

Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere

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Abstract We review the fossil history of seed plant genera that are now endemic to eastern Asia. Although the majority of eastern Asian endemic genera have no known fossil record at all, 54 genera, or about 9%, are reliably known from the fossil record. Most of these are woody (with two exceptions), and most are today either broadly East Asian, or more specifically confined to Sino-Japanese subcategory rather than being endemic to the Sino-Himalayan area. Of the “eastern Asian endemic” genera so far known from the fossil record, the majority formerly occurred in Europe and/or North America, indicating that eastern Asia served as a late Tertiary or Quaternary refugium for taxa. Hence, many of these genera may have originated in other parts of the Northern Hemisphere and expanded their ranges across continents and former sea barriers when tectonic and climatic conditions allowed, leading to their arrival in eastern Asia. Although clear evidence for paleoendemism is provided by the gymnosperms *Amentotaxus*, *Cathaya*, *Cephalotaxus*, *Cunninghamia*, *Cryptomeria*, *Glyptostrobus*, *Ginkgo*, *Keteleeria*, *Metasequoia*, *Nothotsuga*, *Pseudolarix*, *Sciadopitys*, and *Taiwania*, and the angiosperms *Cercidiphyllum*, *Choerospondias*, *Corylopsis*, *Craigia*, *Cyclocarya*, *Davidia*, *Dipelta*, *Decaisnea*, *Diplopanax*, *Dipteronia*, *Emmenopterys*, *Eucommia*, *Euscaphis*, *Hemiptelea*, *Hovenia*, *Koelreuteria*, *Paulownia*, *Phellodendron*, *Platycarya*, *Pteroceltis*, *Rehderodendron*, *Sargentodoxa*, *Schizophragma*, *Sinomenium*, *Tapiscia*, *Tetracentron*, *Toricellia*, *Trapella*, and *Trochodendron*, we cannot rule out the possibility that neoendemism plays an important role especially for herbaceous taxa in the present-day flora of Asia, particularly in the Sino-Himalayan region. In addition to reviewing paleobotanical occurrences from the literature, we document newly recognized fossil occurrences that expand the geographic and stratigraphic ranges previously known for *Dipelta*, *Pteroceltis*, and *Toricellia*.

Key words Cretaceous, eastern Asia, endemic, paleobotany, phytogeography, Tertiary.

Endemism, i.e., the confinement of taxa to a specified geographic region, occurs at various scales over the earth surface. The maiden hair tree (*Ginkgo*) and dawn redwood (*Metasequoia*) are just two examples of genera once widespread in the Northern Hemisphere that are now endemic to eastern Asia. Paleobotanical data confirm that a large number of plant genera now restricted to eastern Asia had broader geographic distribution in the geologic past. Fossil records in North America, Europe, and Asia document patterns of range expansion and reduction and eventual extirpation across large areas, sometimes leaving remnant populations only in eastern Asia (Manchester, 1999; Zhou & Momohara, 2005). In this review, we highlight paleobotanical records from the Northern Hemisphere that we consider to be valid representatives of the genera now confined to eastern Asia in order to illustrate former distribution patterns of these genera in each of the northern continents. These paleobotanical data show the importance of intercontinental dispersal between North America, Europe and

Asia and indicate that the geographic source areas for the evolution of many genera remain in question.

Because some of the East Asian endemic plants have been considered to be phylogenetically primitive, and some are also known from the Asian fossil record, many authors have assumed that these genera originated in the area of their present distribution (e.g., Takhtajan, 1969). Wang (1988), for example, stated that the southern mountains of China may have been the cradle of endemic Chinese genera. However, the fossil record needs to be taken into consideration to evaluate such hypotheses. Many of the genera presently endemic to eastern Asia have excellent fossil records in North America and/or Europe, indicating that the source area of their evolution was not necessarily Asia. The paleobotanical literature abounds with reports of genera identified from the Tertiary of Europe and North America that are now living only in Asia. Some of these reports are well documented, with careful consideration of diagnostic characters of the genera; others are not. Many of the published reports are scattered in the geological literature on individual fossil floras and are not always easy to locate.

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Although often dismissed because of its incompleteness, the fossil record provides hard data on former distribution patterns that cannot come from studies of extant organisms alone. Each fossil occurrence of a taxon, whether positioned within the current distribution area, or beyond the present geographic limits, provides additional data relevant to phytogeographic history. The purpose of this article is to review the paleobotanical records of genera that are now endemic to eastern Asia. This information can be used to track possible routes of intercontinental dispersal and to evaluate different hypotheses on the places of origin of these taxa. We believe that a compilation of reliable fossil accounts of these genera is necessary because there are numerous dubious reports in the literature that are not substantiated by fossils with sufficient diagnostic characters for reliable determination. In addition, many convincingly identified fossils that were previously published have escaped notice by subsequent workers.

A taxon may achieve endemic status through different historical pathways (e.g., Ying & Zhang, 1984; Ferguson et al., 1997). An incipient clade that has not had time to disperse broadly is classified as a “neoen- demic”, whereas a remnant of a once more broadly distributed taxon, now extirpated from all of its former range with the exception of a small area of survival is termed “paleoendemic”. There is a gradient between these situations, but these two terms are conceptually useful. Sometimes a taxon may be inferred to be paleoendemic based on its location, ecological preferences, phylogenetic position and/or presence of “primitive” characters, but the fossil record plays an important role in confirming the status. Most of the examples highlighted in this treatment may be viewed as confirmed paleoendemics in view of their broader geographic distribution during the Tertiary than today.

1 Methods

To address the paleobotanical record of genera now endemic to eastern Asia, the first step was to arrive at a comprehensive listing of all the extant genera regardless of their fossil record. Many sources provide information and examples of plants endemic to eastern Asia, but none are fully comprehensive, because continuing taxonomic and phylogenetic work leads to revision. A taxon formerly considered to lie within the boundaries of “East Asia” may have to be excluded if additional research indicates that it has native populations existing outside the focus area, e.g., in Malesia, Europe, North America or western Asia. The concept of what constitutes a genus in a particular family also changes as phylogenetic studies provide improved understanding of the relationships of the species.

Initially, we focused our attention on genera of seed plants that are primarily restricted in their modern native distribution to China, Korea and Japan, although sometimes passing across these political boundaries into adjacent Vietnam, and India. The compilation of 243 endemic genera of China (Ying et al., 1993) is an excellent guide to the morphology and modern habitats of plants mostly restricted to China. In addition, to achieve a more comprehensive tally of genera endemic to the east Asian region, we must include also those genera that are endemic to Korea (about seven) and Japan (about 14; Xie, 1998), plus genera with occurrences shared in two or more of these areas. Wu (1998) listed 42 genera endemic to Korea plus Japan, the Bonin Islands, and the Ryukyu Islands. Summing these compilations gives an initial estimate of 298 genera of seed plants endemic to the Sino-Japanese flora. However, Qian et al. (2003a) listed 7 additional genera endemic to northeastern Asia including northeastern China, Korea and far eastern Russia, and many additional genera can be included in the East Asian flora when Sino-Himalayan taxa are included (Wu, 1998). Dr. Hong Qian kindly provided a more extensive listing of eastern Asian taxa as used in his comparative investigations with North America and other regions (Qian, 2001, 2002). The compilations of Ying et al. (1993), Wu (1998), Qian (2001; unpubl.), and Qian et al. (2003a, 2003b) aided in preparation of the current list of about 600 genera considered to be endemic to eastern Asia (Table 1). The list includes genera endemic to the broad area of eastern Asia extending from the Himalayas to Mongolia, eastern Russia (east of ca 80°E), Japan, and into Vietnam and Thailand. Criteria for acceptance of particular genera in the dataset were specified by Qian (2001); but we also excluded from the previous lists taxa now considered to extend beyond the boundaries under consideration here, while also introducing some genera that were not previously included (e.g., *Amentotaxus*, *Boehmeriopsis*, *Baimashania*, *Burretiodendron*, *Codonopsis*, *Galitzkya*). Malesia is treated as a separate province beyond the scope of this analysis. This listing of extant eastern Asian endemic genera is provided here with two goals in mind—1) to analyze in terms of the fossil representatives currently known, and 2) to provide a checklist of taxa that paleobotanists should learn to recognize to facilitate the identification of additional examples in the fossil record. General geographic distribution data were obtained from a variety of sources, commonly including Mabberley (1997) and Ying et al. (1993).

Previous surveys of paleobotanical literature that were used in preparing this summary include LaMotte (1952) and Taylor (1990) for North America, Kirchheimer (1957) and Mai (1995) for Europe, Tanai (1994), Liu et al. (1996), and Momohara (1997) for Asia, Manchester (1999) for the Northern Hemisphere records, and Takhtajan

Table 1 List of extant East Asian endemic genera of seed plants, showing familial assignment, modern geographic distribution and growth habit. Genera with accepted fossil records indicated in boldface font with asterisk (*). Genera grouped alphabetically by family. See material and methods for defining boundaries of “East Asia.”

Family	Genus	Geographic distribution	Growth habit	#	Family	Genus	Geographic distribution	Growth habit	#
Acant	<i>Clarkeasia</i>	Nepal to Thailand	shrub	1	Apocy	<i>Parepiginum</i>	China (Yunnan, Guizhou)	liana	47
Acant	<i>Haplanthoides</i>	China (Yunnan)	per herb	2	Arace	<i>Pinellia</i>	China, Japan	herb	48
Acant	<i>Kudoacanthus</i>	China (Taiwan)	per herb	3	Arali	<i>Boninofatsia</i>	Japan (Bonin Islands)	shrub	49
Acant	<i>Paragutzlaffia</i>	SW China	per herb	4	Arali	<i>Fatsia</i>	China (Taiwan), Japan	shrub or small tree	50
Actin	<i>Clematoclethra</i>	WC China	liana	5	Arali	<i>Hunaniopanax</i>	China (Hunan)	epiphytic shrub	51
Adoxa	<i>Sinadoxa</i>	China (Qinghai)	per herb	6	Arali	<i>Kalopanax</i>	E Asia	tree	52
Adoxa	<i>Tetradoxa</i>	China (Sichuan)	per herb	7	Arali	<i>Merrillioanax</i>	Bhutan, Burma, W China, NE India, Nepal	tree, shrub	53
Agava	<i>Anemarrhena</i> (= <i>Terauchia</i>)	China, Korea, Mongolia	herb	8	Arali	<i>Sinopanax</i>	China (Taiwan)	shrub	54
Altin	<i>Semiliquidambar</i>	China	tree	9	Arali	<i>Tetrapanax</i>	S & SC China	tree, shrub	55
Amara	<i>Stilbanthus</i>	Himal	liana	10	Arali	<i>Woodburnia</i>	Burma	?	56
Anaca	<i>Choerospondias</i> *	NE India, N Thailand, SE China, Japan	tree	11	Areca	<i>Guihaia</i>	S China, N Vietnam	palm	57
Anaca	<i>Dobinea</i>	Himal, S China	shrub	12	Areca	<i>Satakentia</i>	Ryukyu Islands	palm	58
Anthe	<i>Comospermum</i>	Japan	herb	13	Areca	<i>Trachycarpus</i>	Himal to E China	tree	59
Apiac	<i>Acronema</i>	Sino-Himal	per, bien herb	14	Arist	<i>Saruma</i>	C & E China	per herb	60
Apiac	<i>Apodicarpum</i>	E Japan	herb	15	Ascle	<i>Belostemma</i>	India, China	twining subshr	61
Apiac	<i>Arcuatopterus</i>	China	per herb	16	Ascle	<i>Biondia</i>	China	per twining herb; liana	62
Apiac	<i>Carlesia</i>	E China	per herb	17	Ascle	<i>Diplolepis</i>	China	liana	63
Apiac	<i>Chaerophyllopsis</i>	W China	ann herb	18	Ascle	<i>Dolichopetalum</i>	China	twining shrub	64
Apiac	<i>Chamaele</i>	Japan	herb	19	Ascle	<i>Graphistemma</i>	China, Vietnam	liana	65
Apiac	<i>Chamaesium</i>	Himal-W China	ann, bien herb	20	Ascle	<i>Jasminanthes</i>	China, Thailand	liana	66
Apiac	<i>Changium</i>	China (Xizang, E)	per herb	21	Ascle	<i>Merrillanthus</i>	Cambodia, China	liana	67
Apiac	<i>Chuanminshen</i>	China	per herb	22	Ascle	<i>Metaplexis</i>	E Asia	liana or scandent subshr	68
Apiac	<i>Cyclorhiza</i>	SW China	per herb	23	Ascle	<i>Pentastelma</i>	China (Hainan)	twining shr	69
Apiac	<i>Dactylaea</i>	C & E China	herb	24	Ascle	<i>Sichuania</i>	China (Sichuan)	liana	70
Apiac	<i>Dickinsia</i>	SW China	ann herb	25	Ascle	<i>Treutlera</i>	E Himal	liana	71
Apiac	<i>Dystaenia</i>	Korea, Japan	per herb	26	Aster	<i>Synurus</i>	China, S Japan, Korea	per herb	72
Apiac	<i>Haloscistrum</i>	E Asia	herb	27	Aster	<i>Ajaniopsis</i>	China (Xizang)	ann herb	73
Apiac	<i>Haplosphaera</i>	Bhutan, China, NE India	per herb	28	Aster	<i>Alfreda</i> (= <i>Xanthopappus</i>)	NW China, Mongolia	per herb	74
Apiac	<i>Harrysmithia</i>	China	ann herb	29	Aster	<i>Atractylodes</i>	China, Korea, Japan, Russia (Siberia)	per herb	75
Apiac	<i>Kedarnatha</i>	Himal	herb	30	Aster	<i>Callistephus</i>	China	herb	76
Apiac	<i>Lalldhwojia</i>	Himal	herb	31	Aster	<i>Chaetoseris</i>	Himal, China	per to ann herb	77
Apiac	<i>Magadania</i>	NE Asia	herb	32	Aster	<i>Codonopsis</i>	E Asia	per herb	78
Apiac	<i>Melanosciadium</i>	China (Guizhou, Sichuan)	per herb	33	Aster	<i>Cremanthodium</i>	Himal, S China	per herb	79
Apiac	<i>Nothosmyrnum</i>	China	per herb	34	Aster	<i>Crepidiastrum</i>	E Asia	ann to per herb	80
Apiac	<i>Notopterygium</i>	China	per herb	35	Aster	<i>Crossostephium</i>	E Asia	shrub	81
Apiac	<i>Physospermopsis</i>	SC China	per herb	36	Aster	<i>Dendrocacalia</i>	Japan (Bonin Islands)	shrub	82
Apiac	<i>Pternopetalum</i>	E Asia, Himal, China	ann, per herb	37	Aster	<i>Dicercocladus</i>	China	per herb	83
Apiac	<i>Pterygopleurum</i>	China, Japan, Korea	per herb	38	Aster	<i>Diplazoptilon</i>	SW China	per herb	84
Apiac	<i>Saposhnikovia</i>	China, Korea, Mongolia, Russia (E Siberia)	per herb	39	Aster	<i>Dolomiaea</i>	China (Xizang), Himal	per herb	85
Apiac	<i>Siniaca</i>	China (Guizhou)	herb	40	Aster	<i>Dubyaea</i>	Himal, W China	per herb	86
Apiac	<i>Sinocarum</i>	W China	per herb	41	Aster	<i>Elachanthemum</i>	China, Mongolia	ann herb	87
Apiac	<i>Sinolimprichtia</i>	SW China	per herb	42	Aster	<i>Endocellion</i>	Russia (Siberia), E Asia	per herb	88
Apiac	<i>Tongoloa</i>	Sino-Himal, mainly in SW China, extending west to C Nepal	per herb	43	Aster	<i>Farfugium</i>	E Asia	herb	89
Apiac	<i>Tordyliopsis</i>	Bhutan, China, Nepal, Sikkim	per herb	44	Aster	<i>Filifolium</i>	NE Asia	herb	90
Apoci	<i>Sindechites</i>	China, Laos, Thailand	liana	45	Aster	<i>Formania</i>	China (Sichuan, Yunnan)	shrub	91
Apocy	<i>Chunechites</i>	SE China	climbing shrub	46					

Table 1 (continued)

Family	Genus	Geographic distribution	Growth habit	#	Family	Genus	Geographic distribution	Growth habit	#
Aster	<i>Heteropappus</i>	C & E Asia	ann herb	92	Brass	<i>Galitzkya</i>	W China, Mongolia, Kazakhstan	per herb	143
Aster	<i>Heteroplexis</i>	China (Guangxi)	per herb	93	Brass	<i>Gorodkovia</i>	Russia (NE Siberia)	per herb	144
Aster	<i>Hololeion</i>	E Asia	per herb	94	Brass	<i>Hemilophia</i>	SW China	per herb	145
Aster	<i>Kalimeris</i>	E Asia	per herb	95	Brass	<i>Lepidostemon</i>	Bhutan, China, Nepal, Sikkim	ann herb	146
Aster	<i>Miricacalia</i>	Japan	per herb	96	Brass	<i>Lignariella</i>	Bhutan, China, Nepal, Sikkim	bien herb	147
Aster	<i>Miyamayomena</i>	Japan	per herb	97	Brass	<i>Megadenia</i>	China, Russia	ann or per herb	148
Aster	<i>Myriopsis</i>	China, Mongolia	shrub	98	Brass	<i>Neomartinella</i>	China	ann herb	149
Aster	<i>Nannoglottis</i>	C & NC China	per herb	99	Brass	<i>Oreoloma</i>	China, Mongolia	per herb	150
Aster	<i>Nemosenecio</i>	China, Japan	per herb	100	Brass	<i>Orychophragmus</i>	China	ann, per herb	151
Aster	<i>Nipponanthemum</i>	Japan	shrub	101	Brass	<i>Pachyneurum</i>	Mongolia, Russia (Altai)	per herb	152
Aster	<i>Notoseris</i>	SC & SE Asia	per herb	102	Brass	<i>Pegaeophyton</i>	C Asia, Himal, to W China	per herb	153
Aster	<i>Nouelia</i>	China (Yunnan, Sichuan)	shrub, tree	103	Brass	<i>Platycraspedum</i>	China	bien, per herb	154
Aster	<i>Opisthopappus</i>	N China	per herb	104	Brass	<i>Pycnophilanthus</i>	China, Kashmir	per herb	155
Aster	<i>Phaeostigma</i>	China	per herb, shr	105	Brass	<i>Sinosophiopsis</i>	China (Qinghai, Sichuan, Xizang)	ann herb	156
Aster	<i>Rhynchospermum</i>	E & SE Asia	per herb	106	Brass	<i>Solms-laubachia</i>	Bhutan, China, Sikkim	per herb	157
Aster	<i>Sheareria</i>	S & SE China	ann herb	107	Brass	<i>Synstemon</i>	NC China	ann or bien herb	158
Aster	<i>Sinacalia</i>	China	per herb	108	Brass	<i>Yinshania</i>	NC China	ann, per herb	159
Aster	<i>Sinoleontopodium</i>	China (S Xizang)	per herb	109	Brets	<i>Bretschneidera</i>	China, Thailand, Vietnam	tree	160
Aster	<i>Soroseris</i>	Himal-W China	herb	110	Calyc	<i>Chimonanthus</i>	China	shrub	161
Aster	<i>Stenoseres</i>	E Asia	per herb	111	Calyc	<i>Sinocalycanthus</i>	China	shrub	162
Aster	<i>Stilpnolepis</i>	China, Mongolia	ann herb	112	Campa	<i>Cyananthus</i>	Himal	per herb	163
Aster	<i>Symphyllocarpus</i>	NE China, Korea, Russia (Siberia)	ann herb	113	Campa	<i>Echinocodon</i>	China	per herb	164
Aster	<i>Syncalathium</i>	China	per herb	114	Campa	<i>Hanabusaya</i>	Korea	per herb	165
Aster	<i>Syneilesis</i>	E Asia	per herb	115	Campa	<i>Leptocodon</i>	Himal	per herb	166
Aster	<i>Synotis</i>	Sino-Himal, China	herb	116	Campa	<i>Platycodon</i>	NE Asia	per herb	167
Aster	<i>Tridactylina</i>	Russia (E Siberia)	ann herb	117	Campu	<i>Homocodon</i>	S China	ann herb	168
Aster	<i>Tugarinovia</i>	Mongolia	per herb	118	Canab	<i>Pteroceltis*</i>	N & C China	tree	169
Aster	<i>Turczaninovia</i>	E Asia	herb	119	Capri	<i>Dipelta*</i>	C & S China	shrub	170
Aucub	<i>Aucuba</i>	Himal-Japan	shrub	120	Capri	<i>Heptacodium</i>	C & SE China	small tree	171
Berbe	<i>Dysosma</i>	E Asia	per herb	121	Capri	<i>Kolkwitzia</i>	C & E China	shrub	172
Berbe	<i>Nandina</i>	India to Japan	shrub	122	Capri	<i>Leycesteria</i>	Himal, SW China	climbing shrub	173
Berbe	<i>Ranzania</i>	Japan	herb	123	Capri	<i>Silvianthus</i>	E India to SE Asia	shrub	174
Betul	<i>Ostryopsis</i>	C China	shrub	124	Capri	<i>Weigela*</i>	E Asia	Shrub	175
Borag	<i>Ancistrocarya</i>	Japan	herb	125	Caryo	<i>Brachystemma</i>	Himal	liana?/ann herb	176
Borag	<i>Antiotrema</i>	SW China	per herb	126	Caryo	<i>Psammosilene</i>	China	per herb	177
Borag	<i>Bothriospermum</i>	Trop, NE Asia	herb	127	Celas	<i>Monimopetalum</i>	China (Anhui, Jiangxi)	climbing shr	178
Borag	<i>Brachybotrys</i>	NE China, Russia (Siberia)	herb	128	Celas	<i>Pottingeria</i>	India (Assam) to NW Thailand	shrub	179
Borag	<i>Chionocharis</i>	Bhutan, China, NE India, Nepal	per herb	129	Celas	<i>Tripterygium*</i>	E Asia	shrub	180
Borag	<i>Ivanjohnstonia</i>	NW Himal	?	130	Cepha	<i>Cephalotaxus*</i>	E Himal through China, Korea, Japan, Vietnam, Burma, Thailand	shrub	181
Borag	<i>Maharanga</i>	Bhutan, India, Nepal, Thailand	per, bien herb	131	Cerci	<i>Cercidiphyllum*</i>	China, Japan	tree	182
Borag	<i>Metaeritrichium</i>	China (Xizang, Qinghai)	ann herb	132	Cheno	<i>Acroglochin</i>	C & E China, Himal	ann herb	183
Borag	<i>Microula</i>	Bhutan, N and NE India, Nepal, Sikkim	bien herb	133	Cheno	<i>Archiatriplex</i>	China (Sichuan)	ann herb	184
Borag	<i>Omphalotrigonotis</i>	China	herb	134	Cheno	<i>Baolia</i>	China	ann herb	185
Borag	<i>Sinojohnstonia</i>	China	per herb	135	Circa	<i>Circaeaster</i>	NW Himal to NW China	ann herb	186
Borag	<i>Thyrocarpus</i>	China, Vietnam	ann herb	136					
Brass	<i>Arcyosperma</i>	Himal	per herb	137					
Brass	<i>Berteroella</i>	Himal to Japan, Korea	ann or bien herb	138					
Brass	<i>Borodinia</i>	Russia (E Siberia)	per herb	139					
Brass	<i>Baimashania</i>	China	per herb	140					
Brass	<i>Dipoma</i>	China	per herb	141					
Brass	<i>Eurycarpus</i>	China (Xizang), Kashmir	per herb	142					

Table 1 (continued)

Family	Genus	Geographic distribution	Growth habit	#	Family	Genus	Geographic distribution	Growth habit	#
Comme	<i>Streptolirion</i>	Bhutan, Burma, China, India, Japan, Korea, Laos, Sikkim, Thailand, Vietnam	per herb	187	Gesne	<i>Bournea</i>	China (Guangdong, Fujian)	per herb	229
Convo	<i>Dinetus</i>	trop Asia	herb twiner	188	Gesne	<i>Briggsia</i>	E Himal, Burma, China	per herb	230
Crass	<i>Kungia</i>	China	per herb	189	Gesne	<i>Briggsiopsis</i>	China	per herb	231
Crass	<i>Meterostachys</i>	S Japan, S Korea	herb	190	Gesne	<i>Cathayanthe</i>	China (Hainan)	per herb	232
Cucur	<i>Actinostemma</i>	India to Japan	liana	191	Gesne	<i>Chiritopsis</i>	China	per herb	233
Cucur	<i>Biswarea</i>	Himal	climber	192	Gesne	<i>Conandron</i>	E China, Japan	herb	234
Cucur	<i>Bolbostemma</i>	China	liana	193	Gesne	<i>Corallodiscus</i>	Himal-NW China, SE Asia	herb	235
Cucur	<i>Edgaria</i>	E Himal	liana	194	Gesne	<i>Dayaoshania</i>	China (E Guangxi)	per herb	236
Cucur	<i>Gomphogyne</i>	E Himal to C China, SE Asia	liana	195	Gesne	<i>Deinocheilos</i>	China	per herb	237
Cucur	<i>Hemsleya</i>	E Asia	liana	196	Gesne	<i>Didymostigma</i>	S China	ann herb	238
Cucur	<i>Herpetospermum</i>	Himal, China	liana	197	Gesne	<i>Dolicholoma</i>	China (Guangxi)	per herb	239
Cucur	<i>Schizopepon</i>	Himal, E Asia	liana	198	Gesne	<i>Gyrocheilos</i>	China	per herb	240
Cupre	<i>Cryptomeria*</i>	Japan, China (Fujian, Jiangxi, Sichuan, Yunnan, Zhejiang)	tree	199	Gesne	<i>Gyrogyne</i>	China	per herb	241
Cupre	<i>Cunninghamia*</i>	China, N Vietnam, Laos	tree	200	Gesne	<i>Hemiboea</i>	China, S Japan, N Vietnam	per herb	242
Cupre	<i>Fokienia</i>	E China, N Laos, Vietnam	tree	201	Gesne	<i>Hemiboeopsis</i>	China, Laos	per herb	243
Cupre	<i>Glyptostrobus*</i>	SE China	tree	202	Gesne	<i>Isometrum</i>	China	per herb	244
Cupre	<i>Metasequoia*</i>	China (SW Hubei, NW Hunan, E Sichuan)	tree	203	Gesne	<i>Lagarosolen</i>	China (S Yunnan)	per herb	245
Cupre	<i>Microbiota</i>	NE Asia	shrub	204	Gesne	<i>Leptoboeria</i>	Bhutan, Burma, China, N India, Sikkim, Thailand	herb, subshr	246
Cupre	<i>Platykladus</i>	China, Korea, E Russia	tree	205	Gesne	<i>Loxostigma</i>	Bhutan, China, India, Burma, Nepal, Sikkim, N Vietnam	per herb	247
Cupre	<i>Taiwania*</i>	N Burma, China (SE Guizhou, SW Hubei, SE Sichuan, W Yunnan, Taiwan, SE Xizang)	tree	206	Gesne	<i>Lysionotus</i>	Bhutan, China, Burma, N India, S Japan, Laos, Nepal, N Thailand, N Vietnam	subshrub, liana	248
Cupre	<i>Thujaopsis*</i>	Japan	tree	207	Gesne	<i>Metabriggsia</i>	China (NW Guangxi)	per herb	249
Diape	<i>Berneuxia</i>	Himal	per herb	208	Gesne	<i>Metapetrocosmea</i>	China (Hainan)	per herb	250
Diape	<i>Diplarche</i>	E Himal, SW China	shrub	209	Gesne	<i>Opithandra</i>	China, Japan	per herb	251
Dipen	<i>Dipentodon</i>	Burma, S China	small tree	210	Gesne	<i>Oreocharis</i>	S China, Thailand, Vietnam	per herb	252
Erica	<i>Bryanthus</i>	Japan, Russia (Kamchatka)	shrub	211	Gesne	<i>Petrocodon</i>	China	per herb	253
Erica	<i>Enkianthus</i>	Himal to Japan	small tree	212	Gesne	<i>Platystemma</i>	Bhutan, China, N India, Nepal	per herb	254
Eucom	<i>Eucommia*</i>	China	tree	213	Gesne	<i>Primulina</i>	China (Guangdong)	per herb	255
Eupho	<i>Cleidiocarpon</i>	Burma, W China	shrub	214	Gesne	<i>Pseudochirita</i>	China (Guangxi)	per herb	256
Eupho	<i>Discocleidion</i>	China, Ryukyu Islands	shrub	215	Gesne	<i>Rehmannia</i>	E Asia	herb	257
Eupho	<i>Speranskia</i>	China	per herb	216	Gesne	<i>Rhabdothamnopsis</i>	China	shrub	258
Eupte	<i>Euptelea*</i>	India (Assam) to SW & C China, Japan	tree	217	Gesne	<i>Schistolobos</i>	China (Guangxi)	per herb	259
Fumar	<i>Dactylicapnos</i>	Himal to SE Asia	liana	218	Gesne	<i>Tengia</i>	China (Guizhou)	per herb	260
Genti	<i>Allocheilos</i>	SW China	per herb	219	Gesne	<i>Thamnocharis</i>	SW China	per herb	261
Genti	<i>Allostigma</i>	S China	per herb	220	Gesne	<i>Titanotrichum</i>	China, Japan	per herb	262
Genti	<i>Ancylostemon</i>	China	per herb	221	Gesne	<i>Tremacron</i>	China	per herb	263
Genti	<i>Latouchea</i>	SE & SW China	per herb	222	Gesne	<i>Whytockia</i>	China (Guizhou, Taiwan, SE Yunnan)	per herb	264
Genti	<i>Lomatogoniopsis</i>	China	ann herb	223	Ginkg	<i>Ginkgo*</i>	China	tree	265
Genti	<i>Megacodon</i>	Bhutan, SW China, India, Nepal, Sikkim	per herb	224	Glauc	<i>Glaucidium</i>	Japan	per herb	266
Genti	<i>Pterygocalyx</i>	China, Japan, Korea, Russia	twining per	225	Hamam	<i>Chunia</i>	China (S Hainan)	tree	267
Genti	<i>Veratrilla</i>	Bhutan, SW China, NE India, Sikkim	per herb	226	Hamam	<i>Corylopsis*</i>	Bhutan to Japan	shrub	268
Gesne	<i>Beccarinda</i>	Burma, S China, N Vietnam	per herb	227	Hamam	<i>Disanthus*</i>	E China, Japan	shrub	269
Gesne	<i>Boeica</i>	China, SE Asia	herb	228	Hamam	<i>Fortunearia*</i>	China	shrub, tree	270
					Hamam	<i>Loropetalum</i>	China, E & N India, Japan	shrub, small tree	271
					Hamam	<i>Mytilaria</i>	China, Laos, N Vietnam	tree	272

Table 1 (continued)

Family	Genus	Geographic distribution	Growth habit	#	Family	Genus	Geographic distribution	Growth habit	#
Hamam	<i>Parrotiopsis</i>	Himal	shrub	273	Lamia	<i>Siphocranion</i>	Burma, China, India, Vietnam	per herb	316
Hamam	<i>Sinowilsonia</i>	C & NC China	tree, shrub	274	Lamia	<i>Skapanthus</i>	China (Sichuan, Yunnan)	per herb	317
Hama	<i>Tetrathyrium</i>	China (Guangxi)	tree, shrub	275	Lamia	<i>Suzukia</i>	China, Japan	herb	318
Helwi	<i>Helwingia</i>	Bhutan, N Burma, China, N India, Japan, S Korea, Nepal, Sikkim, Thailand, N Vietnam	shrub	276	Lamia	<i>Wenchengia</i>	China (Hainan)	subshr	319
Hydra	<i>Cardiandra</i>	E Asia	shrub/subshr	277	Lardi	<i>Akebia</i> *	Temp E Asia	twiner	320
Hydra	<i>Deinathe</i>	C China, Japan	herb	278	Lardi	<i>Decaisnea</i> *	E Himal, C China	shrub	321
Hydra	<i>Kirengeshoma</i>	China, Japan, Korea	per herb	279	Lardi	<i>Holboellia</i>	Himal, SE Asia, China	liana	322
Hydra	<i>Pileostegia</i>	China, E India, Japan, Ryukyu Islands	shrub evergreen, climbing	280	Lardi	<i>Sargentodoxa</i> *	China, Laos, Vietnam	liana	323
Hydra	<i>Platycrater</i>	China, Japan	shrub	281	Lardi	<i>Sinofranchetia</i>	C China	liana	324
Hydra	<i>Schizophragma</i> *	China, Japan, Korea	shrub	282	Lardi	<i>Stauntonia</i>	Burma, China, N India, Japan, Vietnam	liana	325
Icaci	<i>Hosiea</i>	W & C China, Japan	liana	283	Laura	<i>Cinnadenia</i>	E Himal	tree	326
Irida	<i>Belamcanda</i>	India to E Russia, Japan	per herb	284	Laura	<i>Dodecadenia</i>	S Himal	shrub	327
Irida	<i>Pardanthopsis</i>	N China, Mongolia	herb	285	Laura	<i>Parasassafras</i>	Himal, Burma, W China	tree	328
Jugla	<i>Cyclocarya</i> *	China	tree	286	Laura	<i>Sinosassafras</i>	China (W Yunnan)	small tree	329
Jugla	<i>Platycarya</i> *	China, Japan, Korea, Vietnam	tree	287	Legum	<i>Afgekia</i>	Burma, China, Thailand	climbing shrub	330
Labia	<i>Eriophyton</i>	Himal	herb	288	Legum	<i>Chrysorrhiza</i>	S China	liana	331
Lamia	<i>Ajugoides</i>	Japan	herb	289	Legum	<i>Cochlianthus</i>	Himal	liana	332
Lamia	<i>Bostrychanthera</i>	China	per herb	290	Legum	<i>Craspedolobium</i>	W China	liana	333
Lamia	<i>Caryopteris</i>	E Asia	herb, subshr, shrub	291	Legum	<i>Gueldenstaedtia</i>	Sino-Himal to Siberia	per herb	334
Lamia	<i>Chelonopsis</i>	Kashmir to E Asia	herb or shrub	292	Legum	<i>Maackia</i>	E Asia	tree	335
Lamia	<i>Colquhounia</i>	E Himal, SW China	shrub	293	Legum	<i>Piptanthus</i>	Himal	shrub	336
Lamia	<i>Comanthosphace</i>	E Asia	herb	294	Legum	<i>Salweenia</i>	China (Sichuan, Xizang)	shrub	337
Lamia	<i>Craniotome</i>	Himal	herb	295	Legum	<i>Spongiocarpella</i>	Himal to China	herb	338
Lamia	<i>Hanceola</i>	China	per, ann herb	296	Lilac	<i>Nomocharis</i>	Burma, China, India	per herb	339
Lamia	<i>Heterolamium</i>	China	ann herb	297	Lilia	<i>Anemarrhena</i>	China	per herb	340
Lamia	<i>Holocheila</i>	China	per herb	298	Lilia	<i>Cardiocrinum</i>	Himal, E Asia	herb	341
Lamia	<i>Keiskea</i>	China, Japan	herb or subshr	299	Lilia	<i>Chionographis</i>	China, Japan, Korea	per herb	342
Lamia	<i>Kinostemon</i>	C China	per herb	300	Lilia	<i>Diuranthera</i>	China (Guizhou, Sichuan, Yunnan)	per herb	343
Lamia	<i>Lamiophlomis</i>	Bhutan, China, India, Nepal	per herb	301	Lilia	<i>Hosta</i>	China, Japan, Korea, Russia	per herb	344
Lamia	<i>Leucosceptrum</i>	Bhutan, Burma, China, India, Laos, Nepal, Vietnam	shrub	302	Lilia	<i>Milula</i>	China, Nepal	per herb	345
Lamia	<i>Loxocalyx</i>	China	per herb	303	Lilia	<i>Reineckea</i>	China, Japan	per herb	346
Lamia	<i>Marmoritis</i>	China, India	per herb	304	Lilia	<i>Rohdea</i>	China, Japan	per herb	347
Lamia	<i>Microtoena</i>	Asia	herb	305	Lilia	<i>Speirantha</i>	China (Anhui, Jiangxi, Zhejiang)	per herb	348
Lamia	<i>Notochaete</i>	Bhutan, Burma, China, India, Nepal	herb	306	Lilia	<i>Theropogon</i>	Bhutan, China, India, Nepal, Sikkim	per herb	349
Lamia	<i>Ombrocharis</i>	China (Hunan)	per herb	307	Lilia	<i>Tricyrtis</i>	Himal to E Asia	per herb	350
Lamia	<i>Paralamium</i>	Burma, China, Vietnam	per herb	308	Linac	<i>Anisadenia</i>	Himal to C China	herb	351
Lamia	<i>Perilla</i>	India-Japan	ann herb	309	Linac	<i>Reinwardtia</i>	N India, China	shrub	352
Lamia	<i>Perillula</i>	Japan	herb	310	Magno	<i>Kmeria</i>	S China, Indochina	tree	353
Lamia	<i>Rostrinucula</i>	China	shrub	311	Malva	<i>Burretiodendron</i>	Burma, SW China, N Vietnam	tree	354
Lamia	<i>Roylea</i>	Himal	shrub	312	Malva	<i>Corchoropsis</i>	E Asia, Japan	ann herb	355
Lamia	<i>Rubiteucris</i>	China, India	herb	313	Malva	<i>Craigia</i> *	SW China	tree	356
Lamia	<i>Schnabelia</i>	China	per herb	314	Malva	<i>Pityranthe</i> (= <i>Hainania</i>)	China (Guangxi, Hainan)	tree	357
Lamia	<i>Sinopogonantha</i>	China (Anhui, Zhejiang)	herb	315	Malva	<i>Reevesia</i> s*	Himal to China (Taiwan)	tree	358
					Masti	<i>Diplopanax</i> *	SW China, Vietnam	tree	359
					Melan	<i>Japonolirion</i>	Japan	herb	360
					Melas	<i>Barthea</i>	China	shrub	361
					Melas	<i>Bredia</i>	E & SE Asia	herb, shrublets	362
					Melas	<i>Cyphotheca</i>	China (Yunnan)	shrub	363

Table 1 (continued)

Family	Genus	Geographic distribution	Growth habit	#	Family	Genus	Geographic distribution	Growth habit	#
Melas	<i>Fordiophyton</i>	S China, N Vietnam	herb, subshr	364	Oroba	<i>Phacellanthus</i>	China, Japan, Korea, Russian Far East	herb	418
Melas	<i>Stapfiophyton</i>	S China	herb	365	Oroba	<i>Platypholis</i>	Japan (Bonin Islands)	herb	419
Melas	<i>Tigridiopalma</i>	China (Guangdong)	herb	366	Oroban	<i>Mannagettaea</i>	China, Russia	herb	420
Melia	<i>Sphaerosacme</i>	Himal	tree	367	Papav	<i>Dicranostigma</i>	Himal-W China	herb	421
Menis	<i>Eleutharrhena</i>	China, India (Assam)	liana	368	Papav	<i>Eomecon</i>	E China	per herb	422
Menis	<i>Sinomenium*</i>	C China, Japan	liana	369	Papav	<i>Hylomecon</i>	Temp E Asia	per herb	423
Morin	<i>Acanthocalyx</i>	Sino-Himal	herb	370	Papav	<i>Macleaya</i>	Temp E Asia	herb	424
Musac	<i>Musella</i>	China	per herb	371	Papav	<i>Pteridophyllum</i>	Japan	herb	425
Myrsi	<i>Sadiria</i>	E Himal, India (Assam)	?	372	Pinac	<i>Cathaya*</i>	China (NE Guangxi, N Guizhou, S Hunan & SE Sichuan)	tree	426
Myrta	<i>Pyrenocarpa</i>	China (Hainan)	tree	373	Pinac	<i>Keteleeria*</i>	China, Laos, Vietnam	tree	427
Nymph	<i>Euryale*</i>	China, N India, Japan	aquatic herb	374	Pinac	<i>Nothotsuga*</i>	China (NE Guizhou, SW Hunan, N Guangdong, NE Guangxi, S Fujian)	tree	428
Nyssa	<i>Camptotheca</i>	China	tree	375	Pinac	<i>Pseudolarix*</i>	C & SE China	tree	429
Nyssa	<i>Davidia*</i>	China	tree	376	Poace	<i>Acidosasa</i>	S China, Vietnam	herb	430
Olaea	<i>Malania</i>	China (Guangxi, Yunnan)	tree	377	Poace	<i>Ampelocalamus</i>	Himal	bamboo	431
Oleac	<i>Abeliophyllum</i>	Korea	shrub	378	Poace	<i>Anisachne</i>	Himal	per herb	432
Orchi	<i>Aceratorchis</i>	China (Xizang)	herb	379	Poace	<i>Bonia</i>	China	bamboo	433
Orchi	<i>Amitostigma</i>	China, E Asia	herb	380	Poace	<i>Borinda</i>	Himal	bamboo	434
Orchi	<i>Androcorys</i>	India, E Asia	herb	381	Poace	<i>Brylkinia</i>	China, Japan	herb	435
Orchi	<i>Anota</i>	China (Hainan)	herb	382	Poace	<i>Chimonobambusa</i>	Himal to Japan	bamboo	436
Orchi	<i>Anthogonium</i>	E Himal to SE Asia	herb	383	Poace	<i>Ferocalamus</i>	China	shrubby bamboo	437
Orchi	<i>Aorchis</i>	Himal	herb	384	Poace	<i>Gaoligongshania</i>	China (NW Yunnan)	shrubby scrambling bamboo	438
Orchi	<i>Bletilla</i>	Temp E Asia	per herb	385	Poace	<i>Gelidocalamus</i>	S & C China	shrub-bamboo	439
Orchi	<i>Bulleyia</i>	Himal-SW China	per herb	386	Poace	<i>Hakonechloa</i>	Japan	herb	440
Orchi	<i>Chamaegastrodia</i>	Japan	herb	387	Poace	<i>Leptocanna</i>	China (S Yunnan)	bamboo	441
Orchi	<i>Changnienia</i>	China	per herb	388	Poace	<i>Melocalamus</i>	Bangladesh, Burma, S China, India (Assam)	clump-forming climbing bamboo	442
Orchi	<i>Cremastra</i>	E Asia	herb	389	Poace	<i>Monocladus</i>	China (Guangdong, Guangxi, Hainan)	undershrub	443
Orchi	<i>Cryptochilus</i>	Himal	herb	390	Poace	<i>Phaenosperma</i>	China, NE India, Japan, S Korea	herb	444
Orchi	<i>Cyperorchis</i>	China	herb	391	Poace	<i>Phyllostachys</i>	Asia	bamboo	445
Orchi	<i>Dactylostalix</i>	Japan	herb	392	Poace	<i>Pleioblastus</i>	China, Japan, Vietnam	bamboo	446
Orchi	<i>Didickea</i>	Himal to Japan	herb	393	Poace	<i>Pseudodanthonia</i>	NW Himal, W China	herb	447
Orchi	<i>Diphylax</i>	China, NE India	herb	394	Poace	<i>Pseudosasa</i>	China, Japan, Korea	shrub like-arborescent	448
Orchi	<i>Diplandrorchis</i>	NE China	per herb	395	Poace	<i>Pseudostachyum</i>	Bhutan, Burma, China, NE India, Vietnam	shrubby bamboo	449
Orchi	<i>Diplolabellum</i>	Korea	herb	396	Poace	<i>Sasa</i>	China, Japan, Korea, E Russia	shrubby bamboo	450
Orchi	<i>Diplomeris</i>	China	herb	397	Poace	<i>Semiarundinaria</i>	E China, Japan	shrubby bamboo	451
Orchi	<i>Eleorchis</i>	Japan	herb	398	Poace	<i>Setiacis</i>	China (Hainan)	per	452
Orchi	<i>Ephippianthus</i>	Japan, Korea, Russia (Sakhalin)	herb	399	Poace	<i>Shibataea</i>	SE China, SW Japan	shrubby bamboo	453
Orchi	<i>Hancockia</i>	E & SE Asia	herb	400	Poace	<i>Sinobambusa</i>	China (Taiwan), Vietnam	bamboo	454
Orchi	<i>Hemipilia</i>	Himal, E Asia, Thailand	herb	401	Podoc	<i>Hydrobryum</i>	China, S Japan, India (Assam), E Nepal	per herb	455
Orchi	<i>Holcoglossum</i>	China (Taiwan), S Japan	herb	402					
Orchi	<i>Ischnogyne</i>	China	per epiphyte	403					
Orchi	<i>Monomeria</i>	Himal, SE Asia	herb	404					
Orchi	<i>Neofinetia</i>	E Asia	herb	405					
Orchi	<i>Neogyne</i>	SE Asia, China, India	herb	406					
Orchi	<i>Nothodoritis</i>	China (Zhejiang)	per herb	407					
Orchi	<i>Oreorchis</i>	Himal to Japan	herb	408					
Orchi	<i>Ornithochilus</i>	China, India, Thailand	herb	409					
Orchi	<i>Otochilus</i>	E Himal to SE Asia	herb	410					
Orchi	<i>Panisea</i>	India to SE Asia	herb	411					
Orchi	<i>Porolabium</i>	Mongolia	per herb	412					
Orchi	<i>Risleya</i>	Himal, W China	herb	413					
Orchi	<i>Sedirea</i>	E Asia	herb	414					
Orchi	<i>Smithorchis</i>	China (Yunnan)	herb	415					
Orchi	<i>Vexillabium</i>	Japan, Korea	herb	416					
Oroba	<i>Gleadovia</i>	China, India	herb	417					

Table 1 (continued)

Family	Genus	Geographic distribution	Growth habit	#	Family	Genus	Geographic distribution	Growth habit	#
Podos	<i>Terniopsis</i>	China (SW Fujian)	per herb	456	Rubia	<i>Indopolysolenia</i>	E Himal, Burma		502
Polyg	<i>Parapteropyrum</i>	China (SE Xizang)	shrub	457	Rubia	<i>Leptodermis</i>	Himal to Japan	shrub	503
Polyg	<i>Pteroxygonum</i>	China	climbing per herb	458	Rubia	<i>Luculia</i>	Himal, China (Yunnan), Vietnam	shrub	504
Primu	<i>Bryocarpum</i>	E Himal	per herb	459	Rubia	<i>Neohymenopogon</i>	Himal	shrub	505
Primu	<i>Omphalogramma</i>	E Himal, N Burma, W China	per herb	460	Rubia	<i>Pseudopyxis</i>	Japan	herb	506
Primu	<i>Pomatosace</i>	W China	per, bien herb	461	Rubia	<i>Serissa</i>	China	shrub	507
Primu	<i>Stimpsonia</i>	E Asia	ann herb	462	Rubia	<i>Sinoadina</i>	upper Burma, S to SW China, Japan	tree	508
Ranun	<i>Anemoclema</i>	SW China	per herb	463	Rubia	<i>Spermedietyon</i>	India	shrub	509
Ranun	<i>Anemonopsis</i>	Japan	per herb	464	Rubia	<i>Trailliaedoxa</i>	SW China	undershrub	510
Ranun	<i>Asteropyrum</i>	Burma-China	per herb	465	Rusca	<i>Aspidistra</i>	China	herb	511
Ranun	<i>Beesia</i>	N Burma, W & SW China	per herb	466	Rutac	<i>Boenninghausenia</i>	India (Assam) to Japan	sap herb	512
Ranun	<i>Calathodes</i>	Himal-China (Taiwan)	per herb	467	Rutac	<i>Boninia</i>	Japan (Bonin Islands)	shrub	513
Ranun	<i>Chienia</i>	China (Henan)	herb	468	Rutac	<i>Orixa</i>	China, Japan, Korea	shrub	514
Ranun	<i>Dichocarpum</i>	Himal, E Asia	herb	469	Rutac	<i>Phellodendron*</i>	E Asia	tree	515
Ranun	<i>Kingdonia</i>	W & N China	per herb	470	Rutac	<i>Poncirus</i>	China	tree, shrub	516
Ranun	<i>Megaleranthis</i>	S Korea	herb	471	Rutac	<i>Psilopogonum</i>	China (Hubei, Sichuan)	per herb	517
Ranun	<i>Metanemone</i>	China (N Yunnan)	per herb	472	Salic	<i>Idesia*</i>	China, Japan, Korea	tree	518
Ranun	<i>Miyakea</i>	E Russia (Sakhalin)	herb	473	Salic	<i>Poliathyrsis</i>	China	tree	519
Ranun	<i>Paroxygraphis</i>	E Himal	herb	474	Sapin	<i>Delavaya</i>	SW China, N Vietnam	shrub, small tree	520
Ranun	<i>Semiaquilegia</i>	China, Japan, Korea	per herb	475	Sapin	<i>Dipteronia*</i>	C & S China	tree	521
Ranun	<i>Souliea</i>	Bhutan, Burma, China, Sikkim	per herb	476	Sapin	<i>Eurycorymbus</i>	S & SW China (include Taiwan)	tree	522
Ranun	<i>Urophyssa</i>	China	per herb	477	Sapin	<i>Handeliidendron</i>	China (Guangxi, Guizhou)	tree	523
Rhamn	<i>Berchemiella</i>	China, Japan	tree	478	Sapin	<i>Koelreuteria*</i>	S China, Japan, perhaps Fiji	tree or shrub	524
Rhamn	<i>Hovenia*</i>	Bhutan, Burma, China, India, Japan, Korea, Nepal	tree, shrub	479	Sapin	<i>Pavieasia</i>	S China, N Vietnam	tree	525
Rosac	<i>Chaenomeles</i>	E Asia	shrub, small tree	480	Sapin	<i>Sinoradlkofera</i>	China, Vietnam	tree	526
Rosac	<i>Dichotomanthes</i>	SW China	shrub, tree	481	Sapin	<i>Xanthoceras</i>	China	large shrub or small tree	527
Rosac	<i>Docynia</i>	Himal, SE Asia	tree	482	Sapot	<i>Eberhardtia</i>	SE Asia, N Borneo (Sabah), S China	tree	528
Rosac	<i>Eriobotrya</i>	Himal, E Asia, W Malesia	tree, shrub	483	Sauru	<i>Gymnotheca</i>	C & SW China, N Vietnam	per herb	529
Rosac	<i>Kerria</i>	China, Japan	shrub	484	Saxif	<i>Mukdenia</i>	N China, Korea	per herb	530
Rosac	<i>Maddenia</i>	China, Himal	tree, shrub	485	Saxif	<i>Astilboides</i>	N China	herb	531
Rosac	<i>Pentactina</i>	N Korea	shrub	486	Saxif	<i>Oresitrophe</i>	N & NE China	per herb	532
Rosac	<i>Potaninia</i>	China, Mongolia	shrublet	487	Saxif	<i>Peltoboykinia</i>	Japan	herb	533
Rosac	<i>Prinsepia</i>	China, Himal	shrub	488	Saxif	<i>Rodgersia</i>	Himal, E Asia	per herb	534
Rosac	<i>Rhaphiolepis</i>	Japan, S Korea & S China to Thailand & Vietnam	shrub, small tree	489	Saxif	<i>Saniculiphyllum</i>	China (Guangxi, Yunnan)	per herb	535
Rosac	<i>Rhodotypos</i>	China, Japan, Korea	shrub	490	Saxif	<i>Tanakaea</i>	China, Japan	per herb	536
Rosac	<i>Sorbaria</i>	Temp Asia	shrub	491	Sciad	<i>Sciadopitys*</i>	Japan	tree	537
Rosac	<i>Spenceria</i>	China (Sichuan, Yunnan)	per herb	492	Scrop	<i>Phtheirospermum</i>	E Asia	per herb	538
Rosac	<i>Stephanandra</i>	E Asia	shrub	493	Scrop	<i>Deinostema</i>	E Asia	herb	539
Rosac	<i>Stranvaesia</i>	China & Himal to SE Asia	tree, shrub	494	Scrop	<i>Hemiphragma</i>	E China to W Himal	herb	540
Rosac	<i>Taihangia</i>	China (Henan, Hebei)	per herb	495	Scrop	<i>Kashmiria</i>	Himal		541
Rubia	<i>Clarkella</i>	Himal, Thailand	herb	496	Scrop	<i>Lancea</i>	Bhutan, China, India, Mongolia, Sikkim	per herb	542
Rubia	<i>Dammacanthus</i>	E Asia	shrub	497	Scrop	<i>Mimulicalyx</i>	China	per herb	543
Rubia	<i>Dunnia</i>	India, China	undershrub	498	Scrop	<i>Monochasma</i>	China, Japan	per herb	544
Rubia	<i>Emmenopterys*</i>	Burma, China, Thailand	tree	499	Scrop	<i>Neopicrorhiza</i>	Himal	herb	545
Rubia	<i>Hayataella</i>	China (Taiwan)	herb	500	Scrop	<i>Omphalothrix</i>	NE Asia	ann herb	546
Rubia	<i>Himalrandia</i>	Himal	shrub	501	Scrop	<i>Oreosolen</i>	Himal & Qinghai-Xizang Plateau	per herb	547

Table 1 (continued)

Family	Genus	Geographic distribution	Growth habit	#
Scrop	<i>Paulownia</i> *	China, Laos, Vietnam	tree	548
Scrop	<i>Phtheirospermum</i>	E Asia	herb, ann or per	549
Scrop	<i>Pseudobartsia</i>	China	ann herb	550
Scrop	<i>Pterygiella</i>	China	ann herb	551
Scrop	<i>Scrofella</i>	China	per herb	552
Scrop	<i>Trienophora</i>	China	per herb	553
Scrop	<i>Xizangia</i>	China	per herb	554
Solan	<i>Anisodus</i>	Temp E Asia	herb	555
Solan	<i>Archiphysalis</i>	E Asia	ann herb	556
Solan	<i>Atropanthe</i>	China	per herb, subshr	557
Solan	<i>Physaliastrum</i>	Asia	shrub or herb	558
Solan	<i>Przewalskia</i>	China	per herb	559
Stach	<i>Stachyurus</i>	Himal to Japan	shrub/small tree	560
Staph	<i>Euscaphis</i> *	Temp E Asia	tree	561
Styra	<i>Huodendron</i>	E Asia	tree, shrub	562
Styra	<i>Melliiodendron</i>	China	tree	563
Styra	<i>Pterostyrax</i> *	E Asia	tree, shrub	564
Styra	<i>Sinojackia</i>	China	tree, shrub	565
Tapis	<i>Tapiscia</i> *	S & SE China, northernmost Vietnam	tree	566
Taxac	<i>Amentotaxus</i> *	China, Vietnam	tree, shrub	567
Taxac	<i>Pseudotaxus</i>	China	shrub	568
Theac	<i>Apterosperma</i>	China	evergreen tree	569
Theac	<i>Euryodendron</i>	China	tree	570
Theac	<i>Parapyrenaria</i>	China (Hainan)	small tree	571
Thyme	<i>Daphnimorpha</i>	Japan	shrub	572
Thyme	<i>Edgeworthia</i>	China, Japan	shrub	573
Thyme	<i>Stellera</i>	C & E Asia	per herb or shrub	574
Toric	<i>Toricellia</i> *	Bhutan, China, N India, Nepal, Sikkim	tree, shrub	575
Trape	<i>Trapella</i> *	China, Japan, Korea, Russia Far East	aquatic herb	576
Troch	<i>Tetracentron</i> *	N Burma, NW & C China, Nepal	tree	577
Troch	<i>Trochodendron</i> *	southern Japan, southern Korea & China (Taiwan)	tree	578
Ulmac	<i>Hemiptelea</i> *	N China, Korea	tree	579
Urtic	<i>Aboriella</i>	E Himal	per herb	580
Urtic	<i>Archiboehmeria</i>	S China-SE Asia	shrub	581
Urtic	<i>Nanocnide</i>	Temp E Asia	per herb	582
Urtic	<i>Petelotiella</i>	NE Vietnam	herb	583
Valer	<i>Nardostachys</i>	Himal	herb	584
Valer	<i>Triplostegia</i>	SE Asia	per herb	585
Vello	<i>Acanthochlamys</i>	China	per herb	586
Verbi	<i>Tsoongia</i>	Burma, China, Vietnam	shrub/small tree	587
Vitac	<i>Yua</i>	China, India	liana	588
Zingi	<i>Cautleya</i>	Himal	herb	589
Zingi	<i>Curcumorpha</i>	Himal	liana	590
Zingi	<i>Paramomum</i>	China (Yunnan)	per herb	591
Zingi	<i>Pyrgophyllum</i>	China (Sichuan, Yunnan)	per herb	592
Zingi	<i>Roscoea</i>	Himal, W China	herb	593
Zingi	<i>Siliquamomum</i>	China, Vietnam	herb	594
Zygop	<i>Tetraena</i>	China (Nei Mongol)	shrub	595

Genera in boldface and with asterisk (*) are known from the fossil record.

Abbreviations: C, Central; N, North or northern; SC, South Central; SE, southeastern; W, Western; WC, west central. Himal, Himalayas; Temp, temperate; trop, tropical. per herb, perennial herb; ann herb, annual herb; bien herb, biennial herb; shr, shrub; subshr, subshrub. Families are abbreviated by their first 5 characters.

(1963) and Collinson et al. (1993) for worldwide records. These reviews were used as initial guides to the literature; we did not automatically accept the reports presented in these references, but evaluated the reports from primary literature based on published descriptions and illustrations, and where feasible we reexamined the cited specimens.

In evaluating the validity of paleobotanical records, we accepted genera reported in the paleobotanical literature only if: (1) the organ(s) and morphological/anatomical features preserved and described could be considered truly diagnostic to the genus indicated, and (2) the description was accompanied by illustrations showing the diagnostic characters, or we were able to examine the original specimens and agreed with the published assignments. Although there are many extinct genera present in the Cretaceous and Tertiary, we limited our scope in this study to fossils that could be placed with confidence in extant genera. In addition to summarizing occurrences from earlier literature, we document with illustrations new, previously unrecorded occurrences of *Dipelta* (a new record from the Eocene of Mississippi), *Pteroceltis* (new record from the Eocene of Tennessee) and *Toricellia* (the oldest known record, from the Paleocene of North Dakota, USA).

For the examination of fossil specimens, we consulted the following collections: University of California, Berkeley; Denver Museum of Natural History; Florida Museum of Natural History, University of Florida; Peabody Museum of Natural History, Yale University; United States National Museum, Washington, DC; Burke Museum of Natural History and Culture, Seattle; Field Museum, Chicago; Natural History Museum, London; Czech National Museum, Prague; Simon Fraser University, Burnaby, BC, Canada; Senckenberg Museum of Natural History, Frankfurt; Staatliche Museum für Naturkunde in Stuttgart; Humboldt Museum, Berlin; Geological Institute and Geological Museum, Moscow; National Museum of Nature and Science, Tokyo; Institute of Botany, Chinese Academy of Sciences, Beijing; the Shanwang Museum, Shandong.

Institutional abbreviations applied in the figure captions for fossil specimens include, BM (Natural History Museum, London), CMPH (Paleobotanical Herbarium, Institute of Botany, Chinese Academy of Sciences, Beijing), FMNH (Field Museum, Chicago), GINRAS (Geological Institute, Russian Academy of Sciences, Moscow), KRAM-P (Palaeobotanical Museum of the W.

Szafer Institute of Botany, Polish Academy of Sciences, Krakow, Poland, SFU (Simon Fraser University), SMNS (Staatliches Museum für Naturkunde, Stuttgart, Germany), UF (Florida Museum of Natural History, University of Florida), USNM (United States National Museum of Natural History, Smithsonian Institution, Washington, DC), and UWBM (Burke Museum of Natural History and Culture, University of Washington).

The morphology of extant genera was studied for comparison with the fossils, using freshly collected specimens from our own field work when possible. Otherwise, we relied on herbarium specimens observed and photographed at A, GH, K, MO, PE, with supplemental data from plants cultivated in botanical gardens.

We maintain the long-standing useful stratigraphic term, "Tertiary," for the Post-Cretaceous, Pre-Quaternary interval, despite the current notion of many geologists who prefer to replace the term with the more cumbersome phrase "Paleogene and Neogene." The million-year chronology of Tertiary epochs follows Gradstein et al. (2005). The precise age of many floras cannot be specified due to lack of good stratigraphic control or radiometric dates. We tentatively accept the assignments given by the most recent authors, although in some cases there continue to be disagreements among different investigators. We attempt to be conservative in the positioning of stratigraphic ranges; hence the ranges presented here are often shorter (begin later) than those indicated by other authors.

2 Results

In the sections that follow, we attempt to summarize the fossil and modern distribution of each genus, organized by gymnosperms (depicted graphically in Table 2) first followed by angiosperms (Table 3), treated alphabetically by family.

2.1 Gymnosperms

2.1.1 Cephalotaxaceae *Cephalotaxus* has about 10 living species ranging from the eastern Himalaya through China, Korea, Japan, Vietnam, Burma, and Thailand. The fossil record indicates that the genus was widespread across the Northern Hemisphere during the Tertiary. In Asia, the genus is known from the Paleogene of northeastern China (leaf remains with epidermal preservation, He & Tao, 1997), and from the Pliocene and Pleistocene of Japan (seed remains, Miki, 1958). European remains occur in the Miocene and Pliocene (Givulescu, 1973; Meller, 1998). *Cephalotaxus miocenica* (Kräusel) Gregor is recognized on the basis of seeds from brown coal deposits in the Mio-Pliocene of Germany (summarized by Meller, 1998), and *C. rhenana* Gregor seeds occur in the Pliocene of Italy (Martinetto, 2001b). Species known from leaf remains with well preserved epidermal charac-

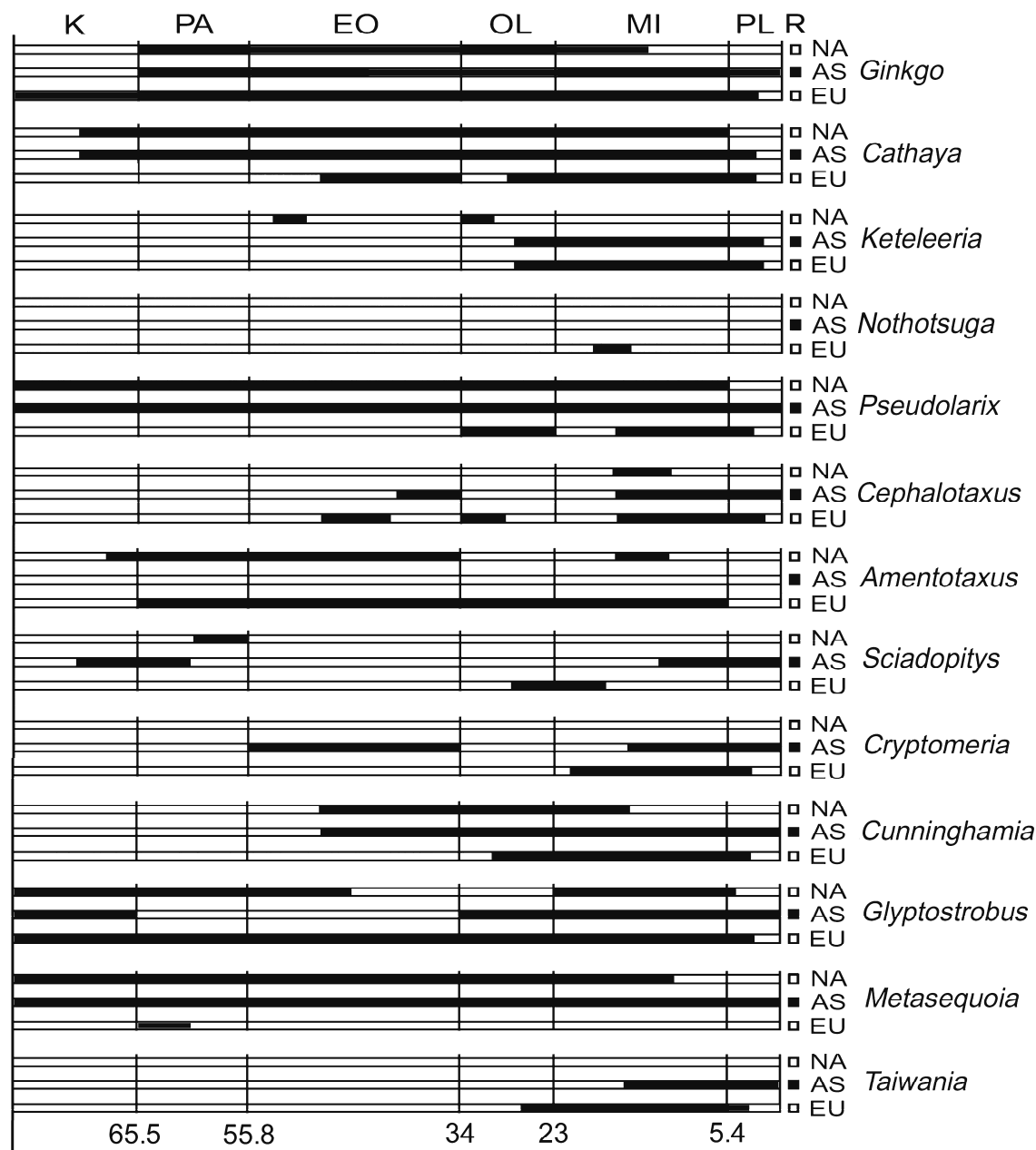
ters include *C. messelensis* Wilde (1989) from the Middle Eocene of Messel, Germany, *C. parvifolia* (Walther) Walther & Kvaček from the Early Oligocene of Kundratice, North Bohemia (Kvaček & Walther, 1998) and the Early Oligocene of Seifhennersdorf, Germany (Walther & Kvaček, 2007), *C. harringtoniana fossilis* K. Koch (Mai & Walther, 1978) from the Neogene sites, and *C. pliocenica* Mädler from the Pliocene of Germany (Mädler, 1939). In North America, the genus is confirmed by leaves with epidermal characters in *C. bonseri* (Knowlton) Chaney & Axelrod from the Miocene of Oregon and Idaho (see Kvaček & Rember, 2000).

2.1.2 Pinaceae Four genera of the pine family are endemic to eastern Asia today: *Cathaya*, *Keteleeria*, *Nothotsuga* and *Pseudolarix*.

Cathaya has one species, *C. argyrophylla* Chun & Kuang, living in the mountains of southwestern and central China in northeastern Guangxi, northern Guizhou, southern Hunan, and southeastern Sichuan (Wu & Raven, 1999). Its bisaccate pollen is distinguished from that of other Pinaceae by the sacci originating at the margins of the corpus, and by the presence of irregularly arranged spinules on both the corpus and sacci, best seen under a scanning electron microscope (Liu et al., 1997; Sivak, 1975). Based upon pollen records that are commonly misinterpreted as *Podocarpus*, reviewed by Liu et al. (1997) and Liu & Basinger (2000), *Cathaya* has occurrences ranging from the Late Cretaceous to Pleistocene in Asia, from the Late Cretaceous to Miocene of North America, and from the Paleocene to Pleistocene in Europe. In Europe, *Cathaya* cones have been identified from the Miocene of Germany, Greece, and France, and from the Pliocene of Germany and Italy (references in Martinetto, 1998; Mai & Velitzelos, 2007). The determination to this genus is supported by leaves with cuticle from the Late Oligocene of Kleinsaubernitz, Germany (Walther, 1999), and by both well preserved cones and anatomically preserved leaves from the Lower Miocene of Wiesa near Kamentz, Saxony, Germany (Kunzmann & Mai, 2005) and by cones from the Pliocene of Italy (Martinetto, 2001b). Well preserved cones and leaves are also recognized from the Miocene of Idaho, USA (Kvaček & Rember, 2000). The genus was confirmed in the Pliocene of Japan based on pollen investigated both by light and scanning electron microscopy (Saito et al., 2001).

Keteleeria has three to five extant species in the broadleaved evergreen forests of China, Laos, and Vietnam. Keys distinguishing the seeds of *Keteleeria* from those of other Pinaceae are provided by Wolfe and Schorn (1990) and Frankis (1989). The genus is known based on distinctive seeds from the Eocene of Quilchena flora of British Columbia (compare Figs. 1 & 2) and Oligocene of Oregon (Meyer & Manchester, 1997). Seeds, needles and male strobili with in situ pollen of *Keteleeria* are known from Upper Oligocene to Miocene

Table 2 Former and present geographic distribution of *Ginkgo* and coniferous genera now endemic to eastern Asia

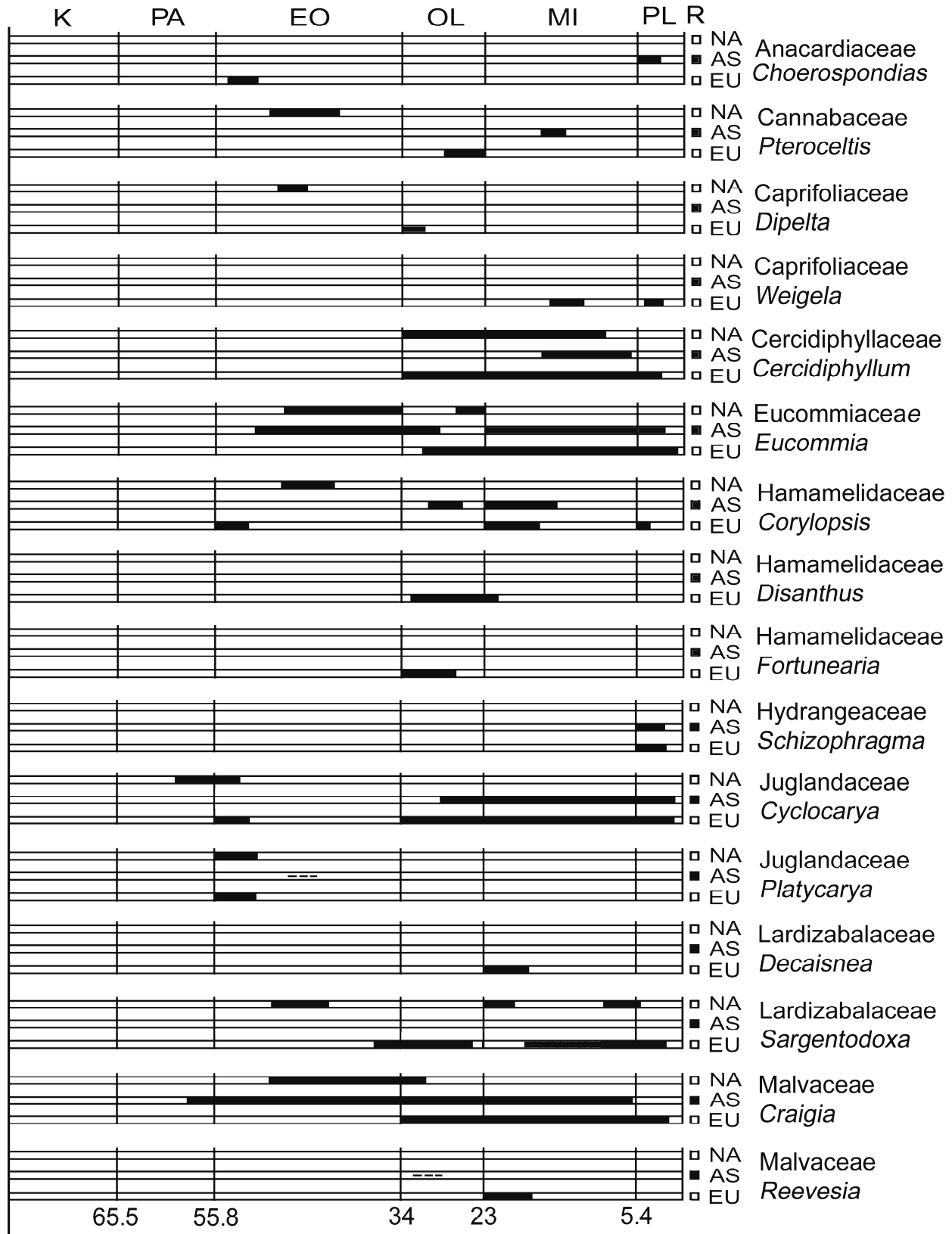


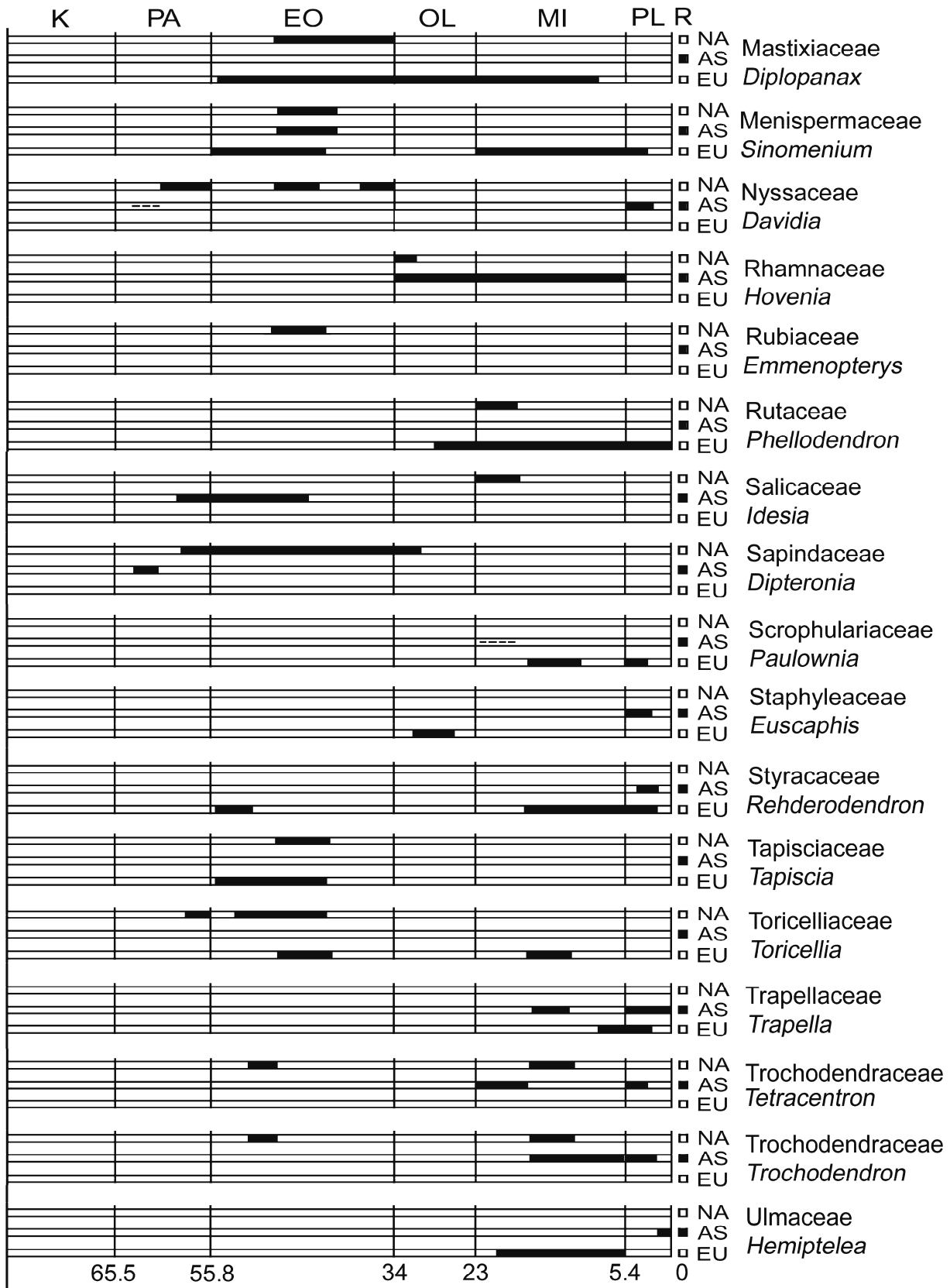
Abbreviations: EO, Eocene; K, Late Cretaceous, beginning 99.5 Ma; MI, Miocene; OL, Oligocene; PA, Paleocene; PL, Pliocene-Pleistocene; R, Recent. AS, eastern Asia; EU, Europe; NA, North America.

sediments of Central Europe (e.g. Kräusel, 1938; Kirchheimer, 1942; Mai, 1964; Mai, 1995; Mai, 1997; Kunzmann & Mai, 2005). Impressions of a cone, seeds and leafy shoots have been recorded from the Miocene Shanwang flora (Wang et al., 2006) and Pliocene of Japan (Miki, 1957). In our opinion, Tanai's *K. ezoana* (1961) needs further examination, including comparison with *Pseudolarix*.

Nothotsuga Hu ex C. N. Page has a single extant species, *N. longibracteata* (W. C. Cheng) Hu ex C. N. Page (1988) distributed in northeastern Guizhou, southwestern Hunan, northern Guangdong, northeastern Guangxi and southern Fujian, China. Formerly treated as a species of *Tsuga*, it is distinguished by radially spreading leaves with stomatal lines on both upper and lower leaf surfaces and erect seed cones (Wu & Raven, 1999).

Table 3 Former and present geographic distribution of angiosperm genera now endemic to eastern Asia (Abbreviations as indicated for Table 2)





Nothotsuga was recently recognized based on the distinctive epidermal anatomy of needles from the upper Lower or lower Middle Miocene of the Hasenberg clay pit near Kamenz, Saxony, Germany (Kunzmann & Mai, 2005).

Pseudolarix is restricted in modern distribution to central and southeastern China, with only one species, *P. amabilis* (J. Nelson) Rehder, living at 100–1500 m in elevation (Wu & Raven, 1999). *Pseudolarix* has an excellent fossil record in the Northern Hemisphere based on its distinctive seeds, cones, and foliage, with earliest records in the Cretaceous of Asia and North America followed by Oligocene establishment in Europe (LePage & Basinger, 1995, Gooch, 1992). It is also documented by well preserved seed cones, seeds, foliage and brachioblasts from the Middle Eocene of Arctic Canada (LePage & Basinger, 1995). Seed cone scales and seeds of *P. schmidtgenii* Kräusel were recovered, for example, from the Middle Miocene of Oberlausitz, Saxony, Germany (Czaja, 2001). The genus became extinct in North America by the middle to late Early Miocene (LePage & Basinger, 1995), and in Europe after the Pliocene (Martinetto, 2001b). It is documented in the Middle Miocene to Pliocene of Japan (Tanai, 1961).

2.1.3 Ginkgoaceae Although possibly wild trees of *Ginkgo biloba* have been found in northeastern Zhejiang Province, the species has a history of cultivation in other provinces of China, such that it is no longer possible to deduce the prehuman natural range of the species (Wu & Raven, 1999). *Ginkgo* is easily recognized by its fan-shaped leaves with subparallel dichotomizing and anastomosing venation, and ovoid drupe-like seeds. The cuticle is relatively resistant and often is preserved on fossil specimens, providing additional diagnostic characters. The record of *Ginkgo* and closely related genera in the Northern Hemisphere extends back to the Jurassic. Its record in the Tertiary indicates relatively late confinement to Asia. Tertiary records in North America extend from the Paleocene of Rocky Mountains and Great Plains (Brown, 1962; Manum, 1966; Crane et al., 1990; McIver & Basinger, 1993) and Middle Eocene of Pacific Northwestern North America (Mustoe, 2002) to the Miocene of Oregon (Chaney, 1920). In Europe it is known also from the Paleocene (Boulter & Kvaček, 1989) to the Early Pliocene (Tralau, 1968; Hably & Kvaček, 1997) and mid-Pliocene (Mädler, 1939). A rare Late Miocene record from Saxony, Germany was documented by Walther (2002). In Asia, *Ginkgo* is well documented from the Paleocene Amur region (Krassilov, 1976) of Koryak Upland, Russia (Golovneva, 1994), the Eocene of Fushun (Endo, 1942; WGCP, 1978), and Huadian (Manchester et al., 2005), China, and from the Eocene to Early Pleistocene of Japan (Uemura, 1997; Yamakawa, 2000). A world-wide review of the stratigraphic distribution of this genus was presented by

Tralau (1968) and a more detailed treatment of the Asian records by Uemura (1997). Although Tertiary leaves similar in appearance to extant *G. biloba* are usually placed in the fossil species *G. adiantoides* Heer, Mustoe (2002) found no significant differences and assigned Eocene leaves to the extant species. The resistant cuticle is often preserved in fossils, and this genus has therefore been a taxon of special interest in assessments of changing CO₂ levels through geologic time.

2.1.4 Sciadopityaceae This family, with only one extant genus, *Sciadopitys*, is endemic to Japan with the single species, *S. verticillata* (Thunb.) Sieb. & Zucc. The earliest fossil record is a seed cone of the family from the Upper Cretaceous of Hokkaido, Japan (Saiki, 1992). Christophel (1973) recognized *Sciadopitys*-like shoots and leaves from the Paleocene Smokey Tower locality in western Alberta, Canada which he referred to the fossil genus, *Sciadopitophyllum*. The long, strap-like leaves of this fossil are attached in apparent whorls subtended by groups of scale leaves, and other scale leaves are borne in loose spirals on the shoots between whorls, as in the extant genus. The branch buds in the axis of scale leaves are in a much less acute angle in *Sciadopitophyllum* than in extant *Sciadopitys*, and the flange of scale leaves found below the newly developed bud in the extant genus is not found in the fossil material. However, Christophel (1973) reasoned that these differences probably do not negate the possibility of a close relationship between the fossil genus and extant *Sciadopitys*. In addition, the extant genus *Sciadopitys* has been confirmed by the epidermal anatomy of well preserved fossil leaves from the Tertiary of Europe (Florin, 1963; Weyland et al., 1967), e.g., *S. tertiaria* from the Lower and Middle Miocene browncoal of Lusatica, Germany (Dolezych & Schneider, 2005) and Late Miocene of Japan (Uemura, 1986).

2.1.5 Taxaceae *Amentotaxus*, with five or six extant species in China and Vietnam, has an excellent fossil record in North America and Europe. It is readily recognized by its broad needle-like leaves with a pair of prominent stomatal bands and distinctive epidermal anatomy (Ferguson et al., 1978). *Amentotaxus* extends from the Upper Cretaceous (Santonian) to Miocene in North America (Kvaček & Rember, 2000) and from the Paleocene to Upper Miocene of Europe (Ferguson et al., 1978; Jähnichen, 1990).

2.1.6 Cupressaceae (incl. Taxodiaceae) This family includes multiple genera now endemic to East Asia, including *Metasequoia*, *Cunninghamia*, *Cryptomeria*, *Glyptostrobus* and *Taiwania*.

Metasequoia, which grows natively in southwestern Hubei, northwestern Hunan, and eastern Sichuan, has become famous as an example of a genus that was formerly widespread in the Northern Hemisphere but is now native only to China. The generic name was

established based on fossil remains in Japan (Miki, 1941) prior to discovery of living trees in central China. Subsequently, the dawn redwood has been recognized to have an excellent Cretaceous and Tertiary record in Asia and North America. A comprehensive review of the modern genus and its Late Cretaceous to Neogene fossil record was provided by LePage et al. (2005). Particularly detailed reports of *Metasequoia* foliage and cones from the Paleocene of Alberta, Canada were provided by Stockey et al. (2001) and from the Paleocene Wuyun Formation of northeastern China by Liu et al. (1999). The record is poor in Europe, except for the occurrences in the Paleocene of Scotland and Eocene of Spitsbergen (Boulter & Kvaček, 1989).

Cryptomeria has a single species today native to Japan and in Fujian, Jiangxi, Sichuan, Yunnan, and Zhejiang provinces of China. The fossil species *C. kamtschatica* Cheleb. is based on leafy twigs from the Eocene of Kamchatka (Budantsev, 1997). In Europe *C. rhenana* Kilpper is known from the Lower and Middle Miocene based on dispersed cuticles (referred to *Enormicutis conferta* Schneider by Dolezych and Schneider, 2005) and from the Late Miocene of Rhein region based on seed cone, seeds, and foliage with cuticle (Kilpper, 1968). The genus extends to the Early and Middle Pliocene of Italy based on cones, seeds and associated twigs (Martinetto, 1998, 2001a). It is also known from the Miocene to Pleistocene of Japan (Miki, 1950; Nishida & Uemura, 1977) and Miocene of Primorye (Klimova, 1975).

In the morphology of foliar twigs, it may be difficult to distinguish *Cryptomeria* from other taxodioid Cupressaceae. A comparison of epidermal anatomy with that of other genera, to aid in the identification of fossil cuticles, is provided by Ma et al. (2007). Ferguson (1967) accepted the record of *C. sternbergii* by Gardner (1886) based on a branched twig with attached cones from the Paleocene of Northern Ireland, as a valid example of the genus. However, Boulter and Kvaček (1989) referred Gardner's *Cryptomeria* to *Glyptostrobus* based mainly on cuticle morphology (see below).

Cunninghamia has one species today occurring in mixed mesophytic and broad-leaved evergreen forests of China and in northern Vietnam and Laos at 200 to 2800 m (Wu & Raven, 1999). It is represented in the fossil record by cones, seeds, and foliage from the Eocene to Miocene of western North America (reviewed in Meyer & Manchester, 1997; Kvaček & Rember, 2000), by foliage twigs with well preserved epidermal anatomy and cones in the upper Lower Oligocene to Pliocene of Europe (reviewed Kovar, 1982; Walther, 1989, 1999), and by leafy twig impressions from Eocene of Kamchatka (Budantsev, 1997). Foliar twigs are also known from the Eocene to Pleistocene of Japan (Matsuo, 1963; Horiuchi, 1996; Miki, 1950).

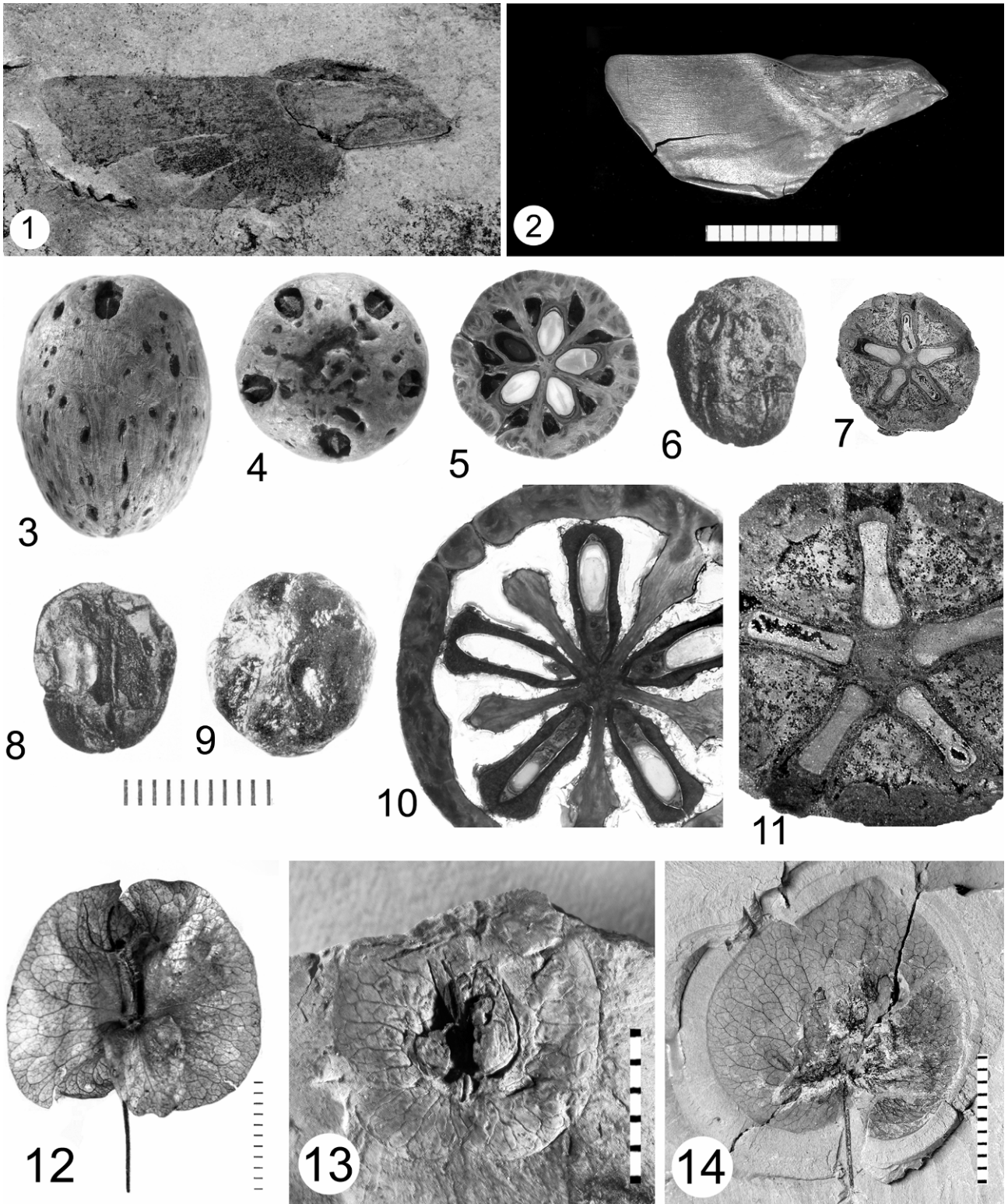
Glyptostrobus is native today only in southeastern China and Vietnam with the single species *G. pensilis*, but it was widespread in the Tertiary. The paleobiogeographic history of the genus was reviewed recently by LePage (2007), who accepts reports as old as the Aptian stage of the Cretaceous from western Canada and Greenland, and later Cretaceous records both in Asia and North America. In contrast to *Metasequoia*, which is almost lacking in the European Tertiary, *Glyptostrobus* is known from numerous European localities, ranging from the Paleocene (Boulter & Kvaček, 1989) to the Pliocene (Mai, 1995; Martinetto, 1998). Beautifully preserved cones and seeds are illustrated as *G. europaea* (Brongn.) Unger by Meller (1998) from the Lower Miocene of Steiermark, Austria. In North America, *Glyptostrobus* is well represented in the Paleocene to Eocene of the Rocky Mountain region (Brown, 1962), and in the Miocene of Idaho, Oregon and Washington (Brown, 1936; Chaney & Axelrod, 1959; Fields, 1996). *Glyptostrobus europaeus* twigs with attached cones are known in the Eocene to Pliocene of Japan (Tanai, 1961) and a permineralized cone was described from the Middle Miocene of central Hokkaido, Japan (Matsumoto et al., 1997).

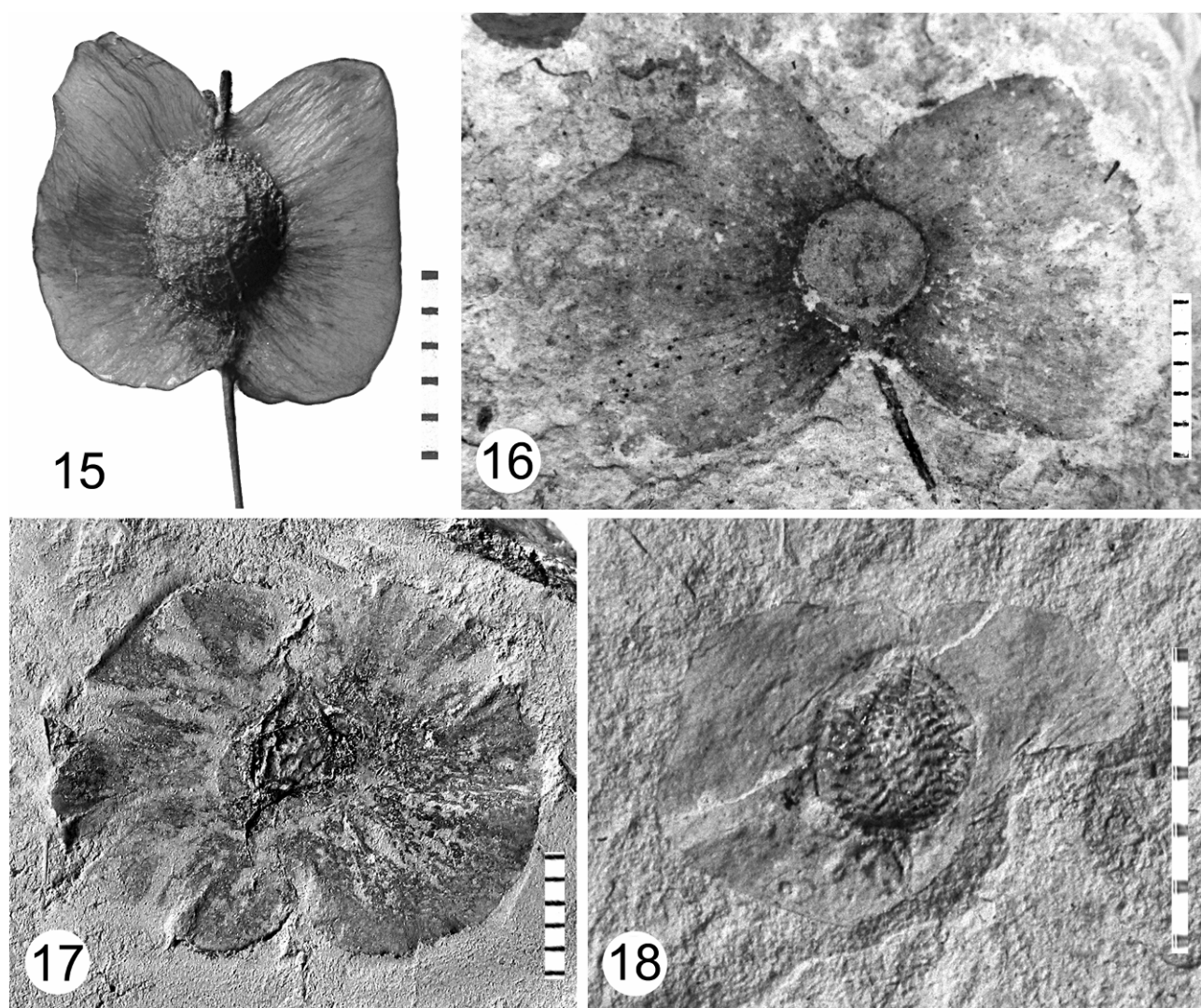
Taiwania has one species native to southeastern Xizang, western Yunnan, SE Sichuan, SW Hubei, SE Guizhou, Taiwan, and northern Burma. Vegetative shoots bearing cones were described and illustrated as *T. schaeferi* from the Paleocene of Spitsbergen by Schloemer-Jäger (1958) and were considered to agree in all respects with those of the modern genus (Ferguson, 1967). Foliar branches with well preserved cuticle have been recognized from the Oligocene-Miocene Weissenster Basin (Mai & Walther, 1991) and from the Late Oligocene of Kleinsaubernitz (Walther, 1999). Kilpper (1968) described a species based on a seed cone and leaf with cuticle from the Late Miocene of Rheinland, and Martinetto (1998) described additional examples from the Pliocene of Italy. The genus is represented in the Neogene of Japan by foliage shoots from the Middle Miocene to Pliocene of Hokkaido and Honshu (Tanai, 1961) and by cones and shoots from the Pliocene of Honshu (Miki, 1954).

Thujopsis. Shoots of *Thujopsis* were reported from the Late Miocene to Pleistocene of Japan (Huzioka & Uemura, 1973). As yet, no fossil cones or seeds have been found for confirmation.

2.2 Angiosperms

2.2.1 Anacardiaceae *Choerospondias*, of the tribe Spondiadeae, with one species distributed in northeastern India, southeastern China and northern Thailand, has distinctive pentalocular, operculate endocarps (Figs. 3–5, 10) readily identifiable as fossils. Well-preserved fruits of *C. sheppeyensis* (Reid & Chandler) Chandler are known from the Lower Eocene London Clay flora of southern England (Figs. 6–9, 11; Reid & Chandler, 1933;





Figs. 15–18. Cannabaceae: Modern and fossil fruits of *Pteroceltis*. **15.** Extant *Pteroceltis tartarinowii*, Botanical Garden, Chinese Academy of Sciences, Beijing. **16.** *P. tertiarum* Weyland, Oligocene of Rott, Germany. *Univ. Köln* 1836. **17.** *Pteroceltis knowltonii* (Berry) comb. nov., Middle Eocene of Puryear, Tennessee, *USNM* 35794 (holotype, Orig. *Dodonaea knowltoni* Berry, 1916). **18.** *Pteroceltis* sp. Middle Eocene of Republic, Washington, *UWBM* 96986. Scale bars calibrated in mm.

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Figs. 1–14. **1, 2.** Pinaceae: Seeds of *Keteleeria*. **1.** Seed from early Eocene Quilchena flora, British Columbia, Canada, photo courtesy of Rolf Mathewes, *SFU s.n.* **2.** Seed of extant *K. fortunei* Carr., Zhejiang, China, *PE* 1600449. **3–11.** Anacardiaceae: Extant and Eocene examples of *Choerospondias*. **3–5.** *Choerospondias axillaris*. **3.** Lateral view showing apically positioned germination valves. **4.** Apical view showing five germination valves. **5.** Transverse section showing five locules with surrounding lacunae. **6–9.** *Choerospondias sheppeyensis* (Reid & Chandler) Chandler, Early Eocene London Clay Formation, Herne Bay, Kent, England, Holotype, *BM* v30105. **6.** Lateral view of abraded exterior, showing a germination valve at upper left. **7.** Same specimen, in transverse section, showing five locules. **8.** Same specimen as 6, rotated to show longitudinally fractured surface with smooth locule lining visible at left. **9.** Another specimen of *C. sheppeyensis*, apical view showing five germination valves, *BM* v30101, figured Chandler 1961, pl. 21, fig. 29. **10.** Enlarged cross section of *C. axillaris*. **11.** Enlargement from 7, showing five locules with intervening parenchyma-filled lacunae. **12–14.** Caprifoliaceae: Modern and fossil fruits of *Dipelta*. **12.** Extant *Dipelta floribunda*, Arnold Arboretum, Massachusetts, *UF ref. coll.* 146. **13.** Holotype of *Dipelta europaea* Reid & Chandler from the Early Oligocene Bembridge flora of southern England, *BM* v17621. **14.** *Dipelta* sp. from Middle or Late Eocene of Bovay Clay Pit, Marshall Co., Mississippi, *UF* 15737–49026. Scale bars=1 cm. The bar in Fig. 2 applies to Figs. 1 and 2, the bar in Fig. 9 applies to Figs. 3–11.

Chandler, 1961). In Japan, fruits of *Choerospondias* are known from the Middle Miocene of central Honshu (reported as *Spondias*, Miki & Sakamoto, 1961), the Pliocene Osaka Group of southwestern Honshu (Fig. 14 in Momohara, 1989) and from several Pliocene localities in central Honshu (as *Spondias* in Miki, 1941).

2.2.2 Caprifoliaceae *Dipelta* has three living species of deciduous shrubs which occur in southwestern and northwestern China, in forest, shrubs, or hill slopes at altitudes from 600 to 3600 m. *Dipelta* fruits are elongate, with persistent epigynous sepals and enlarged bracts that function in wind dispersal (Fig. 12). The characteristic bract-winged fruits have long been known from the Early Oligocene of England (Fig. 13; Reid & Chandler, 1926). In addition, a single specimen from the Middle or Late Eocene of Mississippi, USA conforms in arrangement and venation of the bracts and in the narrow persistent pedicel to extant *Dipelta* (Fig. 14).

Diplodipelta, an extinct genus known from several Late Eocene to Middle Miocene sites in the western United States appears to be the sister genus to *Dipelta* (Manchester & Donoghue, 1995). Both genera have similar elongate fruits with epigynous sepals, but they differ in the morphology of their dispersal units. Whereas the dispersal units of *Dipelta* consist of a single fruit subtended by three enlarged bract wings, *Diplodipelta* dispersal units consist of a pair of fruits subtended by the three bract-wings. The morphological similarity between North American *Diplodipelta* and the Euro-Asian *Dipelta* suggests early Tertiary geographic continuity. Fruits of *Dipelta* and *Diplodipelta* have not been recognized from the Asian fossil record.

Weigela is a genus of deciduous shrubs native to northern China, Korea and Japan. It is distinguished from the related North American genus *Diervilla* by structure of the flowers and fruits and by the presence of membranous wings on the seeds (Lańcucka-Środoniowa, 1967). Seeds are known from the Miocene and Pliocene of Poland (Lańcucka-Środoniowa, 1967), the Miocene of Mammoth Mountain, eastern Russia, the Oligocene and Miocene of western Siberia (Dorofeev, 1957, 1963), and the Miocene of Denmark (Friis, 1985). The fossil seeds of this genus resemble those of extant species of section *Utsugia*, and *W. maximowiczii* which have a thin membranous marginal wing formed of elongated thin-walled cells. Friis (1985) carried out comparative SEM studies and noted that the Miocene seeds are particularly similar to those of extant *W. hortensis*, but differ in having much thinner cell walls. Pollen of *Weigela* has been recognized by light and scanning electron microscopy from the Lower Miocene of Oberdorf, Austria (Meller et al., 1999), but it was not explained how this pollen type may be distinguished from other genera of the family having similar spiny pollen.

2.2.3 Cannabaceae (incl. Celtidaceae) *Pteroceltis*

has one species, *P. tatarinowii* of northern to south-central China and Mongolia, found at altitudes of 100 to 1500 m. It usually grows in valleys and streams of limestone mountains in sparse forest. The fruits consist of a globose endocarp with a pair of finely striate lateral wings (Fig. 15). Perianth parts sometimes persist at the junction of the narrow pedicel with the fruit. *Pteroceltis tertiaris* Weyland is recognized from fruits in the Late Oligocene of Rott, Germany (Fig. 16; Weyland, 1937; Manchester, 1989). These have larger wings than the living species, but appear to be identical to the extant species in wing venation and morphology of the fruit body. Similarly large fruits of *Pteroceltis knowltonii* (Berry) comb. nov. occur in the Middle Eocene of Puryear, Tennessee (Fig. 17). This species, along with one from the Middle Eocene of Republic, Washington (Fig. 18; Pigg & Wehr, 2002) indicate that the genus was formerly distributed in North America as well as Eurasia. *Pteroceltis shanwangensis* Tao & Sun from the Miocene Shanwang flora (Sun et al., 1999) is based on a leaf very similar to that of extant *P. tatarinowii* (see especially, Sun et al., 1999, pl. 6, fig. 4). The leaf could alternatively represent a species of *Celtis*.

Pteroceltis has also been recognized in the Neogene of Korea and Japan, but these records are in need of re-consideration. Oishi and Huzioka (1942) described two winged fruits with photos and drawings “*Pteroceltis* sp. cfr. *P. tatarinowii* Maxim.” from the “Miocene” Kokangen *Engelhardia* bed of North Korea, and “*Pteroceltis* ? sp.” from the Miocene of Abura, Hokkaido, Japan. The published illustration of the Abura fruit resembles a fruit of *Pterocarya* (Juglandaceae), but Oishi and Huzioka stated that it differs completely from that genus in features of the central seed body. We have not observed the specimen and are not sure whether it has distinct venation in the wings (a difference from *Pteroceltis*), or a simple striate pattern (consistent with *Pteroceltis*). In their subsequent treatment of the Abura flora, Tanai and Suzuki (1963, p. 110) regarded Oishi & Huzioka’s *Pteroceltis* ? sp. as *Pterocarya ezoana*). Because Tanai and Suzuki did not mention the feature of fruit/seed body, and Oishi and Huzioka’s original figure (1942, fig. 1) was retouched, re-examination of the original specimen is necessary to confirm or reject this identification.

Oishi and Huzioka’s (1942) Kokangen specimen, “*Pteroceltis* sp. cf. *P. tatarinowii* Maxim.” curiously is not mentioned in Huzioka’s later treatment of the Korean flora (1972). However, the original fragmentary Kokangen specimen appears similar to a more complete specimen named *Carpites kungshimensis* Huzioka (1972, p. 76, pl. 12, figs. 6, 7) from another locality, Kungshim, in the same district of North Korea, and in the same stratum (“*Engelhardia* bed”) as Kokangen. It looks very likely to be *Pteroceltis*—consistent in the globose shape of the

nut, the persisting narrow pedicel, and the wing shape and lack of wing venation. The age of these localities, whether Middle Miocene as originally published, or Oligocene, is still in debate. To be conservative in placement, we have indicated this occurrence as early Middle Miocene in the stratigraphic table (Table 3).

2.2.4 Celastraceae *Tripterygium* is a genus of lianas and scandent shrubs distributed from eastern China to Japan. The distinctive winged fruits were recognized along with fossil leaves attributed to the genus by Ozaki (1991) from the Pliocene Kabutoiwa Formation of Central Honshu, Japan. Other reports of this genus have turned out to be examples of *Craigia* fruits (see Kvaček et al., 2005).

2.2.5 Cercidiphyllaceae Cercidiphyllaceae are represented by one extant genus with two species native to China and Japan (Spongberg, 1979). *Cercidiphyllum* trees grow in the margins of valleys and in forests at 650 to 2700 m. Extant *Cercidiphyllum*, diagnosed on the basis of clustered pod-like fruits and associated elliptical to obovate, serrate leaves like those of the extant species, occur in the Early Oligocene Bridge Creek flora of Oregon (Meyer & Manchester, 1997). In western North America *Cercidiphyllum* was present through the Middle Miocene of Idaho and one specimen is known with attached leaves and fruits (Pl. 4 fig. 8 in Smiley & Rember, 1985). In Europe, *Cercidiphyllum* fruits and leaves extend from the Early Oligocene to Pliocene (Jähnichen et al., 1980; Kvaček & Konzalová, 1996; Kovar-Eder et al., 1998). In Asia, the genus is confirmed by clustered fruits and associated foliage in the Miocene of Korfa, Kamchatka (Chelebaeva, 1971), the Middle Miocene of Hokkaido (Uemura, 1991), and the Middle Pleistocene of central Honshu, Japan (Onoe, 1989). Earlier records of Cercidiphyllaceae from the Cretaceous and Paleocene (which were placed by some authors in the modern genus, *Cercidiphyllum*) belong to extinct genera, with fruits borne in racemes rather than clusters. The isolated leaves are attributed to the fossil genus *Trochodendroides* and the fruits have been *Nyssidium*. In one instance co-occurring leaves of the *Trochodendroides* kind, inflorescences, and infructescences of the *Nyssidium* kind, were used along with associated twig architecture and seedlings, to circumscribe a more complete extinct genus, *Joffrea* (Crane & Stockey, 1985).

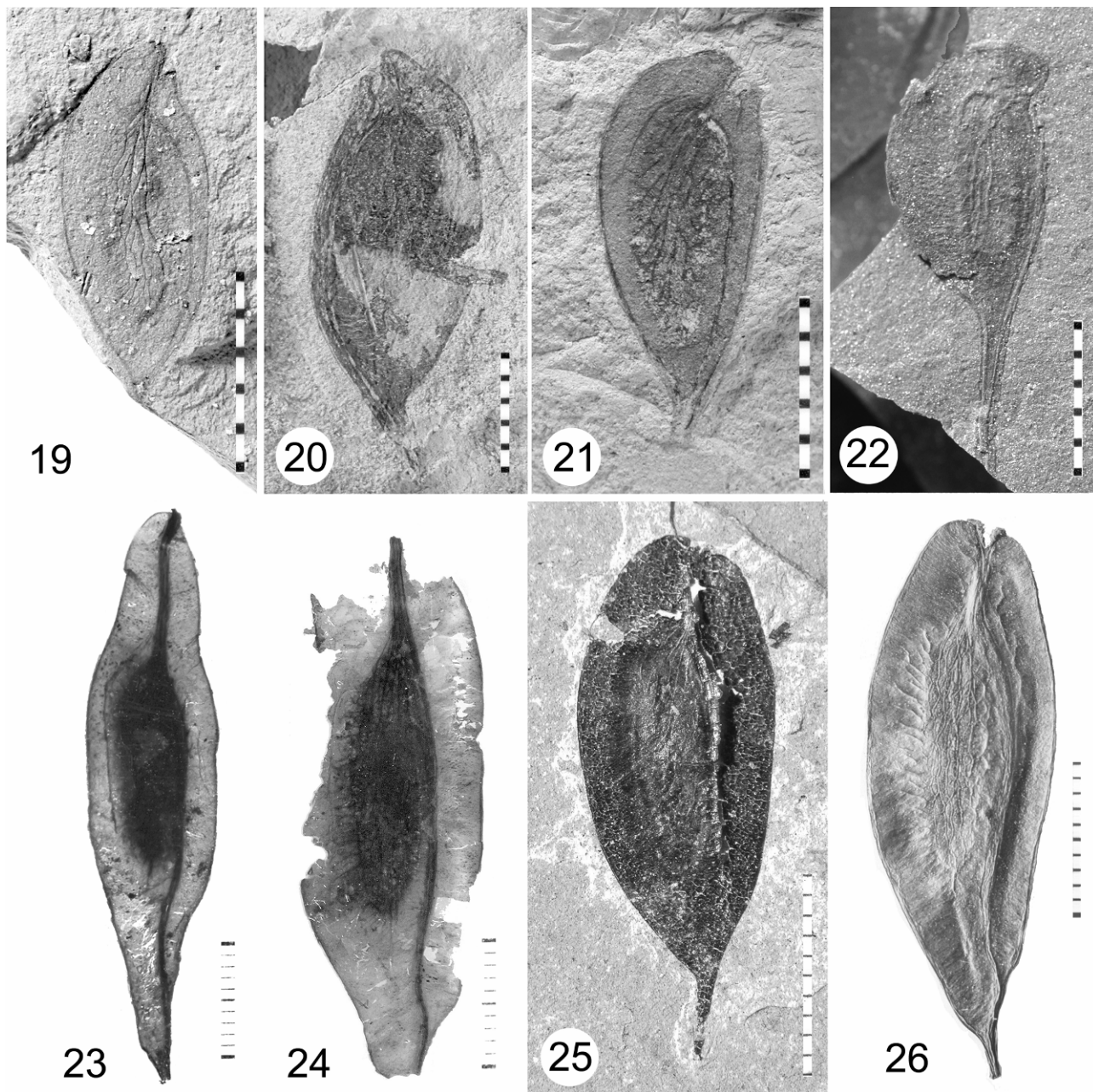
2.2.6 Eucommiaceae *Eucommia* is native to central China today, with a single species, *E. ulmoides*, growing at elevations in the range of 200 to 1740 m. The distinctive samaroid fruits (Fig. 26) have an excellent record in the Northern Hemisphere (Takhtajan, 1974; Guo, 2000). The generic determination of these fruits is secure because of the unique morphology and venation, and the presence of latex strands observable in the fossils that correspond in position to the laticifers of extant fruits (Szafer, 1950, 1954; Tralau, 1963; Call & Dilcher,

1997). The laticifers, whose vulcanized rubber tracts often preserve as a reticulum of fine threads partially free from the surface of the fossil compression or imprint, have also been useful to confirm the generic identity of fossil leaves and wood. In North America, the fruits and rarely leaves are known from the Middle and Late Eocene of the western and southeastern United States (Figs. 19, 20; Call & Dilcher, 1997; Manchester, 2000, 2001), and are also well documented from the Oligocene or Miocene of southern Mexico (Fig. 21; Magallon-Puebla & Cevallos-Ferriz, 1994).

In Asia, *Eucommia* is well documented by fruits in the Eocene of Yubari, Hokkaido, Japan (Huzioka, 1961), and Fushun, Liaoning, China (Fig. 22; Geng et al., 1999), the Lower Oligocene of Kiin-Kerish, Kazakhstan (Akhetiev, 1991), and Kraskino flora from the Khasan Basin, south Primorye, Russia (Ablaev et al., 1993). Several of these occurrences are reviewed in Takhtajan (1974). *Eucommia* was described and illustrated based on a fruit (Fig. 25) and leaves (Sun et al., 1999) and laticiferous wood from the Miocene Shanwang flora of Shandong Province, eastern China (Wang et al., 2003). Fruits occur at many localities in the Miocene to Pliocene of Japan (Tanai, 1961).

The numerous *Eucommia* fruit records in Europe extend from the Oligocene to the Pleistocene (Szafer, 1950, 1954; Tralau, 1963; Mai, 1995), including the Miocene of Moldavia (Negru, 1972). Maps showing the modern and fossil distribution were provided by Tralau (1963) and Ferguson et al. (1997). The North American and Chinese Eocene fruits are about 1/3 as large as those of the extant species, and are somewhat more asymmetrical in the placement of stigma at the fruit apex (Call & Dilcher, 1997). As one follows the record of *Eucommia* fruits through geologic time, a trend of increasing size is obvious, with fruits shorter than 1 cm being prevalent in the Eocene contrasting with larger fruits, e.g., 2.5 cm, in the Miocene. Szafer (1950) pointed out that the Pliocene species, *E. europaea* Mädlér (Figs. 23, 24), has fruits even larger than those of the recent species, *E. ulmoides*. The former range from 4.4–5.5 cm long (avg. 5.07 cm, $n=22$), whereas the latter range from 3.0–4.5 (avg. 3.42 cm, $n=67$) long. Psilate tricolpate or “incipiently tricolpate” pollen closely resembling that of the extant genus occurs in the Upper Paleocene of western North America (Pocknall & Nichols, 1996), but the Paleocene leaves attributed to *Eucommia* by Brown (1962) have been transferred to the unrelated nyssaceous genus *Brownia* (Manchester & Hickey, 2007).

2.2.7 Eupteleaceae This family has one genus and two species distributed from northeastern India to central China and Japan. The early fossil record of this family remains in our opinion uncertain, because the distinctive winged fruits have not been recovered, despite the collection of numerous Tertiary lacustrine deposits in the



Figs. 19–26. Eucommiaceae: *Eucommia*, fossil and modern fruits. **19.** *Eucommia montana* Brown from Late Eocene Whitecap Knoll, Oregon, USA, UF272-26326. **20.** *E. eocenica* fruit from Bovay clay pit, Holly Springs, Mississippi, UF 15737-8219. **21.** *E. constans*, Puebla, Mexico, UF11054. **22.** *E. cf. montana* from the Early Eocene of Fushun, Liaoning, China, CMPH 53959. **23.** *E. cf. europaea* Mädlér from the Pliocene of Auenheim, France, coll. F. Geissert, SMNS P 2096. **24.** *E. europaea* from Mizerna, Poland, KRAMP coll. (Orig. Fig. Szafer 1950, pl. 4, fig. 3). **25.** *Eucommia* fruit from Middle Miocene Shanwang flora, Shandong, China, S2002295. **26.** Extant *Eucommia ulmoides* Oliv. from Lichuan, Hubei, China, PE: G. X. Fu & Z. S. Zhang 1740. Scale bars calibrated in mm.

Northern Hemisphere where such fruits would be expected to be preserved. Leaves have been identified to *Euptelea* from the Eocene and Oligocene of the Pacific Northwestern North America (Wolfe, 1977), but the similarity with leaves of Platanaceae makes it difficult to confirm the identity. Silicified wood of *Euptelea* was identified based on well preserved silicified secondary

xylem from the Middle Eocene of Oregon (Scott & Barghoorn, 1955). Despite some striking similarities between the fossil wood and extant *Euptelea*, differences in the intervacular pitting and perforations acknowledged by the original authors call for caution in accepting the assignment of this wood to Eupteleaceae (Wheeler & Manchester, 2002). Leaves resembling extant

E. polyandra are reported from the Pliocene of central Japan (Ozaki, 1991), but the most reliable record is based on winged fruits and associated leaves from the middle Pleistocene of Shiobara, central Japan (Onoe, 1989).

2.2.8 Hamamelidaceae This family is widely distributed today, but has several genera confined to eastern Asia (Table 1). Seeds of the Hamamelidoideae subfamily, including *Hamamelis*, *Parottia*, and several others have a similar morphology, with a prominent hilar scar and shiny surface related to their dehiscence mode of abrupt ejection from woody capsules. The seeds have converged on very similar morphology related to the constraints of this dispersal mode, and some of the genera might be difficult or impossible to distinguish based on seed morphology alone (Endress, 1989). However, paleobotanists have strained to find characters distinguishing the seeds of this subfamily, and have often made identifications of fossils to extant genera based on configuration of the distinctive hilar scar, overall shape and size (Dorofeev, 1963; Mai, 1987) and course of the raphe impressed on the inside of the seedcoat (Manchester, 1994). Except for some detailed studies of *Corylopsis* seeds in relation to those of other Hamamelidoideae (Zhao & Li, 2008), there has still not been a detailed comparative treatment of all of the genera to show that they can be truly distinguished, so there may be some question remaining about the validity of some of the determinations of *Disanthus*, *Loropetalum*, *Fortunearia*, *Eustigma*, *Sinowilsonia*, *Distylium*, *Sycopsis*, *Hamamelis*, and *Fothergilla*.

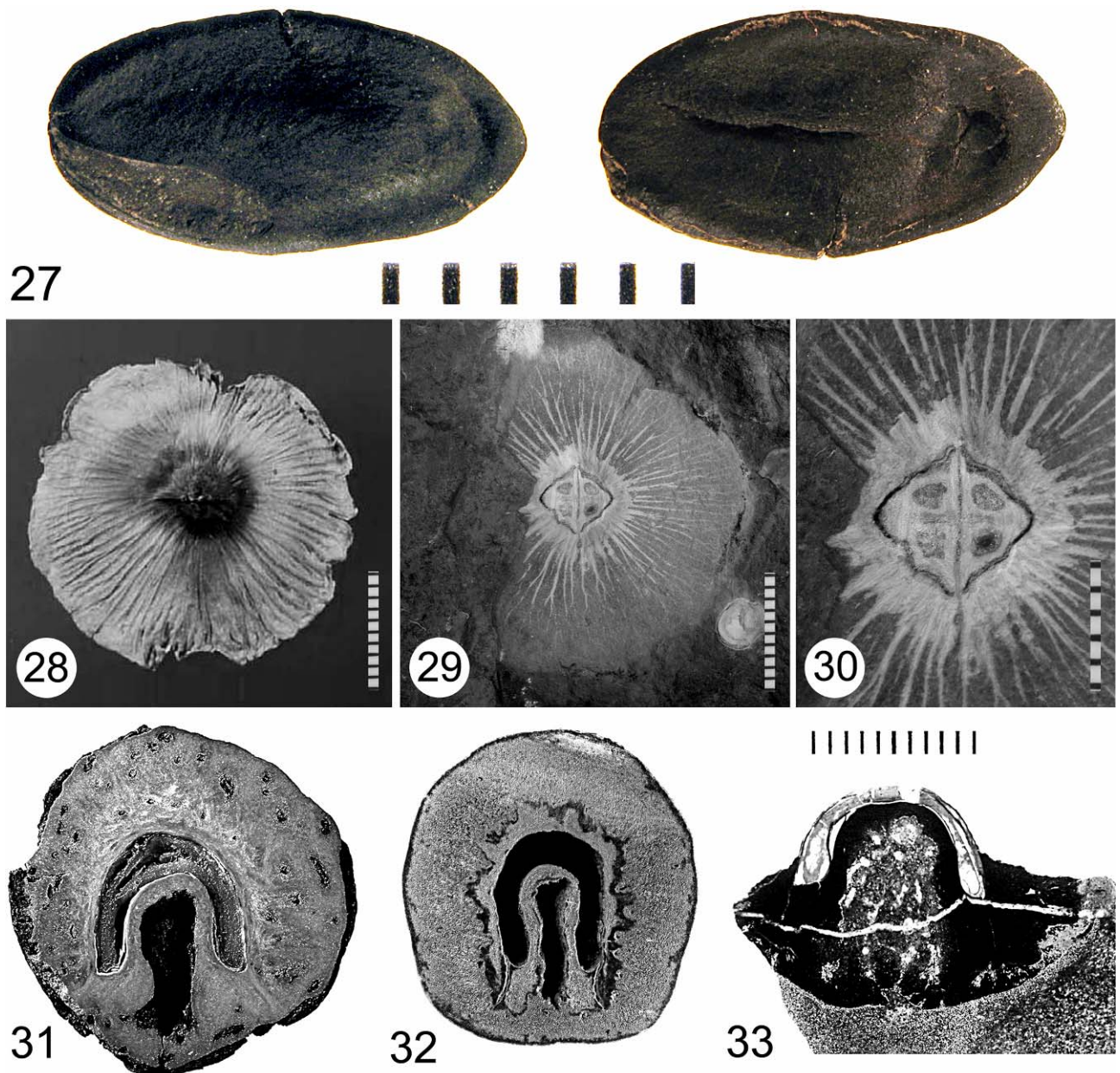
Corylopsis ranges from the Himalayas to Japan today with about 30 species, including 20 in southwestern and southeastern China. It was formerly distributed in Europe and North America. The global fossil record of the genus, with occurrences in North America, and Europe as well as Asia, was reviewed by Zhao and Li (2008). The oldest known record is the species *C. venablesi* Chandler based on seeds with a basilateral hilar scar 1/2 to 1/4 the length of the seed one side and a facet on the opposite side, from the Early Eocene of London Clay flora of southern England (Chandler, 1961). Grote (1989) recognized *Corylopsis* on the basis of seeds from the Middle Eocene of Tennessee (e.g., Fig. 27). He noted that a distinctive asymmetrical hilar scar facilitates the discrimination of *Corylopsis* seeds from seeds of other extant genera of the Hamamelidoideae. Leaves of *Corylopsis* were recognized from the Eocene of Republic, Washington, USA by Radtke et al. (2005) and from the Oligocene of western Japan (Hori, 1987; Uemura et al., 1999). Zhao and Li (2008) identified well-preserved seeds of *Corylopsis* from beds of probable Miocene age in southwestern Yunnan, China. In addition, they provided a table with characters distinguishing seeds of some other extant genera of Hamamelidoideae. According to their analysis, there are two

distinct scars in *Sinowilsonia*, *Distylium* and *Corylopsis*, one on each side near the base but not united over it. The *Corylopsis* seeds can be distinguished by a narrow sunken asymmetric hilar scar on one side and a marked facet on the other.

Disanthus is another genus of Hamamelidoideae with one extant species now confined to eastern China and Japan. In Germany, *D. bavaricus* was recognized from Oligo-Miocene of Schwandorf (Gregor, 1977), and from Early Oligocene Haselbach series (Mai & Walther, 1978). Knobloch and Mai (1986) recognized hamamelidaceous seeds with the distinctive hilar scars from the Late Cretaceous of Austria and Germany and named them to extant *Disanthus*, but without detailed justification regarding the generic assignment. *Disanthus austriacus* was described as an exceptionally small-seeded species from the Campanian-Maastrichtian of Sievering, Austria and *D. hercynicus* was described based on larger, multifaceted seeds from the Maastrichtian of Eisleben (Knobloch & Mai, 1986). An additional species was named from the Paleocene of Germany (Mai, 1987). Until a more thorough morphological and anatomical comparative treatment of extant and fossil seeds is conducted, we consider these geologically older records to be provisional.

Fortunearia is a genus of shrubs distributed in central and eastern China. Dorofeev (1963) identified seeds similar to those of extant *F. sinensis* from near the River Tym of western Siberia. A fossil seed species named *F. altenburgensis* Mai occurs in the middle to Lower Oligocene of Haselbach Series, Germany (Mai & Walther, 1978), but the justification for placement in this genus was not presented. Subsequently, Mai (1998) recognized the same species from the middle Oligocene Calau beds in Brandenburg, Germany, but he indicated that the seeds "either belong to a *Fortunearia* or *Sinowilsonia* species with small seeds". The genus has been identified in Japan on the basis of Pliocene leaves (Ozaki, 1984) and seeds (Miki, 1941). Infructescences of the fossil genus *Fortunearites* from the Eocene of Oregon bear seeds with a combination of characters found today only in the Asian endemic sister genera *Fortunearia* and *Sinowilsonia* (Manchester, 1994).

2.2.9 Hydrangeaceae *Schizophragma* is a genus of woody climbers extending from the Himalayas through Japan, with 11 species, 9 of which occur in China, ranging from 200 to 2900 m in elevation. It has capsular fruits, with united styles terminating in a large capitate stigma; the capsule dehisces by decay of intercostal tissue. *Schizophragma* is recognized based on immature fruits from the Pliocene Kroskienko flora of southern Poland by Mai (1985) and is known from well preserved fruiting heads in the Pliocene of northern Italy (Martinetto, 2001a). In Japan, fossil leaves closely similar to those of extant *S. hydrangeoides* were identified from the



Figs. 27–33. 27. Hamamelidaceae. Seed of *Corylopsis* sp. from the Eocene of Tennessee, USA, viewed ventrally and dorsally with hilar scar oriented to the left, det. P. Grote, *UF 15803-9115*. Scale bar calibrated in mm. 28–30. Juglandaceae: Extant and fossil *Cyclocarya*. 28. Extant *Cyclocarya paliurus*, A: S. C. Sun 1296, Anhui, China, *UF Ref. coll. 4000*. 29. *C. brownii* Manchester & Dilcher from the Paleocene of North Dakota, USA, *UF 15722-4039*. 30. Detail of nutlet in 29, with base of nutshell abraded to reveal 4-lobes of the base of locule, and orthogonal intersection of primary and secondary septa. Scale bars calibrated in mm. 31–33. Mastixiaceae: Fruits of Recent and fossil *Diplopanax* in transverse section. 31. Extant *Diplopanax stachyanthus* Vinh Phu (Tam Dao II), northern Vietnam, *Nguyen Tien Ban 121*; Komarov Inst., St Petersburg. 32. *Tectocarya rhenana* from Düren, Germany, *Staatliche Museum für Naturkunde in Stuttgart s.n.* 33. *Diplopanax* sp. from Late Eocene Quimper Sandstone, Oak Bay, Jefferson Co., Washington, USA, coll. J. Goedert 1988, *UWBM 36892*. All at same magnification (scale bar=1 cm).

Pliocene Kabutoiwa Formation of Central Honshu (Ozaki, 1991). Also, a leaf attributed to the modern species *S. hydrangeoides* was described from the middle Pleistocene of Shiobara, central Honshu (Onoe, 1989).

Although *Hydrangea* is geographically widespread with numerous species in the Northern Hemisphere, and

extends into South America, *H. anomala* constitutes a distinct clade called subsection *Calyptranthe* by McClintock (1957) which is confined to eastern Asia (Eastern Himalaya, central China, Korea, Japan). This is the only species of *Hydrangea* with seeds having an encircling wing. Silicified *Hydrangea* fruits containing

winged seeds indistinguishable from those of *H. anomala* were described from the Eocene of western North America (Manchester, 1994).

2.2.10 Juglandaceae The Juglandaceae include two genera endemic to eastern Asia: *Cyclocarya* and *Platycarya*. *Pterocarya* is also mostly eastern Asian in distribution, but with an additional species living in the Caucasus region. Although pollen and leaflets may be readily recognized to this family and subclades, the generic distinctions are based primarily on fruit characters. Because of overlapping foliar and pollen morphological characters among the extant genera as well as with some extinct genera of the family, we confine our attention to records confirmed on the basis of fossil fruits.

Cyclocarya is distributed today in southern, central and north-central China (Iljinskaya, 1953; Manning, 1975; Ying et al., 1993). It has distinctive fruits consisting of a small nutlet, surrounded by a prominent, circular disk-like wing with radiating dichotomous venation (Fig. 28). Care must be taken, however, to distinguish *Cyclocarya* fruits from morphologically convergent fruits *Paliurus* (Rhamnaceae), which also has a widespread Tertiary fossil record (Burge & Manchester, 2008), and *Dioncophyllum* (Dioncophyllaceae). Although *Cyclocarya* is most easily identified when both the wing and the nut are preserved (Iljinskaya, 1994), it is also possible to recognize based on the morphology of isolated nuts (Dorofeev, 1970, 2004). *Cyclocarya* fruits are common in the Paleocene of the North American Great Plains region (Figs. 29, 30; Manchester & Dilcher, 1982; Manchester, 1987), extending to the Early Eocene (Burge & Manchester, 2008). *Cyclocarya* ranges from the Oligocene to Upper Pliocene in Europe and Asia (Manchester, 1987; Iljinskaya, 1994), with the Asian records from western Siberia (Dorofeev, 1970), Kazakhstan and Primorye (Iljinskaya, 1994) and Japan (Miki, 1955; Ozaki, 1991). Isolated nutlets with wings absent and apparently abraded away, called *Juglandicarya depressa* Chandler, common in the Early Eocene London Clay flora of England, show internal structure consistent with that of *Cyclocarya*. A Paleocene fruit impression from northeastern China was described as *C. macroptera* by Tao and Xiong (1986), but it corresponds rather to the circular-winged fruit of the Dioncophyllaceae (*Dioncophyllites amurensis* Fedotov) recently recognized from the Eocene Raitschicha flora of the Amur region, southeastern Russia (Budantsev, 2005, p. 30, pl. 4). A juglandaceous locule cast with four basal lobes indicating development of the secondary as well as primary septum, was described as *Platycarya cordiformis* Mai (1987) from the Lower Paleocene of Gonna; however, the cast matches more closely those of *Cyclocarya*.

Platycarya has three species of deciduous trees distributed in China, Vietnam, Korea and Japan at eleva-

tions of 500–1300 m. The modern species typically have imparipinnately compound leaves, but *P. simplicifolia* has simple leaves. The fruits are bi-winged nuts borne in globose to elongate-ellipsoidal cone-like infructescences. Infructescences with intact fruits are known from the Early Eocene of England (Reid & Chandler, 1933 as *Petrophylloides*; Manchester, 1987) and North Dakota (Wing & Hickey, 1984). The extinct fruit genera *Hoo-leya* from the Eocene of North America (Manchester, 1987; Wing & Hickey, 1984) and the Eocene to Oligocene of Europe (Reid & Chandler, 1926; Rasky, 1956) and *Paleoplatycarya* from Paleocene of North America show affinities with *Platycarya* (Wing & Hickey, 1984; Manchester, 1987). The triporate pollen of *Platycarya* has the usual diagnostic features of Juglandaceae (porate with ornamentation of evenly distributed scabrae) but is distinctive among other extant juglandaceous pollen by the presence of pseudocolpi, a pair of thin oblique troughs in the exine on both polar hemispheres. The same kind of pollen co-occurs with the extinct fruit genera, indicating that such pollen is diagnostic of the tribe, but not to genus, when the Tertiary record is considered. Hence, the fossil genus name *Platycaryapollenites* Nagy is preferred for fossil pollen grains. *Platycaryapollenites* has been reported from the Eocene of North China sea (Song et al., 1999, 2004), as well as from Paleogene of North America and Europe. Despite the occurrence of juglandaceous leaflets assigned by some authors to *Platycarya*, the diagnostic infructescences of *Platycarya* have not been found in the Asian Tertiary.

2.2.11 Lardizabalaceae This family is disjunct today between South America and Asia, but most of the genera are endemic to eastern Asia: *Akebia*, *Decaisnea*, *Holboellia*, *Sargentodoxa*, *Sinofranchetia*, and *Stauntonia*.

Akebia has five species living today in eastern Asia. Mai (2001a) identified seeds of *Akebia*, *A. parvisemina* Mai, from the Upper Miocene of the Bröthen clay pit. He indicated that the fossils correspond in morphology to the seeds of all three extant species of *Akebia*, but anatomical details were not presented, and diagnostic features for seeds of *Akebia*, which would allow them to be distinguished from seeds of all other angiosperm genera, were not mentioned. Therefore, these fossils are in need of more detailed comparative work to confirm their identity.

Decaisnea has two extant species in the eastern Himalayan region and central China. The fruits of this genus are leathery follicles with seeds mainly in two rows surrounded by white pulp. The seeds of this genus are laterally compressed, and obovoid to oblong in outline with a thin testa consisting of an outer layer of isodiametric cells and an inner layer of radially elongate cells. In contrast to other genera of the family, it lacks a prominent hilar marking. Mai (1980) recognized a fossil

species based on seeds from the Lower Miocene of Borna-Ost, near Leipzig, Germany, *D. bornensis* Mai. The fossil species corresponds to the extant genus in morphology, including placement and size of the hilum, raphe and micropylar point and in anatomy of the seed coat. According to Mai, the fossil seeds of *D. bornensis* deviate from extant *D. fargesii* Franch. seeds by having smaller width in relation to length and the more distinctly inclined, subapical chalazal region, supporting separate species status.

Sargentodoxa is a genus of two species of deciduous lianas ranging from south-central to eastern China to northern Laos. It grows in forests and in thickets at forest margins, usually climbing on other vegetation, in soils with a pH from 4.5 to 6.0, at elevations of (130–)400–1900(–2400) m. The leaves are estipulate and simple to digitately trifoliolate with entire-margins. *Sargentodoxa* has distinctive shiny seeds with a rounded base and slightly oblique apical truncation, described in detail by Tiffney (1993). In North America the fossil seeds are known from the Middle Eocene of Oregon (Manchester, 1999), the Early Miocene Brandon lignite of Vermont (Tiffney, 1993), and the late Miocene or Pliocene Gray site in Tennessee (Yu-Sheng Liu, pers. comm., 2007). Seeds of *S. lusatica* (Mai) Mai have been recognized from the Late Eocene to Late Oligocene of northwest Saxony and Middle Miocene of Lausitz, Germany (Mai, 2001a). Well-preserved *Sargentodoxa* seeds have also been found in the uppermost Miocene-Lower Pliocene dredging flora of Alsace and the Pliocene of Italy (Martinetto, 2001b).

2.2.12 Malvaceae This family (incl. Tiliaceae, Sterculiaceae, Bombacaceae as well as traditional Malvaceae—Bayer & Kubitzki, 2003) is widespread particularly in the tropics today, but has only a few genera endemic to eastern Asia.

Extant *Craigia*, traditionally placed in the Tiliaceae, has two species: *C. yunnanensis* W. W. Smith & W. E. Evans of southern China (Guangxi, Guizhou, Yunnan, southeastern Xizang), and northern Vietnam, and *C. kwangsiensis* Hsue of Guangdong Province, China. It grows in broadleaved evergreen and deciduous mixed forests and seasonally wet forests in limestone areas, in soils with a pH ranging from 6.0 to 7.5 at elevations of 1400–1700 m. The genus was widely distributed through the Tertiary (its fruits were formerly considered to be an extinct genus, *Pteleaecarpum*; Bůžek et al., 1989). With the recognition that the fossil fruits represent *Craigia* (Kvaček et al., 1991), it has been possible to document an extensive history of this genus throughout the Northern Hemisphere with many fruit records in western North America, Europe, and Asia (Kvaček et al., 2005). The distinctive fruit valves are known from the Late Eocene or Early Oligocene of Spitsbergen and the Middle Eocene to Early Oligocene of Western North America,

but in Europe, the fruit records extend from the Oligocene to the Pliocene. In Asia, *Craigia* fruits have the greatest stratigraphic range, from the Paleocene in Kamchatka to the Late Miocene of Sikhote-Alin (Kvaček et al., 2005).

The genus *Reevesia* Lindley, originally based on the species distributed from the eastern Himalaya to Taiwan and Yunnan, has been recognized by some authors to include the central American genus *Veeresia*. The status of *Reevesia* as a genus endemic to eastern Asia depends, however, on whether *Veeresia* is treated as a distinct entity or not. If *V. clarkii* Monach. & Moldenke of southern Mexico is treated as an American representative of *Reevesia*, the genus would be considered disjunct between the two continents, rather than endemic to eastern Asia (Mabberley, 1997). *Reevesia* has been recognized in the Tertiary of Europe based on pollen (*Reevesiapollis* Krutzsch) corroborated by both light and scanning electron microscopy from the Lower Miocene of Oberdorf, Austria (Meller et al., 1999) and by an association of leaves, fruit valves and winged seeds from the Miocene of Bilina, Czech Republic (Kvaček, 2006). Woods anatomically similar to *Reevesia* are known from the Paleogene and Miocene of Japan (Terada & Suzuki, 1998).

2.2.13 Mastixiaceae *Diplopanax*, with two extant species, is distributed in China (Guangxi, Guangdong, Hunan, Yunnan), Vietnam and Cambodia. Although this tree was originally thought to belong to the Araliaceae, fruit morphology, and molecular sequence data indicate that it belongs within the Cornales as a sister to *Mastixia* (Eyde & Xiang, 1990; Fan & Xiang, 2003) in the Mastixiaceae clade. *Diplopanax* fruits are easily recognized by their ellipsoidal woody fruits with a single-seeded boat shaped locule and elongate germination valve. In transverse section, the fruits are circular with a C-shaped locule (Fig. 31). *Diplopanax* fruits are similar to those of *Mastixia*, but have numerous scattered vascular bundles rather than a single pair of ovular bundles. The margins of the germination valve are perpendicular to, rather than tangential to the limbs of the locule. In Europe, most of the fruits attributed to *Mastixicarpum* (a fossil fruit genus established before *Diplopanax* was known) probably also belong to *Diplopanax* (Eyde & Xiang, 1990; Czaja, 2003; Ševčík et al., 2007), indicating a stratigraphic range from Early Eocene to Miocene. The fossil genus *Tectocarya* (Fig. 32) is also very similar to, and likely congeneric with, *Diplopanax*. *Diplopanax* has been recognized based on fruits from the Middle and Late Eocene of Oregon (as *Mastixicarpum*, Manchester, 1994; Tiffney & Haggard, 1996; Manchester & McIntosh, 2007) and the Middle Eocene of British Columbia, Canada (Stockey et al., 1998). An additional occurrence from the Late Eocene of Washington recently came to light (Fig. 33). As yet, neither *Diplopanax* nor

Mastixia has been recognized in the Asian fossil record.

2.2.14 Menispermaceae This family is well distributed in tropical regions today, but has only one genus that is endemic to eastern Asia: *Sinomenium* which has one extant species in central China and Japan. *Cyclea* extends from China to the Philippines, and hence exceeds our area of emphasis, but also has fossil records in Europe (Martinetto, 2001a, b). *Diploclisia* extends into Malesia as well as China, and has Eocene fossil occurrences in North America (Manchester, 1994). These genera, like most in the family, are readily recognizable based on endocarp morphology. *Sinomenium* endocarps were first recognized in the European Tertiary based on endocarps from the Pliocene of Poland (Szafer, 1947) and are now known from several more occurrences in the Miocene of Europe, as reviewed by Kirchheimer (1957), and in the Pliocene of Italy (Martinetto, 1998). Dorofeev (1963) recognized the species *S. cantalense* (E. M. Reid) Dorof. based on fruits from the Pliocene of Pont-de-Gail, France, the Kroskienka flora of Poland, and from western Siberia. Another species, *S. militzeri* Kirchheimer (1957) has endocarps that are also close to extant *S. acutum* and to the fossil *S. cantalense*, but differs from both of these species by having higher protuberances of the external and lateral crests. Mai (1997) considers that characteristics of the endocarps of the Eocene fossil genera *Palaeosinomenium* Chandler, and *Wardensheppeya* Eyde (= *Wardenia* Chandler) differ only in specific, rather than generic characters, from *Sinomenium*. He therefore considers that *Sinomenium* extends from the Eocene to the Pliocene of Europe. *Palaeosinomenium* endocarps were also recognized from the Middle Eocene of Oregon, USA (Manchester, 1994) and Huadian, Jilin, China (Manchester et al., 2005).

2.2.15 Nymphaeaceae *Euryale* is the only member of the water lily family confined to eastern Asia. The distinctive seeds of *Euryale* facilitate recognition and distinction of paleobotanical records. While many other genera of the family have excellent fossil records, the fossil record of extant *Euryale* has proven elusive. *Euryale nodulosa* seeds from the Pliocene of Netherlands and Italy are similar to those of living *E. ferox* in macroscopic shape and general structure, "but with shorter and broader elliptic embryotega, finer cell sculpture and more prominent nodules on the external surface. In addition, they show a different testa structure in cross section" (Martinetto, 2001b, p. 156). This species could alternatively fit the diagnosis for the form genus *Paleoeuryale* Dorofeev. Seeds assigned to an extinct genus, *Susiea* from the Paleocene of North America, appear to have their closest similarity to *Euryale* among extant genera. *Susiea* differs, however, by having rectangular, rather than polygonal, epidermal cells and in the thickness of the seed coat and raphe morphology (Taylor et al., 2006). Miki (1960) described 4 species of *Euryale*

based on seed remains at many localities of the Pliocene and Pleistocene of Japan. Three species were identified to European fossil species (*E. europaea* Weber, *E. lissa* Reid, *E. nodulosa* Reid), and one to the modern species, *E. ferox*.

2.2.16 Nyssaceae This family includes the extant genera *Nyssa*, *Camptotheca*, and *Davidia*, plus the extinct genera *Amersinia* and *Browniea* (Manchester & Hickey, 2007).

Davidia has one species, *D. involucrata*, native to the broad-leaved forests or evergreen forests, at altitudes of 1100–2600 m in southwest and west Hubei Province, China. It has a distinctive ellipsoidal fruit with a woody stone containing several single-seeded locules, each with an elongate dorsal germination valve. An extinct species, *Davidia antiqua* (Newberry) Manchester, was common in the Paleocene of North America, based on well preserved leaves and fruits from the Paleocene of Wyoming, Montana and North Dakota (Manchester, 2002). Similar leaves and fruits occur in the Paleocene of southeastern Russia (Manchester, 2002). In North America, silicified fruits indicate that the genus survived at least to the Late Eocene in Oregon (Manchester & McIntosh, 2007). Leaves virtually indistinguishable from those of extant *Davidia* were described as a fossil genus, *Tsukada*, from the Middle Eocene of Republic, Washington (Wolfe & Wehr, 1987). No occurrences of *Davidia* have been found in the paleobotanical record of Europe despite conditions favorable for the preservation of woody fruits. In Japan, *Davidia* fruits and leaves indistinguishable from the modern Chinese species occur in the Pliocene of central Honshu (Kokawa, 1965; Ozaki, 1984; Tsukagoshi et al., 1997). The extinct fruit genus *Amersinia* combines characters of *Camptotheca* and *Davidia*. Along with the associated foliage, *Beringiaphyllum*, these fruits were widespread in the Paleocene of eastern Asia and North America (Manchester et al., 1999).

Wood conforming anatomically to *Camptotheca* was described from the Oligocene of Tsuyazaki, northern Kyushu, Japan (Suzuki, 1975), but the wood is also anatomically similar to other genera. The distinctive fruits of *Camptotheca* have not been found in the fossil record. The extinct Paleocene genus *Browniea* has infructescences and fruits similar to those of *Camptotheca*, but *Browniea* had fruits with persistent perianth lobes not present in the extant genus, as well as different foliage and pollen (Manchester & Hickey, 2007).

2.2.17 Rhamnaceae *Hovenia* is a genus of deciduous trees and shrubs with five species ranging from the Himalayas to Japan; in southwest to eastern China it occurs at altitudes of 200 to 2100 m. The leaves are distinctive in their ovate outline, serrate margin with small glandular teeth, asymmetrical base and peculiar venation in which the lower margin of the lamina is delimited by the lowermost pair of secondary veins

(Figs. 34–36). Fossil leaves occur in the Oligocene of Oregon, USA (Figs. 35, 38; Meyer & Manchester, 1997), and the Middle Miocene Shanwang flora of Shandong Province, China (Fig. 36; Hu & Chaney, 1940; Sun et al., 1999). Wood conforming anatomically to *Hovenia* has been described from the Oligocene of northern Kyushu (Suzuki, 1982) and Lower Miocene of southwestern Honshu (Watari, 1952), Japan. We exclude from the genus, leaves described as *H. cuneiformis* from the Paleogene of South Primorye (Ablaev, 2000) because they do not show the base of the lamina outlined by the basal pair of secondary veins—an important feature of *Hovenia* and a few other genera of Rhamnaceae. From the prominence of glandular teeth and transverse arrangement of tertiary veins, the species appears instead to represent the Salicaceae.

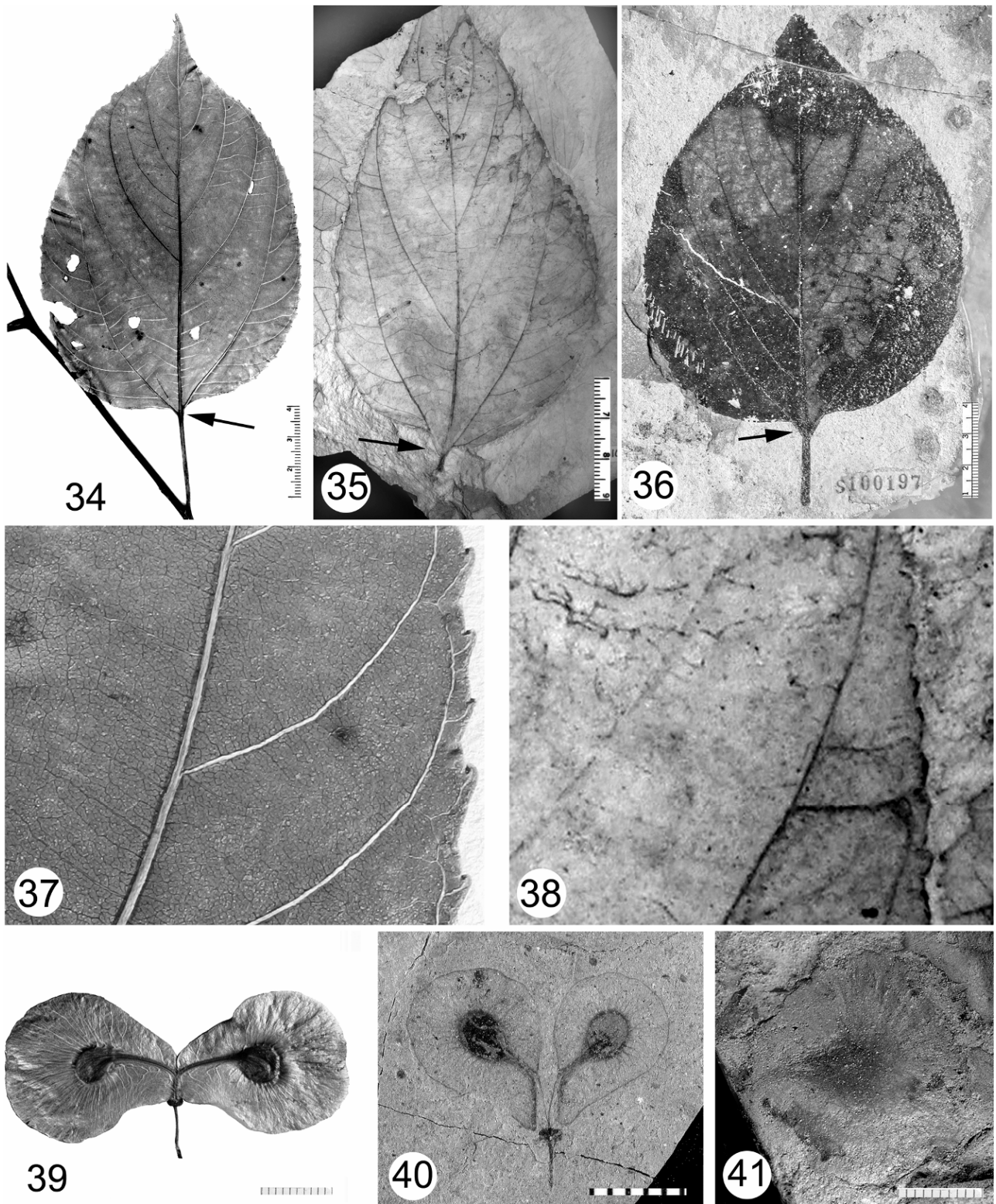
2.2.18 Rubiaceae *Emmenopterys* has one extant species, *E. henryi*, native to western to eastern China. It grows in broadleaved evergreen and mixed broadleaved evergreen and deciduous forest with pH 5–6, at elevations of 700 to 1300 m but usually 300 m in southeastern China and 1600 m in south-central China. This genus belongs to the tribe Cinchoneae which is characterized by elongate bilocular capsules with winged seeds and axile placentation (Andersson & Persson, 1991). *Emmenopterys dilcheri*, from the Eocene of Oregon based on well preserved infructescences containing anatomically preserved winged seeds, corresponds closely to extant *E. henryi* in infructescence branching pattern, inferior ovary, elongate bilocular fruits, axial placentation, and the morphology a pattern of reticulate thickening on the seed coat cells of the winged seeds (Manchester, 1994). A similar infructescence was also illustrated from the Middle Eocene of Eckfeld, Eifel, Germany (Pl. V, fig. 10 in Wilde & Frankenhäuser, 1998), but a broader study of the fruits and seeds of extant Cinchoneae is needed to ascertain its position.

2.2.19 Rutaceae The Tertiary record of Europe and North America includes many occurrences of rutaceous seeds as has been reviewed by Tiffney (1980) and Gregor (1989). Some of these genera are widely distributed today in warm regions, e.g., *Zanthoxylum* and *Toddalia*, but *Phellodendron* is limited to eastern Asia including far eastern Russia, China, Korea, and Japan (Tiffney, 1980). Although some members of the family are easily recognized based on seed morphology, several extant genera are similar and perhaps overlapping in seed morphological characters. The form genus *Rutaspermum* has thus been applied to some of the fossil species. Nevertheless, extant *Phellodendron* seeds are sufficiently distinctive that it has been possible to recognize fossil seeds with some confidence. This genus is confined to eastern Asia today with about 10 species. Fossil seeds of *Phellodendron* have been identified from the Neogene of Europe and Asia, and the Miocene Brandon Lignite

(Tiffney, 1980). Tiffney (1981) challenged the prior identification of *Phellodendron* from the Eocene of southern England, observing characters supporting reassignment of those fossils to *Euodia*, but in the same investigation he accepted the other European records of the *Phellodendron* from the review of Kirchheimer (1957). Tralau (1963) provided a map and review of the numerous European records of *Phellodendron* seeds, extending from the Oligocene to Pliocene. The seeds are found to the end of the Pliocene in central Europe and to the Early Pleistocene in Italy (Martinetto, 1998). Leaves reported as *Phellodendron* from China and Russia are in our opinion questionable.

2.2.20 Salicaceae *Idesia* is a genus now endemic to China, Korea and Japan. Its fruits are berries, unlike the capsules characteristic of related *Populus* and *Poliothyrsis*. *Idesia* is identified based on leaves with well-preserved venation from the northern California Weaverville flora (MacGinitie, 1937) of probable Early Miocene age (Barnett, 1989). *Idesia* leaves are similar to *Populus* in glandular teeth, but the laminae have truly palmate primary venation, without decurrence of lateral primaries along the midvein. According to MacGinitie, every character of the fossil leaves of *I. cordata* MacGinitie is matched in the leaves of extant *I. polycarpa* Maxim. If correctly determined, this western North American fossil species indicates that this genus, now endemic to China, crossed between Asia and North America sometime during the Tertiary. In Asia, the genus has been identified by leaf impressions from the Paleocene to Lower Eocene of Andyrka, Kiin Kerish (Iljinskaya in Budantsev, 2005; Chelebaeva in Budantsev, 2005).

2.2.21 Sapindaceae *Dipteronia*, the sister genus of *Acer*, has two extant species endemic to China with distinctive schizocarpic winged fruits (Fig. 39). This genus has an excellent fossil fruit record in North America, beginning in the Late Paleocene and continuing through the Early Oligocene (McClain & Manchester, 2001). Several complete fruit specimens from the Middle Eocene of Oregon, Washington, and British Columbia show that the mericarps were commonly borne in schizocarps of three (a typical feature of Sapindaceae) as well as in pairs (e.g., Fig. 40), in contrast to the modern species which usually have only paired mericarps. *Dipteronia* has not been observed in the Tertiary of Europe, despite the excellent record there of *Acer* and other kinds of winged fruits. The fossil record of *Dipteronia* in Asia is not well known. A figured *Dipteronia* fruit specimen reported to have come from the Eocene of Fushun, Liaoning, China (Manchester, 1999) was later discredited as being a misplaced museum specimen actually from the Eocene of western Canada (McClain & Manchester, 2001). However, a mericarp was subsequently discovered during fieldwork by Akhmetiev and



Figs. 34–41. 34–38. Rhamnaceae: *Hovenia*, fossil and Recent leaves. 34. Extant *Hovenia acerba* Lindl., Fenyé Co., Kiangsi, A: K. Yao & K. Yao 9109. 35. *H. oregonensis* Meyer & Manch. Early Oligocene Bridge Creek flora, Oregon, UF 243-10731. 36. *H. miodulcis* Hu & Chaney, Middle Miocene Shanwang flora, Shandong, China. S100197. 37. Enlargement from 34. 38. Enlargement from 35. Scale bars 3 cm in figs. 34–36. 39–41. Sapindaceae: Recent and fossil fruits of *Dipteronia*. Scale bars calibrated in mm. 39. Extant schizocarp of *D. sinensis* with two fully developed mericarps, A: B. Bartholomew et al., 1063, Hubei, China. 40. *Dipteronia brownii* McClain & Manch. from Early Eocene of McAbee, British Columbia, UWBM 97675. 41. Mericarp of *Dipteronia* sp. from the Paleocene of Archara Bogochan coal mine, Zeya Bureya basin, GINRAS ab 5-11.

Manchester from the Paleocene Tsagayan Formation of Amur region, southeastern Russia (Fig. 41; Akhmetiev et al., 2002), confirming an early presence of the genus in Asia.

Koelreuteria, with three extant species, is native today in China. Although one species is also found disjunct to Fiji, we have included the genus in this treatment as being “almost” endemic to east Asia. The genus has a good fossil record in North America, Europe and Asia, especially supported by the distinctive fruit remains (Fig. 11 in Manchester, 1999). *Koelreuteria* fruits are inflated, bladder-like capsules with reticulate venation. The seeds are attached on an incomplete septum 1/3 to 1/2 of the fruit length from the base. The oldest North American examples are from the Middle Eocene of the Green River Formation (Fig. 11 A in Manchester, 1999) and there are impressive examples from the Late Eocene Florissant Formation (MacGinitie, 1953, 1969). In Europe the oldest known examples are from the Oligocene of Rott, Germany (Weyland, 1937), extending to the Miocene of Randecker Maar, Germany (Rüffle, 1963), and Bohemia (Bůžek, 1971). In Asia, the fruit valves have been recognized from the Middle Eocene of Huadian in southern Jilin Province, China (Manchester et al., 2005), from the Paleogene of southern Primorye (Ablaev, 2000), as well as from the Miocene Shanwang flora of Shandong Province, China (Hu & Chaney, 1940) and Late Miocene Tatsumitoge flora of southwestern Honshu, Japan (Ozaki, 1980). In some instances fruit valves of *Craigia* (= *Ptelea*) have been mistaken for *Koelreuteria*, but they can be distinguished by the serial attachment of seeds, the complete septum and more elongated areoles in the fruit valve venation. *Koelreuteria* has an incomplete septum with seeds borne at a single level within the pod.

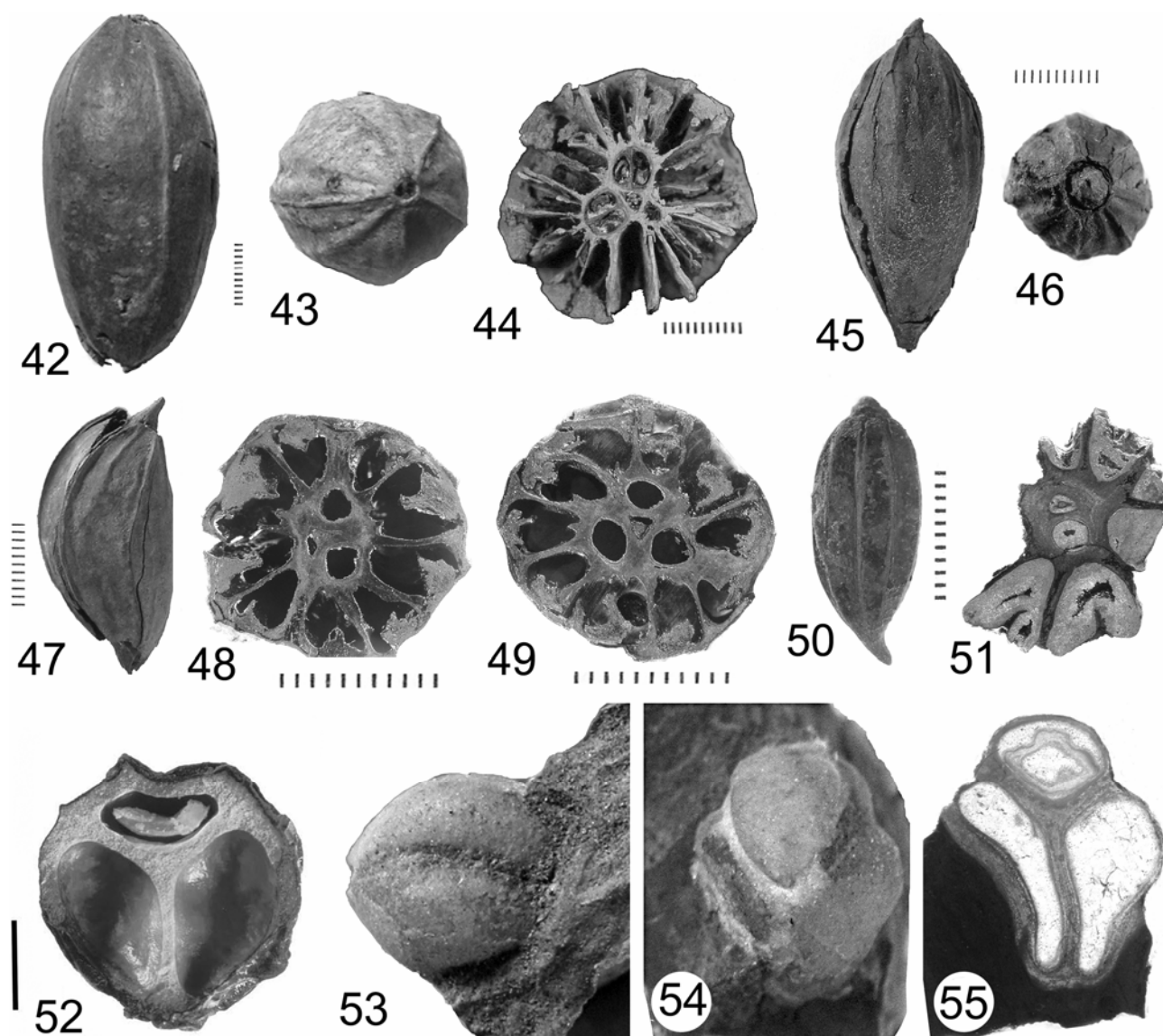
Sinoradlkofera F. Meyer (syn. *Boniodendron*), with one species in China and Vietnam is a segregate from *Koelreuteria* Laxm. that differs by its paripinnate leaves, regular flowers, and the absence of an androgynophore (Meyer, 1976; Buijssen et al., 2003). In addition, mature capsules of *S. minor* are about half the size of those in *Koelreuteria* species. Some of the fossil fruits previously assigned to *Koelreuteria* conform more closely to *Sinoradlkofera*, and might represent that genus, although more detailed comparative work is needed. These include *Koelreuteria arnoldii* Becker from the Oligocene of Ruby, Montana (Becker, 1961), and Republic, Washington (Wolfe & Wehr, 1987).

2.2.22 Scrophulariaceae Although most members of this family are herbaceous, *Paulownia* is a species of trees native to eastern Asia. It has large, distinctive bivalved loculicidally dehiscent capsules and tiny winged seeds. Fossil representatives have been confirmed by sedimentary casts of the characteristic fruit valves from the Middle Miocene of Bavaria, Germany

(Butzmann & Fischer, 1997). In addition, isolated winged seeds are known from Early and Middle Pliocene sites in northern Italy (Martinetto, 1998). Seeds denuded of the wing have been identified to *P. cantalensis* (Reid) Mai from the Pliocene of Cantal, France, to Lower Miocene of the Lausitz region (Mai, 2001a). Watari (1948, 1952) described wood conforming anatomically to *Paulownia* from the Lower Miocene of southwestern Honshu, Japan.

2.2.23 Staphyleaceae This family includes the genera *Euscaphis*, *Staphylea*, and *Turpinia*. Simmons (2006) prefers to sink *Euscaphis* and *Turpinia* within *Staphylea* based on inferences from molecular data, but these genera are distinguished morphologically by their fruit types which are baccate in *Turpinia*, bladder-like in *Staphylea*, and dehiscent follicles in *Euscaphis*. The spherical shape and small hilum of the seed distinguishes *Euscaphis* from seeds of the other two genera (Tiffney, 1979). *Euscaphis* has one extant species endemic to eastern Asia. The seed is lenticular in form because it lacks any pressure marks from adjacent seeds (a distinction from *Turpinia* which bears multiple seeds per fruit that crowd each other in development) and has a thin shiny sarcotesta and a large hilum with 5 vascular bundle scars, but not with the surrounding bulge seen in *Staphylea* seeds (Mai, 1980). Fossil seeds conforming to *Euscaphis* have been identified based on morphology and seed coat anatomy from the middle Oligocene of Nerchau, Saxony, Germany (Mai, 1980). In Asia, the seeds are known from the Pliocene of Yahata, Iki, Kyushu, Japan (Miki & Kokawa, 1962). In older classifications, *Tapiscia* was placed in the Staphyleaceae, but it is now treated in a separate family (see Tapisciaceae, below).

2.2.24 Styracaceae *Rehderodendron* is related to *Halesia*, but has unwinged, buoyant fruits (Figs. 42, 43). The fruits are 2–3 locular with prominent lacunae radiating from the central area (Fig. 44). The genus includes four species of deciduous shrubs and trees distributed in southwestern China (Yunnan, Guizhou, Sichuan, Guangxi, Guangdong and Hunan) and Vietnam, occurring in dense forests at elevations from 100–1500 m. The genus is confirmed by well preserved fruits from the Tertiary of Europe, including the Early Eocene London Clay of England (Figs. 50, 51; Mai, 1970), the Miocene of Germany (Figs. 45–49; Mai, 1970), the Pliocene of Germany and Italy (Geissert & Gregor, 1981; Martinetto, 1998), and the Upper Pliocene of Romania (Mai & Petrescu, 1983). A morphological key to the fossil species was provided by Mai and Petrescu (1983). *Melliodendron* was recognized based on degraded fruits from the Plio-Pleistocene of Japan (Miki, 1968), however the illustrated specimens show radiating longitudinal blades of sclerified tissue coinciding with *Rehderodendron* rather than *Melliodendron*. Transverse sections of the



Figs. 42–55. 42–51. Styracaceae: Recent and fossil fruits of *Rehderodendron*. Scale bars calibrated in mm. 42, 43. Lateral and apical view of fruit of extant *Rehderodendron* sp. from N Burma, BM: F. Kingdon-Ward 22086. 44. Transverse section of extant *Rehderodendron macrocarpus* Hu, Sichuan, China, PE 55291: T. U. Tu 730 showing three locules and radiating blades of endocarp tissue with and intervening lacunae. 45–49. *R. ehrenbergii* (Kirchheimer) Mai from Mine Alfred, Düren, Germany, coll. Claire A. Brown 1952. 45, 46. Fruit in lateral and apical view, USNM 537358. 47, 48. Fruit in lateral view and in transverse section, showing two well developed locules. USNM 537359. 49. Transverse section of the specimen in 46, showing three well developed locules. 50, 51. *R. stonei* (Reid & Chandler) Mai from the Early Eocene London Clay. 50. Lateral view showing meridional ribs and apical protuberance, BM v30451, Herne Bay, England. 51. Specimen in transverse section showing one well developed locule and an axial canal, BM v30347. 52–55. Toricelliaceae: Fruits of extant and Paleocene *Toricellia*. All at same magnification (scale bar=1 mm). 52. *Toricellia tiliaefolia*, transverse section of fruit, showing three chambers: two large and empty, one smaller and containing a seed, Yunnan, China, MO 52556: A Henri 11907. 53–55. *Toricellia bonesii* (Manch.) Manch., permineralized fruit in front, lateral, and transversely sectioned views, Late Paleocene of Almont, North Dakota, USA, FMNH pp22421.

fruit would be required to verify the assignment to *Melliiodendron*.

Pterostyrax is native in eastern Asia from Burma to Japan. Mai (1998) recognized fossil fruits of *Pterostyrax* from the Oligocene Calau beds of Brandenburg, Germany, and called attention to another species, *P. europaea* Zablocki (1930). Mai stated that the fossils

“display a ring of calyx lobes surrounding an obtuse styler cone and an almost inferior drupe. These typical characteristics place the fossils unequivocally in the genus *Pterostyrax* Sieb. & Zucc.” A twig with attached fruits and leaves of this genus was illustrated and described from the middle Pleistocene of Shiobara, central Honshu, Japan (Onoe, 1989).

2.2.25 Tapisciaceae *Tapiscia* is a monotypic genus of deciduous trees with odd-pinnately compound estipulate leaves distributed across southern and southeastern China south of Yellow River, and northernmost Vietnam. It occurs today in the mixed mesophytic forests of China, in soils with pH 4.5 to 5.5 at elevations of 720–2550 m. Although formerly placed in the Staphyleaceae, molecular and morphological studies indicate that *Tapiscia*, and the neotropical genus *Huerteia*, form an unrelated family (Soltis et al., 2005). *Huerteia* and *Tapiscia* share distinctive subglobose seeds with a prominent concave chalaza, rounded base and pointed micropylar end, but those of *Huerteia* are larger and less sharply pointed (Manchester, 1988). *Tapiscia* seeds are known as fossils from the Eocene of England, Germany (Mai, 1980), and in western North America (Oregon: Manchester, 1988, 1994). Reports of the genus based on foliage from the Miocene Shanwang flora (WGCP, 1978) and from the Paleocene of Canada (Chandrasekharam, 1974) are unconvincing. The latter record was reassigned to the extinct nyssa-ceous genus *Brownia* Manchester & Hickey (2007).

2.2.26 Toricelliaceae *Toricellia* is a genus of small trees with three species distributed in northern India and southwestern China. The fruits, like those of the related Madagascan genus *Melanophylla*, are distinguished by endocarps of three chambers: a small central chamber containing a seed, and two large lateral chambers that are empty; there is no central vascular strand, and the endocarp wall and septa are composed of isodiametric sclereids (Fig. 52; Manchester, 1999; Meller, 2006). Fossil endocarps of *Toricellia* are known from the Eocene of Oregon and Washington, USA (Manchester, 1999), as well as from the Eocene of Messel, Germany and the Miocene of Oberdorf, Austria (Meller, 2006). The oldest known occurrence is from the Paleocene of Almont, North Dakota, USA, based on the single specimen illustrated here (Figs. 53–55).

2.2.27 Trapellaceae The genus *Trapella* includes aquatic perennial herbs distributed in eastern Asia. The distinctive spiny fruits of *Trapella* are recognized in the Pliocene of western Germany (Tralau, 1964, 1965) and the Miocene of Siberia (Dorofeev, 1963). Another occurrence is known from the Late Miocene of Hungary (Bůžek unpublished, Mai, 1995). Fruits of *Trapella*, including three extinct species, plus examples of the extant species, *T. sinensis* Oliv., were also recorded from the Pliocene and Pleistocene at many localities in central Honshu and Shikoku, Japan (Miki, 1961).

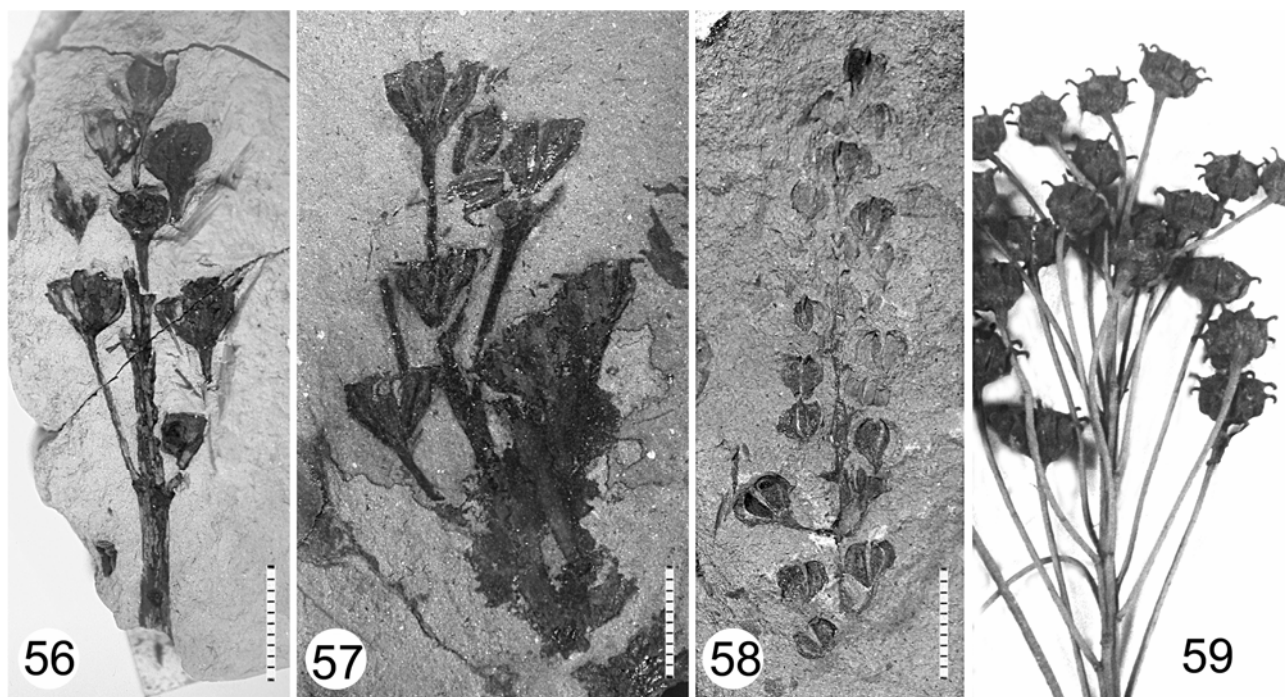
2.2.28 Trochodendraceae This family includes the extant east Asian vesselless genera *Trochodendron* and *Tetracentron*.

Trochodendron has one species, *T. aralioides*, distributed in Japan, Korea, and China (Taiwan) at elevations of 300 to 2700 m. It is an evergreen tree found in broadleaved forest or mixed broadleaved and evergreen

forest. In the paleobotanical record, *Trochodendron* is known based on fruiting racemes from the Eocene of Washington (Fig. 58; Pigg et al., 2001) and British Columbia (Pigg et al., 2007), the Miocene of Idaho and Oregon (Fig. 56: Manchester et al., 1991; Fields, 1996: 304–307), the Miocene of Kamchatka (Fig. 57; Chelebaeva & Chigayeva, 1988) and Japan (Manchester et al., 1991). In Japan, the genus is also known from the mid-Pleistocene of central Honshu (leaf and fruits, Onoe, 1989) and Upper Pleistocene of Bosa Peninsula (fruits with seeds, Kokawa, 1966). Leaves found in association with the *Trochodendron* infructescences from the Middle Eocene of Republic, Washington (Pigg et al., 2001) resemble those of extant *Trochodendron* in thick texture (probably evergreen) and small appressed teeth typically confined to the apical half of the lamina, but they differ from leaves of the single extant species of the genus by having palmate venation, which is presumed to be a primitive character, shared also with *Tetracentron*. The leaves from the Middle Eocene of McAbee, British Columbia are more similar in venation to those of the extant species, but frequently differ by the presence of a pair of basilaminar extensions (Pigg et al., 2007)

Tetracentron has one extant species, *T. sinense*, which is a deciduous tree that lives in southern China, Bhutan, northeastern India, northern Burma, eastern Nepal, and northern Vietnam. *Tetracentron* has been recognized on the basis of its characteristic leaves from the Eocene of Princeton, British Columbia and Republic, Washington (Pigg et al., 2007) and from the Middle Miocene to Late Pliocene of Japan (Ozaki, 1987). The distinctive vesselless xylem of *Tetracentron* was also identified from the Miocene of Japan and carefully distinguished from that of *Trochodendron* (Suzuki et al., 1991). This genus has also been confirmed from the Miocene of Idaho, USA, based on well preserved infructescences (Manchester & Chen, 2006). The fruit morphology of the fossil matches that of the extant species, and the characteristic persistent recurved styles of these fossils bear adhering pollen matching that of extant *Tetracentron*. Similar fruits, along with *Tetracentron* leaves and dispersed pollen, have more recently been recognized from the Miocene of Iceland (Grímsson et al., 2008), indicating that the genus may have passed into Europe as well, but no fossil records are yet known from Europe.

2.2.29 Ulmaceae *Hemiptelea* has one extant species, *H. davidii*, distributed from northeastern to southern China and Korea at elevations up to 2000 m. The fruits have curved endocarps with an enveloping asymmetrical wing. Such fruits are confirmed from the Miocene of Poland (Lańcucka-Środoniowa, 1967) and Ukraine (Dorofeev, 1982). Fruits and wood from the Pleistocene of central Honshu (Minaki et al., 1988) indicate that the Asian range of this genus formerly extended to Japan.



Figs. 56–59. Trochodendraceae: Extant and fossil infructescences of *Trochodendron*. **56.** *Trochodendron* sp. Middle Miocene of Emerald Creek, Idaho, *UF 9575*. **57.** *T. kamtschaticum* Cheleb. & Chig. from early Middle Miocene of Kavavlya, Central Kamchatka, *GINRAS 725-121*. **58.** *T. nastae* Pigg, Wehr, Ickert-Bond from early Middle Eocene of Republic, Washington, USA, *USNM 537360*. **59.** Extant *T. aralioides*. Scale bars=1 cm.

2.3 Patterns Observed

Table 1 provides a listing of the extant endemic genera of seed plants from eastern Asia, highlighting those which are also known from the fossil record, and summarizing their modern geography range, and growth form. Despite the emphasis that has often been given to endemic taxa represented in the broader paleobotanical record, it is obvious from this compilation that only a small fraction of the genera endemic to eastern Asia have confirmed fossil occurrences. Excluding the genera whose recognition in the fossil record remains tentative (e.g., Appendix 1), we calculate that only about 9 percent of those now endemic to eastern Asia are represented in the fossil record (54 genera known as fossils, of 596 extant genera).

Among the eastern Asian endemic seed plant genera known from the fossil record, 13 are gymnosperms, i.e., *Ginkgo* and conifers (Table 2), and 36 are angiosperms (including those in Table 3, plus *Euptelea*, *Euryale*, *Koelreuteria*, *Pterostyrax*, and *Tripterygium*). Most are woody, including trees, shrubs, and, in the case of *Sargentodoxa* and *Sinomenium*, lianas. Only 4% of those known in the fossil record (*Euryale* and *Trapella*) are herbaceous, whereas among all the extant endemic genera (including those for which no fossil record is confirmed), 358 (60%) are herbaceous. Given that herbaceous genera are, in general, poorly represented as

fossils, regardless of whether one focuses on regional endemics or on particular systematic groups, it is also of interest to examine the statistics with attention to the woody representatives. Of the 238 extant woody genera endemic to eastern Asia (Table 1), 52 genera (21%) are known in the fossil record.

The eastern Asian endemic plants considered here are a subset of a larger group of Asian endemics that include plants extending farther southward. Thorne (1999) listed additional oriental taxa whose area of endemism extends southward to Malaysia. These tend to be plants with preference for tropical conditions. Examples of such genera distributed now in southeast Asia, which also have good fossil records in the Tertiary of North America and/or Europe, include *Actinidia*, *Anamirta*, *Castanopsis*, *Cyclea*, *Diploclisia*, *Mastixia*, *Nypa*, *Rhodoleia*, and *Sabia* (e.g., Mai, 1980, 2001b; Manchester, 1999). These and others, some with ranges extending even to New Guinea and/or Australia, are outside the scope of the present treatment.

2.3.1 Collective fossil histories Tables 2 and 3 (pp. 11–13) summarize the geographic and stratigraphic records of gymnosperm and angiosperm genera endemic to eastern Asia with accepted fossil records. These tables are similar to those presented by Mai (1980, 1995) and Manchester (1999) but emended to include newly recognized occurrences, and taxonomic and stratigraphic

revisions. The data and references used to draw the ranges of each genus are summarized in the preceding section of this article. Although this study is mainly concerned with comparisons at the generic level, we acknowledge that the genus rank is an artificial category of taxonomic convenience, and that taxonomic ranking traditions differ among different clades of angiosperms. Thus, it is not surprising that similar geographic patterns may be observed at different taxonomic levels. The mono- and oligotypic families Trochodendraceae, Cephalotaxaceae, Cercidiphyllaceae, Eucommiaceae, and Ginkgoaceae, are eastern Asian in modern distribution, but were widespread in the Northern Hemisphere during the Tertiary. At the infrageneric level, subsection *Calyptranthes* of *Hydrangea* illustrates the same geographic pattern.

Another point for consideration is the inherent bias of this study toward “living fossils”, i.e., extant genera for which morphological stasis has applied, allowing them to be recognized far back into the Tertiary, and, in the case of some conifers, even to the Cretaceous. This means these taxa have survived for millions of years, essentially unchanged in a suite of diagnostic morphological characters, in order for the fossils to be directly recognizable through comparisons with extant taxa. Extinct genera, including taxa that may have belonged to more rapidly evolving clades, are, by default, excluded from this treatment. Extinct genera commonly co-occur in fossil assemblages alongside the extant genera considered here (e.g., Reid & Chandler, 1933; Manchester, 1994). Northern Hemisphere examples of extinct genera showing various patterns of disjunction and endemism at different intervals of the Tertiary were summarized previously (Manchester, 1999).

It is clear from Tables 2 and 3 that most of these genera have a refugial modern distribution that arose when formerly widespread genera became extinct over large parts of their original distribution, but were able to survive in parts of eastern Asia. This is parallel to the history of some of the modern genera endemic to North America such as *Sequoia*, *Decodon*, and *Comptonia* (Ferguson et al., 1997; Thorne, 1999). The effects of cooling climate and glaciation through the Pliocene-Pleistocene interval explains many of the geographic range reductions of the particularly in Europe and North America, that resulted in the survival of these taxa in relictual areas.

2.3.2 Subregional distribution of paleoendemic genera The eastern Asian endemic genera represented in the fossil record may be classified into geographic subgroups according to their modern characteristic distribution (Wu, 1998), of which three patterns are most prominent: Sino-Japanese, Sino-Himalayan, and broadly distributed eastern Asian.

The Sinojapanese region, in which the following

genera occur, *Cercidiphyllum*, *Cryptomeria*, *Disanthus*, *Euscaphis*, *Hemiptelea*, *Hovenia*, *Paulownia*, *Phellodendron*, *Platycarya*, *Schizophragma*, *Tripterygium*, and *Weigela*, includes many more genera with known fossil representatives than does the Sino-Himalayan region. Among the numerous Himalayan and Sino-Himalayan genera (149 listed by Wu, 1998), only *Tetracentron* and *Toricellia* are known as fossils. Among the genera that are endemic exclusively to the Korea-Japan region (42 genera listed by Wu, 1998), *Sciadopitys* is the only one confirmed in the fossil record. Among the extant genera “characteristic of the Central China Province” (Wu, 1998) several have good fossil records: *Cathaya*, *Davidia*, *Dipteronia*, *Eucommia*, *Metasequoia*, *Sargentodoxa*, and *Tapiscia*. Genera with a broader “eastern Asian pattern of distribution” (87 listed by Wu, 1998) that are recognized in the fossil record include *Actinidia*, *Cephalotaxus*, *Choerospondias*, and *Koelreuteria*. In terms of numbers of surviving genera, the central part of China, such as Hubei and eastern Sichuan, may be regarded as a hot spot for the survival of these paleoendemics. Did they also originate there?

2.3.3 Exotic vs eastern Asian origins Although most of the conifers now endemic to eastern Asia have long records in Asia as well as Europe and North America (Table 2), most of the angiosperm examples have only later occurrences in Asia. In many instances the earliest available fossil records of the “east Asian endemics” are in other northern continents but not Asia (Tables 2, 3). This may be due in part to less intensive-sampling of the Asian fossil record, and it does not refute the possibility of Asian origins for these genera. However, if the discrepancy is taken at face value, it implies that many of these genera arrived relatively recently in Asia after an earlier history in Europe and/or North America, which would imply that they evolved outside of Asia. *Euptelea* and *Thujopsis* are the only examples we encountered of genera now endemic to eastern Asia whose fossil records are apparently confined to eastern Asia. Qian (2001) listed *Actinodaphne*, *Machilus*, *Platycladus* as additional examples of this pattern, but we have been unable to confirm the validity of those paleobotanical identifications.

Citing similar observations on Chinese endemic genera and their widespread fossil occurrences, Ferguson et al. (1997, p. 360) concluded “Many botanists have been misled by the presence of numerous relict genera in southern and western China into thinking that this area represents the centre of origin of these taxa.” The paleobotanically represented genera summarized here mostly have fossil ranges outside of Asia, indicating that the present distribution is more a matter of place of survival than place of origin.

On the other hand, we cannot ignore the high proportion of extant genera endemic to eastern Asia with no

known fossil record (92%, Table 1). These include most of the herbaceous representatives, and it is likely that many of them originated in eastern Asia as previously proposed (e.g., Takhtajan, 1969; Wang, 1988), in association with uplift of the Himalayas. This tectonism created new environments that may have been responsible for a high level of East Asian neoendemism (Lu, 1999).

2.3.4 Routes of Intercontinental Dispersal The dynamic patterns of geographic dispersal of plants through the Tertiary are well illustrated by plants with modern disjunct distributions in the Northern Hemisphere (Latham & Ricklefs, 1993; Milne & Abbott, 2002; Donoghue & Smith, 2004). Such cases of disjunction, as well as endemism, reflect changing configurations of land and sea, and climate. Barriers to dispersal may have been oceans and straits, and in some cases, desert areas (Tiffney, 1985; Tiffney & Manchester, 2001). Range expansion between Asia and other northern continents was controlled in part by: 1) the Turgai seaway which isolated Europe from Asia from the Late Cretaceous to early Tertiary, and 2) the Bering land bridge. The relatively high latitude of the Bering connection apparently excluded or at least “filtered” the transfer of thermophilic plants between North America and Asia, but apparently did not impede the spread of Pinaceae and Cupressaceae. The early Tertiary North Atlantic Land Bridge, providing a route of connection between North America and Europe, was at lower latitude than the Bering Land Bridge (Tiffney & Manchester, 2001). It is possible that some of the thermophilic genera shared between extant flora of China and the early Tertiary of western North America may have traveled “the long way around”: via the North Atlantic Land Bridge, with subsequent spread across Europe and the Turgai region to reach Asia. For example, *Tapiscia*, and *Sargentodoxa*, well documented from the Eocene of western North America, likely reached Asia via Europe, where they are also known as fossils, rather than by direct connection between Asia and North America.

The tectonic and climate influences on Tertiary plant distribution in the Northern Hemisphere were summarized by Tiffney and Manchester (2001). The main points are: Beringial crossings were possible (land connection, or only narrow separation) through much of the Tertiary, but the high paleolatitude may have been limiting to broadleaved evergreen trees due to cooler climate and/or winter darkness. Connection between North America and Europe is postulated to have occurred via the North Atlantic Land Bridge, connecting North America, Greenland, Iceland and Europe prior to the rifting apart of these land areas in the Late Eocene. The North Atlantic connection was at lower latitude than Beringia, and may have permitted the passage of more thermophilic plants. Connection between Europe and

Asia became possible as the Turgai seaway retreated. Summarizing geological and paleontological evidence, Kubitzki and Krutzsch (1996) noted that during the climatic optimum of the Eocene “a belt of warm temperate climate in southern Laurasia, which bordered the Sea of Tethys, permitted the development of an exuberant laurophyllous flora. At this time many taxa now distributed in eastern Asia were present in North America and Europe. Eastern Asia was apparently excluded from participation in this floristic belt due to its pronounced aridity.”

Based on the geographic and stratigraphic distribution of genera, it is possible to infer some of the routes of dispersal important in the history of Asian paleoendemic genera. The Beringial connection linking eastern Asia and western North America appears to have been responsible for the passage of *Davidia*, *Dipteronia*, and *Trochodendron*, because there is no record of these genera as fossils in Europe, despite their high preservation potential (based on frequency of recovery in North American and Asian deposits). In other cases, colonization of Asia appears to have been from Europe as the Turgai seaway receded (e.g., *Cyclocarya*, *Hemiptelea*, *Paulownia*). The occurrence of *Cercidiphyllum* in eastern Asia during the Miocene could indicate immigration of the genus either from North America or from Europe, where species were already established in the Oligocene.

However, the record does not prove the directionality of movements. Finding a taxon at two different geographic locations A and B, indicates that there was a direct or indirect linkage between these places through time, but it does not specify whether the population at A, emigrated and colonized B, or vice versa. The recovery of older fossils from location A, than from B provides only weak evidence for directionality because the fossil record is so incomplete. Phylogenetic studies of extant genera with disjunctions across the northern continents may yield hypotheses of the directionality of prior intercontinental exchanges (Donoghue & Smith, 2004). Because the molecular phylogenetic approach requires extant species in multiple disjunct regions for comparative analyses, it cannot be directly applied in the case of endemic genera like those considered here; however the pathways illustrated by broader phylogenetic studies may include general patterns that were important in the history of endemic as well as disjunct genera.

2.3.5 Comparisons between Eastern Asia and North America Qian (2001) compared patterns of endemism between eastern Asia and North America (north of Mexico) utilizing his database of extant genera of vascular plants. The study did not specifically compare eastern North America with eastern Asia, so it may be biased by including ocean-exposed western North America in comparisons with the landlocked western margin of eastern Asia. When these two areas were rigorously

compared in terms of numbers of endemic genera, Qian found a significantly higher diversity of endemic angiosperm genera in North America (981) than in eastern Asia (710), but a markedly higher diversity of coniferous endemic genera in eastern Asia (16) than in North America (4). Qian's analysis was taken to indicate that "in contrast to East Asia, which tends to have more paleoendemic genera, North America tends to have more neoendemic genera". This hypothesis requires scrutiny from different approaches. From current data, we infer that only a small fraction of eastern Asian endemic genera are paleoendemic. There also appears to be a large number of neoendemic genera, not represented in the fossil record, that may have evolved along with the shifting environments associated with the Himalayan orogeny.

Appendix 1

Here we comment on additional Asian endemic genera that have been reported or suggested to be represented in the fossil record. In these instances, we explain why the fossil identifications are not accepted in this review.

Heptacodium (Caprifoliaceae) was identified based on leaves and fruiting calyces by Ozaki (1980). However, we have reexamined the fruits, and found that they have two whorls of persistent perianth, including an unlobed calyx which forms a rim around the apical edge of the fruit, and an inner whorl of persistent corolla with 5 prominent lobes, unlike the fruits of *Heptacodium* and other Caprifoliaceae, which have an impersistent campanulate corolla and 5-lobed persistent calyx. Another difference is that the fossil fruits are borne on long slender pedicels, rather than sessile. The affinities of these fruits do not appear to be with Caprifoliaceae. The leaves are similar to those of *Heptacodium* but without the corroborating fruit remains; we consider the identification to be questionable.

Hosiea (Icacinaeae) endocarps were identified by Mai (1987) from the Upper Paleocene of Gonna, Germany. However, the endocarps display overlapping characters of the extant genera *Iodes*, *Hosiea* and *Natsiatum*, and were subsequently placed in a fossil genus, *Palaeohosiea* by Kvaček and Bůžek (1995).

Fossil seeds attributed to *Poliothyrsis* (Flacourtiaceae) by Mai (1980), lack the diagnostic wing, and are therefore difficult to diagnose as this genus rather than other related Salicaceae/Flacourtiaceae. Although the fossils which have been attributed to this genus have been illustrated and described in excellent detail both with light and SEM microscopy (Mai, 1980; Friis, 1985; Ferguson et al., 1998; Arbutova in Budantsev, 2005), nobody has documented the seeds of extant *Poliothyrsis*

in comparable detail to justify the assignment.

Kalopanax (Araliaceae) was recognized based on leaves from the Miocene Shanwang flora of China (Hu & Chaney, 1940) based on leaves. These leaves have 5 palmate lobes with widely spaced serrations (in contrast to the closely spaced, sharp teeth of extant *Kalopanax* species). Hu and Chaney (1940) did not provide characters to distinguish the leaves from those of *Liquidambar*, and it remains unclear if the generic assignment of the fossil leaves is correct. More recently, well preserved umbellate infructescences have been illustrated under the same name, *Kalopanax acerifolium*, also from Shanwang flora (Sun et al., 1999; pl. 45, fig. 1, pl. 37, fig. 1). The fruits are circular to ovoid in lateral compression, with an apical perianth bulge and at least two divergent styles. These infructescences clearly conform to the Araliaceae, but the generic assignment is in our opinion less certain.

Although *Fokienia* (Cupressaceae) was identified from the Paleocene of North America (Brown, 1962; McIver, 1992), closer study of anatomically preserved foliage, and new specimens with attached cones, (Guo SX, Kvaček Z, and Manchester S, in preparation) indicates that these species represent not extant *Fokienia*, but the extinct Cupressaceous genus, *Ditaxocladus* Guo & Sun (Guo et al., 1984).

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References

- Ablaev AG. 2000. Paleogene biostratigraphy of the coastal region in South Primorye. Vladivostok: Russian Academy of Sciences Far Eastern Branch, Pacific Institute of Oceanography. (In Russian)
- Ablaev AG, Sin En U, Vassiliev IV, Lu ZM. 1993. Miocene of the North Korea and the South Primorye (Beds with Engelhardia). Vladivostok: Russian Academy of Sciences Far-eastern Branch, Pacific Institute of Oceanography, Dalnauka. (In Russian)
- Akhmetiev MA. 1991. Early Oligocene flora of Kiin-Kerish and its comparison with other Paleogene floras. In: Zhilin

- SG ed. Development of the flora in Kazakhstan and Russian Plain from the Eocene to the Miocene. Leningrad: Kryshstofovich Lecture Series no. 2. Reports delivered on December 27, 1988, at the Second Kryshstofovich Lecture Series, Academy of Sciences of the USSR. Komarov Botanical Institute. 134. (In Russian).
- Akhmetiev MA, Kezina TV, Kodrul TM, Manchester SR. 2002. Stratigraphy and flora of the Cretaceous-Paleogene boundary layers in the southeast part of the Zeya-Bureya sedimentary basin. In: Akhmetiev MA, Doludenko MP, Herman AB, Ignatiev IA eds. Special volume dedicated to the memory of the corresponding member of the USSR Academy of Sciences, Professor Vsevolod Andreevich Vakrameev (to the 90th anniversary of his birth). Moscow: Geological Institute, Russian Academy of Sciences. 275–315. (In Russian).
- Andersson L, Persson CS. 1991. Circumscription of the tribe Cinchoneae (Rubiaceae)—a cladistic approach. *Plant Systematics and Evolution* 178: 65–94.
- Barnett J. 1989. Palynology and paleoecology of the Tertiary Weaverville Formation, northwestern California. *U.S.A. Palynology* 13: 195–246.
- Bayer C, Kubitzki K. 2003. Malvaceae. In: Kubitzki K, Bayer C eds. The families and genera of vascular plants. Vol. 5. Berlin: Springer. 225–311.
- Becker HF. 1961. Oligocene plants from the upper Ruby River Basin, southwestern Montana. *Geological Society of America Memoir* 82: 1–127.
- Berry EW. 1916. The lower Eocene floras of southeastern North America. *U.S. Geological Survey Professional Paper* 91: 1–481.
- Boulter MC, Kvaček Z. 1989. The Palaeocene flora of the Isle of Mull. *Palaeontological Association Special Papers in Palaeontology* 42: 1–149.
- Brown RW. 1936. The genus *Glyptostrobus* in America. *Journal of the Washington Academy of Sciences* 26: 353–357.
- Brown RW. 1962. Paleocene floras of the Rocky Mountains and Great Plains. *U.S. Geological Survey Professional Paper* 375: 1–119, pls. 1–69.
- Budantsev LY. 1997. Late Eocene flora of western Kamchatka. *Proceedings of Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg, Issue* 19. (In Russian)
- Budantsev LY ed. 2005. Magnoliophyta Fossilia Rossiae et Civitatum Finitimarum. Vol. 4. Nyctaginaceae-Salicaceae. Komarov Botanical Institute, Russian Academy of Sciences, St Petersburg. 184, 140 pls. (In Russian)
- Buijssen JRM, Van Welzen PC, Van der Ham RWJM. 2003. A phylogenetic analysis of *Harpullia* (Sapindaceae) with notes on historical biogeography. *Systematic Botany* 28 (1): 106–117.
- Burge DO, Manchester SR. 2008. Fruit morphology, fossil history, and biogeography of *Paliurus* (Rhamnaceae). *International Journal of Plant Sciences* 169: 1066–1085.
- Butzmann R, Fischer TC. 1997. Description of the fossil fruit *Paulownia inopinata* nov. sp. from the Middle Miocene of Unterwohnbach (Bavaria) and other possible occurrences of the genus in the Tertiary. *Documenta Naturae* 115: 1–13.
- Bůžek Č. 1971. Tertiary flora from the northern part of the Pětipsy area (North-Bohemian Basin). *Rozpravy Ústředni Ústavu Geologického, Praha*. 36: 1–118, 52 pls.
- Bůžek Č, Kvaček Z, Manchester SR. 1989. Sapindaceous affinities of the *Pteleaearpum* fruits from the Tertiary of Eurasia and North America. *Botanical Gazette* 150: 477–489.
- Call VB, Dilcher DL. 1997. The fossil record of *Eucommia* (Eucommiaceae) in North America. *American Journal of Botany* 84: 798–814.
- Chandler MEJ. 1961. The Lower Tertiary floras of southern England. 1. Paleocene Floras. London Clay Flora (Supplement). Text and Atlas. London: British Museum (Natural History).
- Chandrasekharam A. 1974. Megafossil flora from the Genessee Locality, Alberta, Canada. *Palaeontographica Abt. B* 147: 1–41.
- Chaney RW. 1920. The flora of the Eagle Creek Formation. *Contributions from the Walker Museum* 2: 115–181.
- Chaney RW, Axelrod DI. 1959. Miocene floras of the Columbia Plateau. *Carnegie Institution of Washington Publication* 617: 89–108.
- Chelebaeva AI. 1971. Questions of the stratigraphy of the continental Cenozoic. Academy of Sciences of the USSR Siberian Department, Institute of Volcanology. Leningrad: Nauka. (In Russian)
- Chelebaeva AI, Chigayeva GB. 1988. The genus *Trochodendron* (Trochodendraceae) in Miocene of Kamchatka. *Botanicheskii Zhurnal* 73: 315–318. (In Russian with English summary).
- Christophel DC. 1973. *Sciadopitophyllum canadense* gen. et sp. nov.: A new conifer from western Alberta. *American Journal of Botany* 60: 61–66.
- Collinson ME, Boulter MC, Holmes PL. 1993. Magnoliophyta ('Angiospermae'). In: Benton MJ ed. *The Fossil Record* 2. London: Chapman and Hall. 809–840.
- Crane PR, Manchester SR, Dilcher DL. 1990. A preliminary survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota. *Fieldiana Geology, New Series*, no. 20: 1–63.
- Crane PR, Stockey RA. 1985. Growth and reproductive biology of *Joffrea speirsii* gen. et. sp. nov., a *Cercidiphyllum*-like plant from the Late Paleocene of Alberta, Canada. *Canadian Journal of Botany* 63: 340–364.
- Czaja A. 2001. Koniferen aus dem Mittelmiozän der Tongrube Tetta-Buchholz in der Oberlausitz (Sachsen). *Eröff. Museum Westlausitz Kamenz* 23: 23–38.
- Czaja A. 2003. Paläokarpologische Untersuchungen von Taphozöosen des Unter- und Mittelmiozäns aus dem Braunkohlentagebau Berzdorf/Oberlausitz (Sachsen). *Palaeontographica, Abt. B* 265: 1–148.
- Dolezych M, Schneider W. 2005. Taxonomie und Taphonomie von Braunkohlenhölzern und Cuticulae dispersae von Koniferen im 2. Lausitzer Flözhorizont (Miozän) des Senftenberger Reviers. In: Dolezych M ed. *Koniferenhölzer im 2. Lausitzer Flöz und ihre ökologische Position. LPP Contributions Series* 19: 19–115.
- Donoghue MJ, Smith SA. 2004. Patterns in the assembly of temperate forests around the Northern Hemisphere. *Philosophical Transactions of the Royal Society of London B* 359: 1633–1644.
- Dorofeev PI. 1957. Contributions to the knowledge of western

- Siberian Tertiary flora (fossil flora of S. Yekaterina near Mt. Tara). A. N. Krishtofovich memorial volume. Moscow-Leningrad: Akademia Nauk SSSR. 277–312. (In Russian)
- Dorofeev PI. 1963. Tertiary Floras of Western Siberia. Moscow-Leningrad: Akademia Nauk SSSR. (In Russian)
- Dorofeev PI. 1970. A contribution to the taxonomy of certain fossil Juglandaceae. *Botanicheskii Zhurnal* 55: 1596–1604 (In Russian)
- Dorofeev PI. 1982. *Hemiptelea* Planch., II. Description of the fruits. In: Takhtajan A ed. *Magnoliophyta fossilia URSS*. Leningrad: Nauka. 2: 18. (In Russian)
- Dorofeev PI. 2004. *Cyclocarya* Iljinskaya species established on the fruits and the endocarp. In: Budantsev L ed. *Magnoliophyta fossilia Rossiae et Civitatum finitimarum*. Leitneriaceae-Juglandaceae. St Petersburg: Komarov Botanical Institute. 3: 42–48. (In Russian)
- Endo S. 1942. On the fossil flora from the Shulan Coal-field, Kirin Province and the Fushun Coal-field, Fengtien Province. *Bulletin Central National Museum Manchoukou* 1942 (3): 33–47.
- Endress PK. 1989. Phylogenetic relationships in the Hamamelidoideae. In: Crane PR, Blackmore S eds. *Evolution, systematics, and fossil history of the Hamamelidae*. Vol. 1. Introduction and “lower” Hamamelidae. New York: Oxford University Press. 227–248
- Eyde RH, Xiang QY. 1990. Fossil mastixioid (Cornaceae) alive in eastern Asia. *American Journal of Botany* 77: 689–692.
- Fan CZ, Xiang QY. 2003. Phylogenetic analyses of Cornales based on 26S rDNA and combined 26S rDNA-matK-rbcL sequence data. *American Journal of Botany* 90: 1357–1372.
- Ferguson DK. 1967. On the phytogeography of Coniferales in the European Cenozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 3: 73–110.
- Ferguson DK, Jähnichen H, Alvin KL. 1978. *Amentotaxus* Pilger from the European Tertiary. *Feddes Repertorium* 89: 379–410.
- Ferguson DK, Liu YS, Zetter R. 1997. The paleoendemic plants of East Asia: evidence from the fossil record for changing distribution patterns. In: Jablonski NG ed. *The Changing Face of East Asia during the Tertiary and Quaternary*. Hong Kong: Centre of Asian Studies, The University of Hong Kong. 359–371.
- Ferguson DK, Pingen M, Zetter Z, Hofmann C-C. 1998. Advances in our knowledge of the Miocene plant assemblage from Kreuzau, Germany. *Review of Palaeobotany and Palynology* 101: 147–177.
- Fields PH. 1996. The Succor Creek flora of the Middle Miocene Sucker Creek Formation, southwestern Idaho and eastern Oregon: systematics and paleoecology. Ph.D. Dissertation. East Lansing: Michigan State University.
- Florin R. 1963. The distribution of conifer and taxad genera in time and space. *Acta Horti Bergiani* 20: (4).
- Frankis MP. 1989. Generic inter-relationships in Pinaceae. *Notes from the Royal Botanical Garden Edinburgh* 45: 527–548.
- Friis EM. 1985. Angiosperm fruits and seeds from the Middle Miocene of Jutland (Denmark). *Biologiske Skrifter* 24 (3): 1–165.
- Gardner JS. 1886. A monograph of the British Eocene flora. London: Palaeontographical Society.
- Geissert F, Gregor H-J. 1981. Einige interessante und neue sommergrüne Pflanzenelemente (Fruktifikationen) aus dem Elsässer Pliozän (Genera *Sabia* Colebr., *Wikstroemia* Endl., *Alangium* Lam., *Nyssa* L., *Halesia* Ellis, *Rehderodendron* Hu). *Mitteilungen des Badischen Landesvereins für Naturkunde und Naturschutz N.F.* 12: 233–239.
- Geng B-Y, Manchester SR, Lu AM. 1999. The first discovery of *Eucommia* fruit fossil in China. *Chinese Science Bulletin* 44: 1506–1509.
- Givulescu R. 1973. Die fossilen Koniferen des Fundortes Chiusbaia. *Memorii. Institutul de Geologie si Geofizica* 19: 31–34.
- Golovneva LB. 1994. Maastrichtian-Danian floras of Koryak Upland. *Russian Academy of Sciences, Proceedings of the Komorov Botanical Institute Issue 13*, St. Petersburg. (In Russian)
- Gooch NL. 1992. Two new species of *Pseudolarix* Gordon (Pinaceae) from the Middle Eocene of the Pacific Northwest. *PaleoBios* 14: 13–19.
- Gradstein FM, Ogg JG, Smith AG, Agterberg FP, Bleeker W, Cooper RA, Davydov V, Gibbard P, Hinnov LA, House MR, Lourens L, Luterbacher HP, McArthur J, Melchin MJ, Robb LJ, Shergold J, Villeneuve M, Wardlaw BR, Ali J, Brinkhuis H, Hilgen FJ, Hooker J, Howarth RJ, Knoll AH, Laskar J, Monechi S, Plumb KA, Powell J, Raffi I, Ro U, Sadler HP, Sanfilippo A, Schmitz B, Shackleton NJ, Shields GA, Strauss H, Van Dam J, Van Kolfshoten T, Veizer J, Wilson D. 2005. A geologic time scale 2004. Cambridge, UK: Cambridge University Press.
- Gregor H-J. 1977. Subtropische Elemente im europäischen Tertiär II (Fruktifikationen). Die Gattungen *Quercus* (Fagaceae), *Myristicacarpum* (Myristicaceae), *Brueckelholzia* und *Cyclea* (Menispermaceae), *Disanthus* und *Fortunearia* (Hamamelidaceae), *Frangula* (Rhamnaceae), *Palaeocayratia* (Vitaceae) und *Acanthopanax* (Araliaceae). *Paläontologische Zeitschrift* 51: 196–226.
- Gregor H-J. 1989. Aspects of the fossil record and phylogeny of the family Rutaceae (Zanthoxylae, Toddalioidae). *Plant Systematics and Evolution* 162: 251–265.
- Grímsson F, Denk T, Zetter R. 2008. Pollen, fruits, and leaves of *Tetracentron* (Trochodendraceae) from the Cainozoic of Iceland and western North America and their palaeobiogeographic implications. *Grana* 47 (1): 1–14.
- Grote PJ. 1989. Selected fruits and seeds from the Middle Eocene Claiborne Formation of Southeastern North America. Ph.D. Dissertation. Bloomington: Indiana University.
- Guo SX. 2000. Evolution, palaeobiogeography and paleoecology of Eucommiaceae. *The Palaeobotanist* 49 (2): 65–83.
- Guo SX, Sun ZH, Li HM, Dou YW. 1984. Palaeocene flora Altai in Xinjiang, Northwest China. *Bulletin of Nanjing Institute of Geology and Palaeontology, Academia Sinica* 8: 119–146. (In Chinese with English summary)
- Hably L, Kvaček Z. 1997. Early Pliocene plant megafossils from the volcanic area in west Hungary. In: Hably L ed. *Early Pliocene volcanic environment, flora and fauna from Transdanubia, West Hungary*. Hungarian Natural History

- Museum Budapest Studia Naturalia 10: 5–152.
- He CX, Tao JR. 1997. A study on the Eocene flora in Yilan County, Heilongjiang. *Acta Phytotaxonomica Sinica* 35: 249–256.
- Hori J. 1987. Plant fossils from the Miocene Kobe flora. Fukusaki, Japan: Hyogo Biological Society. (In Japanese)
- Horiuchi J. 1996. Neogene floras of the Kanto District. *Science Reports of the Institute of Geoscience, University of Tsukuba, sec. B, Geological Sciences* 17: 109–208.
- Hu HH, Chaney RW. 1940. A Miocene flora from Shantung Province, China. *Carnegie Institute of Washington Publication* 507: 1–147.
- Huzioka K. 1961. A new Paleogene species of the genus *Eucommia* from Hokkaido, Japan. *Transactions and Proceedings of Palaeontological Society of Japan, New Series* 41: 9–12.
- Huzioka K. 1972. The Tertiary floras of Korea. *Journal of the Mining College of Akita University, series A* 5: 1–83, pls. 1–14.
- Huzioka K, Uemura K. 1973. The Late Miocene Miyata flora of Akita Prefecture. Northeast Honshu, Japan. *Bulletin of the National Science Museum, Tokyo* 16: 661–738, pls. 1–18.
- Ilijinskaya IA. 1953. Monograph of the genus *Pterocarya* Kunth. *Trudy Botanical Institute, Academy of Nauk SSSR Ser. 1, Flora Sistematika Vysshikh Rastenii* 10: 7–123. (In Russian, translated, U.S. Department of Commerce, IPST Catalog 5622)
- Ilijinskaya IA. 1994. *Cyclocarya* Ilijinskaja species established on leaves and imprints of fruits. In: Budantsev L ed. *Magnoliophyta fossilia Rossiae et Civitatum finitimarum. Leitneriaceae-Juglandaceae*. St Petersburg: Komarov Botanical Institute. 3: 42–52.
- Jähnichen H. 1990. New records of the conifer *Amentotaxus gladifolia* (Ludwig) Ferguson, Jähnichen and Alvin, 1978, from the Polish and Czechoslovakian Tertiary and its recognition in Canada, North America and Europe. *Tertiary Research* 12: 69–80.
- Jähnichen H, Mai DH, Walther H. 1980. Blätter und Früchte von *Cercidiphyllum* Siebold & Zuccarini im mitteleuropäischen Tertiär. *Schriftenreihe der Geologischen Wissenschaften Berlin* 16: 357–399.
- Kilpper K. 1968. Koniferen aus den tertiären Deckschichten des niederrheinischen Hauptflöztes, 3. Taxodiaceae und Cupressaceae. *Palaeontographica Abt. B* 121 (4–6): 102–111.
- Kirchheimer F. 1942. Zur Kenntnis der Alttertiärflora von Wiesa bei Kamenz (Sachsen). *Planta* 32: 418–446.
- Kirchheimer F. 1957. Die Laubgewächse der Braunkohlenzeit. *Verb Wilhelm Knapp Verlag, Halle (Salle)*.
- Klimova RS. 1975. Miocene conifers from Rettikhovka. *Proceedings of the Institute of Biology and Pedology, Far Eastern Scientific Center, Academy of Sciences of the USSR, New Series* 27: 84–92, pls. 16–19. (In Russian with English summary)
- Knobloch E, Mai DH. 1986. Monographie der Früchte und Samen aus der Kreide von Mitteleuropa. *Rozprawy Ústřední Ústavu Geologického* 47: 1–219, 56 pls.
- Kokawa S. 1965. Fossil endocarp of *Davidia* in Japan. *Journal of Biology, Osaka City University* 16: 45–51, 4 pls.
- Kokawa S. 1966. Late Cenozoic floras of the Bosa Peninsula, Japan. I. Upper Pleistocene floral change. *Journal of Biology, Osaka City University* 17: 1–45.
- Kovar JB. 1982. A leaf-flora recovered from Late Oligocene (Egerian) marine sediments of the Central Paratethys, surroundings of Linz (Austria). *Beiträge zur Paläontologie von Österreich* 9: 1–209. (In German)
- Kovar-Eder J, Meller B, Zetter R. 1998. *Cercidiphyllum crenatum* (Unger) R. W. Brown in der kohleführenden Abfolge von Oberdorf N Voitsberg, Steiermark. *Mitteilungen des Referates für Geologie und Paläontologie am Landesmuseum Joanneum, Graz* SH 2: 239–263.
- Krassilov VA. 1976. The Tertiary flora of Amur region. Moscow: Nauka Press, *Academic Sciences of USSR*, 92, 43 pls. (In Russian)
- Kräusel R. 1938. Die tertiäre Flora der Hydrobrienkalke von Mainz-Kastel. *Palaeontologische Zeitschrift* 20: 9–103.
- Kubitzki K, Krutzsch W. 1996. Origins of east and south east Asian plant diversity. In: Zhang A, Wu S eds. *Proceedings of the International symposium on floristic characteristics and diversity of east asian plants*. Berlin: Springer. 56–70.
- Kunzmann L, Mai DH. 2005. Die Koniferen der Mastixioideen-Flora von Wiesa bei Kamenz (Sachsen, Miozän) unter besonderer Berücksichtigung der Nadelblätter. *Palaeontographica B* 272: 67–135.
- Kvaček Z. 2006. Fossil fruits of *Reevesia* (Malvaceae, subfam. Helicteroideae) and associated plant organs (seeds, foliage) from the Lower Miocene of North Bohemia. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 2006: 431–448.
- Kvaček Z, Bůžek Č. 1995. Endocarps and foliage of the flowering plant family Icacinaceae from the Tertiary of Europe. *Tertiary Research* 15: 121–138.
- Kvaček Z, Bůžek Č, Manchester SR. 1991. Fossil fruits of *Ptelea carpum* Weyland—Tiliaceous, not sapindaceous. *Botanical Gazette* 152: 522–523.
- Kvaček Z, Manchester SR, Akhmetiev MA. 2005. Review of the fossil history of *Craigia* (Malvaceae s.l.) in the northern hemisphere based on fruits and co-occurring foliage. In: Akhmetiev MA, Herman AB eds. *Modern problems of Palaeofloristics, Palaeophytogeography, and Phytostratigraphy*. Moscow: GEOS. 114–140.
- Kvaček Z, Konzalová M. 1996. Emended characteristics of *Cercidiphyllum crenatum* (Unger) R. W. Brown based on reproductive structures and pollen *in situ*. *Palaeontographica, Abt. B*. 239: 147–155.
- Kvaček Z, Rember WC. 2000. Shared Miocene conifers of the Clarkia flora and Europe. *Acta Universitatis Carolinae Geologica* 44: 75–85.
- Kvaček Z, Walther H. 1998. The Oligocene volcanic flora of Kundratice near Litoměřice České středohoří Volcanic Complex (Czech Republic)—a review. *Acta Musei Nationalis Pragae, Ser. B, Historia Naturalis Ser. B*. 54: 1–42.
- LaMotte RS. 1952. Catalogue of the Cenozoic plants of North America through 1950. *Memoirs of the Geological Society of America* 51: 1–381.
- Lańcucka-Srodoniowa M. 1967. Two new genera: *Hemiptelea* Planch. and *Weigela* Thumb. in the younger Tertiary of Poland. *Acta Palaeobotanica* 8: 1–17.
- Latham RE, Ricklefs RE. 1993. Continental comparisons of

- temperate-zone tree species diversity. In: Ricklefs RE, Schluter D eds. *Species diversity in ecological communities*. Chicago: University of Chicago Press. 294–314.
- LePage BA. 2007. The Taxonomy and Biogeographic History of *Glyptostrobus* Endlicher (Cupressaceae). *Bulletin of the Peabody Museum of Natural History* 48: 359–426.
- LePage BA, Basinger JF. 1995. Evolutionary history of the genus *Pseudolarix*. *International Journal of Plant Sciences* 156: 910–950.
- LePage BA, Yang H, Matsumoto M. 2005. The evolution and biogeographic history of *Metasequoia*. In: LePage BA, Williams C, Yang C eds. *The Geobiology and Ecology of Metasequoia*. New York: Springer. 3–114.
- Liu Y-J, Li C-S, Wang Y-F. 1999. Studies on fossil *Metasequoia* from Northeast China and their taxonomic implication. *Botanical Journal of the Linnean Society* 130: 267–297.
- Liu Y-S, Basinger JF. 2000. Fossil *Cathaya* (Pinaceae) pollen from the Canadian high arctic. *International Journal of Plant Sciences* 161: 829–847.
- Liu Y-S, Guo S-X, Ferguson DK. 1996. Catalogue of Cenozoic megafossil plants in China. *Palaeontographica*, Abt. B. 238: 141–179.
- Liu Y-S, Zetter R, Ferguson DK. 1997. Fossil pollen grains of *Cathaya* (Pinaceae) in the Miocene of eastern China. *Proceedings 4th Eur. PPC. Mededelingen Nederlands Instituut voor Toegepaste Geovetenschappen TNO*, Nr 58 1997.
- Lu A-M. 1999. *The geography of spermatophytic families and genera*. Beijing: Science Press.
- Ma Q-W, Li C-S, Li F-L. 2007. Epidermal structures of *Cryptomeria japonica* and implications to the fossil record. *Acta Palaeobotanica* 47: 281–289.
- Mabberley DJ. 1997. *The Plant Book. A portable dictionary of the vascular plants*. 2nd ed. Cambridge: Cambridge University Press.
- MacGinitie HD. 1937. The flora of the Weaverville beds of Trinity County, California with descriptions of plant-bearing beds. *Carnegie Institute of Washington Publication* 465: 84–151.
- MacGinitie HD. 1953. Fossil plants of the Florissant beds, Colorado. *Carnegie Institute of Washington Publication* 599: 1–198, pls. 1–75.
- MacGinitie HD. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. *University of California Publications in Geological Sciences* 83: 1–140.
- Mädler K. 1939. Die pliozänen Floren von Frankfurt am Main. *Abhandlungen der Senckenbergische Naturforschende Gesellschaft* 446: 1–202.
- Magallon-Puebla S, Cevallos-Ferriz SRS. 1994. *Eucommia constans* n. sp. fruits from upper Cenozoic strata of Puebla, Mexico: Morphological and anatomical comparison with *Eucommia ulmoides* Oliver. *International Journal of Plant Sciences* 155: 80–85.
- Mai DH. 1964. Die Mastixioideen-Floren im Tertiär der Oberlausitz. *Paläontologische Abhandlungen* Abt. B 2: 1–192, 16 pls.
- Mai DH. 1970. Subtropische Elemente im europäischen Tertiär I. Die Gattungen *Gironniera*, *Sarcococca*, *Illicium*, *Evodia*, *Ilex*, *Mastixia*, *Alangium*, *Symplocos* und *Rehderodendron*. *Paläontologische Abhandlungen* Abt. B 3: 441–503, pls. 58–69.
- Mai DH. 1980. Zur Bedeutung von Relikten in der Florengeschichte. 100 Jahre Arboretum (1879–1979). Berlin: Humboldt Universität zu Berlin. 281–307.
- Mai DH. 1985. Beiträge zur Geschichte einiger holziger Saxifragales-Gattungen. *Gleditschia* 13: 75–88.
- Mai DH. 1987. Neue Früchte und Samen aus paläozänen Ablagerungen Mitteleuropas. *Feddes Repertorium* 98: 197–229, pls. 12–21.
- Mai DH. 1995. *Tertiäre Vegetationsgeschichte Europas*. Jena: Gustav Fischer.
- Mai DH. 1997. Floras from the Upper Oligocene at the northern margin of Lausitz, Saxony. *Palaeontographica* Abt. B. 244: 1–124.
- Mai DH. 1998. Contribution to the flora of the Middle Oligocene Calau Beds in Brandenburg, Germany. *Review of Palaeobotany and Palynology* 101: 43–70.
- Mai DH. 2001a. Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz Teil II: Dicotyledonen. *Palaeontographica* Abt. B 257: 35–174, 35 pls.
- Mai DH. 2001b. The fossils of *Rhodoleia* Champion (Hamamelidaceae) in Europe. *Acta Palaeobotanica* 41: 161–175.
- Mai DH, Petrescu I. 1983. Eine neue *Rehderodendron*-Art (Styracaceae) aus dem oberen Pliozän des Barolt-Beckens (SR Rumänien). *Zeitschrift für geologische Wissenschaften*, Berlin 11: 915–925.
- Mai DH, Velitzelos E. 2007. The fossil flora of Kallithea (Rhodes, Greece) at the Pliocene/Pleistocene boundary. *Palaeontographica* Abt. B. 277: 75–99.
- Mai DH, Walther H. 1978. Die Floren der Haselbacher Serie im Weißelster-Becken (Bezirk Leipzig, DDR). *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* 28: 1–200.
- Mai DH, Walther H. 1991. Die oligozänen und untermiozänen Floren NW-Sachsens und des Bitterfelder Raumes. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* 38: 1–230.
- Manchester SR. 1987. The fossil history of the Juglandaceae. *Missouri Botanical Garden Monographs* 21: 1–137.
- Manchester SR. 1988. Fruits and seeds of *Tapiscia* (Staphyleaceae) from the Middle Eocene of Oregon, USA. *Tertiary Research* 9: 59–66.
- Manchester SR. 1989. Systematics and fossil history of the Ulmaceae. In: Crane PR, Blackmore S eds. *Evolution, systematics, and fossil history of the Hamamelidae*. Vol. 2. “Higher” Hamamelidae, Systematics Association Special Volume no. 40B. Oxford: Clarendon Press. 221–252.
- Manchester SR. 1994. Fruits and seeds of the Middle Eocene Nut Beds flora, Clarno Formation, Oregon. *Palaeontographica Americana* 58: 1–205.
- Manchester SR. 1999. Biogeographical relationships of North American Tertiary floras. *Annals of the Missouri Botanical Garden* 86: 472–522.
- Manchester SR. 2000. Late Eocene fossil plants of the John Day Formation, Wheeler County, Oregon. *Oregon Geology* 62: 51–63.
- Manchester SR. 2001. Update on the megafossil flora of Florissant, Colorado, USA. In: Evanoff E, Gregory-Wodzicki KM, Johnson KR eds. *Fossil flora and stratigraphy of the Florissant Formation, Colorado*.

- Proceedings of the Denver Museum of Nature and Science, Series 4, 1: 137–161.
- Manchester SR. 2002. Leaves and fruits of *Davidia* from the Paleocene of North America. *Systematic Botany* 27: 368–382.
- Manchester SR, Chen I. 2006. *Tetracentron* fruits from the Miocene of western North America. *International Journal of Plant Sciences* 167: 601–605.
- Manchester SR, Chen Z-D, Geng B-Y, Tao J-R. 2005. Middle Eocene flora of Huadian, Jilin Province, Northeastern China. *Acta Palaeobotanica* 45: 3–26.
- Manchester SR, Crane PR, Dilcher DL. 1991. *Nordenskiöldia* and *Trochodendron* (Trochodendraceae) from the Miocene of northwestern North America. *Botanical Gazette* 152: 357–368.
- Manchester SR, Crane PR, Golovneva L. 1999. An extinct genus with affinities to extant *Davidia* and *Camptotheca* (Cornales) from the Paleocene of North America and eastern Asia. *International Journal of Plant Sciences* 160: 188–207.
- Manchester SR, Dilcher DL. 1982. Pterocaryoid fruits (Juglandaceae) in the Paleogene of North America and their evolutionary and biogeographic significance. *American Journal of Botany* 69: 275–286.
- Manchester SR, Donoghue M. 1995. Winged fruits of Linnaean (Caprifoliaceae) in the Tertiary of western North America: *Diplodipelta* gen. nov. *International Journal of Plant Sciences* 156: 709–722.
- Manchester SR, Hickey LJ. 2007. Reproductive and vegetative organs of *Browniea* gen. n. (Nyssaceae) from the Paleocene of North America. *International Journal of Plant Sciences* 168: 229–249.
- Manchester SR, McIntosh WC. 2007. Late Eocene silicified fruits and seeds from the John Day Formation near Post, Oregon. *PaleoBios* 27: 7–17.
- Manning WE. 1975. An analysis of the genus *Cyclocarya* Iljinskaya (Juglandaceae). *Bulletin of the Torrey Botanical Club* 102: 157–166.
- Manum S. 1966. *Ginkgo spitsbergensis* n. sp. from the Paleocene of Spitsbergen and a discussion of certain Tertiary species of *Ginkgo* from Europe and North America. Oslo: Norsk Polarinstitut. 49–58.
- Martinetto E. 1998. East Asian elements in the Plio-Pleistocene floras of Italy. In: Zhang A-L, Wu SG, and others eds. *Proceedings of the First International Symposium of Floristic Characters and Diversity of East Asian Plants*, Kunming, China. Berlin: Springer-Verlag; Beijing: China Higher Education Press. 71–87.
- Martinetto E. 2001a. The role of central Italy as a centre of refuge for thermophilous plants in the Late Cenozoic. *Acta Palaeobotanica* 41: 299–319.
- Martinetto E. 2001b. Studies on some exotic elements of the Pliocene floras of Italy. *Palaeontographica Abt. B*, 259: 149–166.
- Matsumoto M, Ohsawa TA, Nishida M, Nishida H. 1997. *Glyptostrobus rubenosawaensis* sp. nov., a new permineralized conifer species from the Middle Miocene, Central Hokkaido, Japan. *Paleontological Research* 1: 81–99.
- Matsuo H. 1963. The Notonakajima flora of Noto Peninsula. In: *Tertiary floras of Japan Miocene floras*. Tokyo: The collaborating association to commemorate the 80th Anniversary of the Geological Survey of Japan. 219–258.
- McClain AM, Manchester SR. 2001. *Dipteronia* (Sapindaceae) from the Tertiary of North America and implications for the phytogeographic history of the Aceroideae. *American Journal of Botany* 88: 1316–1325.
- McClintock E. 1957. A monograph of the genus *Hydrangea*. *Proceedings of the California Academy of Sciences*, fourth series, 29: 147–256.
- McIver EE. 1992. Fossil *Fokienia* (Cupressaceae) from the Paleocene of Alberta, Canada. *Canadian Journal of Botany* 70: 742–749.
- McIver EE, Basinger JF. 1993. Flora of the Ravenscrag Formation (Paleocene) southwestern Saskatchewan, Canada. *Palaeontographica Canadiana* 10: 1–167.
- Meller B. 1998. Systematisch-taxonomische Untersuchungen von Karpo-Taphocenosen des Köflich-Voitsberger Braunkohlenrevieres (Steiermark, Österreich; Untermiozän) und ihre paläoökologische Bedeutung. *Jahrbuch der Geologischen Bundesanstalt Wien* 140: 497–655.
- Meller B. 2006. Comparative investigation of modern and fossil *Toricellia* fruits—a disjunctive element in the Miocene and Eocene of Central Europe and the USA. *Beiträge zur Paläontologie von Österreich* 30: 315–327.
- Meller B, Kovar-Eder J, Zetter R. 1999. Lower Miocene leaf, palynomorph, and diaspore assemblages from the base of the lignite-bearing sequence in the opencast mine Oberdorf, N. Voitsberg (Styria, Austria) as an indication of “Younger Mastixioid” vegetation. *Palaeontographica Abt. B*, 252: 123–179, 11 pls.
- Meyer FG. 1976. A revision of the genus *Koelreuteria* (Sapindaceae). *Journal of the Arnold Arboretum* 57: 129–166.
- Meyer HW, Manchester SR. 1997. The Oligocene Bridge Creek flora of the John Day Formation, Oregon. *University of California Publications in Geological Science* 141: 1–195.
- Miki S. 1941. On the change of flora in eastern Asia since the Tertiary period (1). The clay or lignite beds flora in Japan with special reference to the *Pinus trifolia* beds in Central Hondo. *Japanese Journal of Botany* 11: 237–303, pls. 4–7. [plate numbers are beyond the page numbers—Author]
- Miki S. 1950. Taxodiaceae of Japan, with special reference to its remains. *Journal of the Institute of Polytechnics, Osaka City University*, series D 1: 63–77.
- Miki S. 1954. The occurrence of the remains of *Taiwania* and *Palaeotsuga* from Pliocene beds in Japan. *Proceedings of the Japan Academy* 30: 976–981.
- Miki S. 1955. Nut remains of Juglandaceae in Japan. *Journal of the Institute of Polytechnics, Osaka City University*, Series D 6: 130–144, 3 pls.
- Miki S. 1957. Pinaceae of Japan, with special reference to its remains. *Journal of the Institute of Polytechnics, Osaka City University*, series D 8: 221–272, pls. 1–10.
- Miki S. 1958. Gymnosperms in Japan, with special reference to its remains. *Journal of the Institute of Polytechnics, Osaka City University*, Series D 9: 221–272.
- Miki S. 1960. Nymphaeaceae remains in Japan, with new fossil genus *Eoeryale*. *Journal of the Institute of Polytechnics, Osaka City University*, series D 11: 63–78, pls. 1–5.
- Miki S. 1961. Aquatic floral remains in Japan. *Journal of Biology, Osaka City University* 12: 91–121.

- Miki S. 1968. *Paleodavidia*, synonym of *Melliodendron* and fossil remains in Japan. Bulletin of the Mukogawa Women's University 16: 287–291.
- Miki S, Kokawa S. 1962. Late Cenozoic floras of Kyushu, Japan. Journal of Biology, Osaka City University 13: 65–86.
- Miki S, Sakamoto T. 1961. Neogene flora from Sasazu in Toyama Pref., Japan. Prof. Jiro Makiyama Commemorative Volume. 259–264. (In Japanese with English abstract)
- Milne RI, Abbott RJ. 2002. The origin and evolution of Tertiary relict floras. Advances in Botanical Research 38: 282–314.
- Minaki M, Noshiro S, Suzuki M. 1988. *Hemiptelea mikii* sp. nov. (Ulmaceae), fossil fruits and woods from the Pleistocene of central Japan. Botanical Magazine, Tokyo 101: 337–351.
- Momohara A. 1989. Pliocene *Carya* nuts (Juglandaceae) from the Osaka Group, Southwest Japan. Journal of Phytogeography and Taxonomy 37: 107–112.
- Momohara A. 1997. Cenozoic history of evergreen broad-leaved forest in Japan. Natural History Research 4: 141–156.
- Mustoe GE. 2002. Eocene *Ginkgo* fossils from the Pacific Northwest. Canadian Journal of Botany 80: 1078–1087.
- Negru AG. 1972. Early Sarmatian flora of northeastern Moldavia. Academy of Sciences of Moldavskoi SSR Botanical Garden. Kishinev: Shtiinstsa Publishing House. (In Russian)
- Nishida H, Uemura K. 1977. Phytogeographic history of Taxodiaceae and importance of preserving mixed broad-leaved deciduous/evergreen forest. Tropics 6: 413–420.
- Oishi S, Huzioka K. 1942. On *Pteroceltis* from the Tertiary of Hokkaido and Tyosen. Journal of the Geological Society of Japan 49: 177–179.
- Onoe T. 1989. Palaeoenvironmental analysis based on the Pleistocene Shiobara flora in the Shiobara volcanic basin, central Japan. Report, Geological Survey of Japan, Tsukuba 269: 1–207. (In Japanese with English abstract and systematic descriptions)
- Ozaki K. 1980. Late Miocene Tatsumitoge flora of Tottori Prefecture, Southwest Honshu, Japan (III). Science Reports of the Yokohama National University Sec. 2, no. 27: 19–45.
- Ozaki K. 1984. Two new fossil species of *Fortunearia* and *Davidia* from the upper Motojuku (Kabutoiwa) Formation in Central Japan. Memoirs of the Institute of Field Education, Yokohama National University 2: 1–8.
- Ozaki K. 1987. *Tetracentron* leaves from the Neogene of Japan. Transactions and Proceedings of the Palaeontological Society, Japan, NS 146: 77–87.
- Ozaki K. 1991. Late Miocene and Pliocene floras in central Honshu, Japan. Bulletin of Kanagawa Prefectural Museum Natural Science Special Issue, Yokohama, Japan.
- Page CR. 1988. New and maintained genera in the conifer families Podocarpaceae and Pinaceae. Notes from the Royal Botanic Garden, Edinburgh 45: 317–305 (published 1989).
- Pigg KB, Dillhoff RM, DeVore ML, Wehr WC. 2007. New diversity among the Trochodendraceae from the Early/Middle Eocene Okanogan Highlands of British Columbia, Canada, and northeastern Washington State, United States. International Journal of Plant Sciences 168: 521–532.
- Pigg KB, Wehr WC. 2002. Tertiary flowers, fruits, and seeds of Washington State and Adjacent Areas—Part III. Washington Geology 30 (3/4): 3–16.
- Pigg KB, Wehr WC, Ickert-Bond SM. 2001. *Trochodendron* and *Nordenskioldia* (Trochodendraceae) from the Middle Eocene of Washington State, USA. International Journal of Plant Sciences 162: 1187–1198.
- Pocknall DT, Nichols DJ. 1996. Palynology of coal zones of the Tongue River Member (Upper Paleocene) of the Fort Union Formation, Powder River Basin, Montana and Wyoming. American Association of Stratigraphic Palynologists Contribution Series 32: 1–58.
- Qian H. 2001. A comparison of generic endemism of vascular plants between east Asia and North America. International Journal of Plant Sciences 162: 191–199.
- Qian H. 2002. Floristic relationships between eastern Asia and North America: test of Gray's hypothesis. American Naturalist 160: 317–332.
- Qian H, Krestov P, Fu PY, Wang QL, Song JS, Chourmouzis C. 2003a. Phytogeography of Northeast Asia. In: Kolbek J, Šrůtek M, Box EO eds. Forest vegetation of Northeast Asia. Dordrecht: Kluwer Academic Publishers. 51–91.
- Qian H, Yuan X-Y, Chou Y-L. 2003b. Forest vegetation of Northeast China. In: Kolbek J, Šrůtek M, Box EO eds. Forest vegetation of Northeast Asia. Dordrecht: Kluwer Academic Publishers. 181–230.
- Radtke MG, Pigg KB, Wehr WC. 2005. Fossil *Corylopsis* and *Fothergilla* leaves (Hamamelidaceae) from the Lower Eocene flora of Republic, Washington, U.S.A., and their evolutionary and biogeographic significance. International Journal of Plant Sciences 166: 347–356.
- Rasky K. 1956. Fossil plants from the marl formation of the environs of Budapest. Bulletin of the Hungarian Geological Society 86: 167–179. (In Hungarian with English summary)
- Reid EM, Chandler MEJ. 1926. Catalogue of Cainozoic Plants in the Department of Geology. Vol. 1. The Bembridge Flora. London: British Museum (Natural History).
- Reid EM, Chandler MEJ. 1933. The London Clay Flora. London: British Museum (Natural History). 561, 33 pls.
- Rüffle L. 1963. Die Obermiozäne Flora vom Randecker Maar. Paläontologische Abhandlungen 1 (3): 139–296.
- Saiki K. 1992. A new sciadopityaceous seed cone from the Upper Cretaceous of Hokkaido, Japan. American Journal of Botany 79: 989–995.
- Saito T, Momohara A, Yamakawa C. 2001. Discovery of *Cathaya* (Pinaceae) pollen from the Pliocene Koka Formation, Kobiwako Group, Shiga Prefecture, Japan. Journal of the Geological Society of Japan 107: 667–670. (In Japanese with English abstract)
- Schloemer-Jäger A. 1958. Altteriäre Pflanzen aus Flözen der Brögger-Halbinsel Spitzbergens. Palaeontographica Abt. B104: 39–103.
- Scott RA, Barghoorn ES. 1955. The occurrence of *Euptelea* in the Cenozoic of western North America. Journal of the Arnold Arboretum 36: 259–265.
- Ševčík J, Kvaček Z, Mai DH. 2007. A new mastixioid florula from tektite-bearing deposits in South Bohemia, Czech Republic (Middle Miocene Vrábče Member). Bulletin of Geosciences 82: 429–436.

- Simmons SL. 2006. Staphyleaceae. In: Kubitzki K ed. Families and genera of vascular plants. Vol. XIII. Flowering Plants, Eudicots: Berberidopsidales, Buxales, Crossosomatales, Fabales P.P., Geraniales, Gunnerales, Myrtales P.P., Proteales, Saxifragales, Vitales, Zygophyllales, Clusiaceae Alliance, Passifloraceae Alliance, Dilleniaceae, Huaceae, Picramniaceae, Sabiaceae. Berlin: Springer. 440–445.
- Sivak J. 1975. Les caractères de diagnose des grains de pollens à ballonnets. *Pollen et Spores* 17: 349–421.
- Smiley CJ, Rember WC. 1985. Composition of the Miocene Clarkia flora. In: Smiley CJ ed. Late Cenozoic history of the Pacific Northwest. San Francisco: Pacific Division, American Association for the Advancement of Science. 95–112.
- Soltis DE, Soltis PS, Endress PK, Chase MW. 2005. Phylogeny and evolution of angiosperms. Sunderland, MA: Sinauer.
- Song Z-C, Zheng Y-H, Li M-Y, Zhang Y-Y, Wang W-M, Wang D, Zhao C-B, Zhou S-F, Zhu Z-H, Zhao Y-N. 1999. Fossil spores and pollen of China. Vol. 1. The Late Cretaceous and Tertiary Spores and Pollen. Beijing: Science Press.
- Song Z-C, Wang W-M, Huang F. 2004. Fossil pollen records of extant angiosperms in China. *Botanical Review* 70: 425–458.
- Spongberg SA. 1979. Cercidiphyllaceae hardy in temperate North America. *Journal of the Arnold Arboretum* 60: 367–376.
- Stockey RA, LePage BA, Pigg KB. 1998. Permineralized fruits of *Diplopanax* (Cornaceae, Mastixioideae) from the Middle Eocene Princeton chert of British Columbia. *Review of Palaeobotany and Palynology* 103: 223–234.
- Stockey RA, Rothwell GW, Falder A. 2001. Diversity among taxodioid conifers: *Metasequoia foxii* sp. nov. from the Paleocene of central Alberta, Canada. *International Journal of Plant Sciences* 162: 221–234.
- Sun B, Tao J-R, Wang X-Z, Li J-Y. 1999. Plant fossils from Shanwang. Jinan: Science and Technology Publishing House. (In Chinese with English summaries)
- Suzuki M. 1975. Two new species of nyssaceous fossil woods from the Palaeogene of Japan. *Journal of Japanese Botany* 50: 228–238, pls. 3, 4.
- Suzuki M. 1982. Some fossil woods from the Palaeogene of Northern Kyushu, II. *Botanical Magazine Tokyo* 95: 281–294.
- Suzuki M, Joshi L, Noshira S. 1991. *Tetracentron* wood from the Miocene of Noto Peninsula, Central Japan, with a short revision of homoxylic fossil woods. *Botanical Magazine Tokyo* 104: 34–48.
- Szafer W. 1947. The Pliocene flora of Krościenko in Poland. *Rozpraw Wydziału matematyczno-przyrodniczego* 72 B (1–2): 1–213.
- Szafer W. 1950. The family Eucommiaceae in the Tertiary of Europe. *Kosmos A*: 378–409. (In Polish with English summary)
- Szafer W. 1954. Pliocene flora from the vicinity of Czorsztyn (West Carpathians) and its relationship to the Pleistocene. *Instytut Geologiczny Prace* 11: 1–238.
- Takhtajan A. 1963. Chief editor. *Osnovi Palaeontology. Gymnosperms and angiosperms*. Governmental Scientific-Technological Publisher of Literature on Geology and Preservation of Mineral Wealth, Moscow. (In Russian)
- Takhtajan A. 1969. Flowering plants: Origin and dispersal. Washington: Smithsonian Institution Press.
- Takhtajan A ed. 1974. *Magnoliophyta Fossilia URSS Volumen I Magnoliaceae-Eucommiaceae*. Leningrad: NAUKA.
- Tanai T. 1961. Neogene floral changes in Japan. *Journal of the Faculty of Science, Hokkaido University series 4, Geology and Mineralogy* 11 (2): 120–400.
- Tanai T. 1994. Bibliography of Cenozoic paleobotany in Japan through 1992 (exclusive of the Holocene and palynological articles). *Japanese Journal of Historical Botany* 2: 1–92.
- Tanai T, Suzuki N. 1963. Miocene floras of southwestern Hokkaido, Japan. In: Tertiary floras of Japan Miocene floras. Tokyo: Collaborative Association Commemorating 80th Anniversary of the Geological Survey of Japan. 9–152.
- Tao J-R, Xiong X-Z. 1986. The latest Cretaceous flora of Heilongjiang Province and the floristic relationship between East Asia and North America. *Acta Phytotaxonomica Sinica* 24: 1–15; 121–135.
- Taylor DW. 1990. Paleobiogeographic relationships of angiosperms from the Cretaceous and early Tertiary of the North American area. *Botanical Review* 56: 279–417.
- Taylor W, DeVore ML, Pigg KB. 2006. *Susiea newsalemae* gen. et sp. nov. (Nymphaeaceae): *Euryale*-like seeds from the Late Paleocene Almont Flora, North Dakota, U.S.A. *International Journal of Plant Sciences* 167: 1271–1278.
- Terada K, Suzuki M. 1998. Revision of the so-called “*Reevesia*” fossil woods from the Tertiary in Japan—a proposal of new genus *Wataria* (Sterculiaceae). *Review of Palaeobotany and Palynology* 103: 235–251.
- Thorne RF. 1999. Eastern Asia as a living museum for archaic angiosperms and other seed plants. *Taiwania* 44: 413–422.
- Tiffney BH. 1979. Fruits and seeds of the Brandon lignite III. *Turpinia* (Staphyleaceae). *Brittonia* 31: 39–51.
- Tiffney BH. 1980. Fruits and seeds of the Brandon lignite, 5. Rutaceae. *Journal of the Arnold Arboretum* 61: 1–63.
- Tiffney BH. 1981. *Euodia costata* (Chandler) Tiffney (Rutaceae) from the Eocene of southern England. *Paläontologische Zeitschrift* 55: 185–190.
- Tiffney BH. 1985. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. *Journal of the Arnold Arboretum* 66: 243–273.
- Tiffney BH. 1993. Fruits and seeds of the Tertiary Brandon Lignite. VII. *Sargentodoxa* (Sargentodoxaceae). *American Journal of Botany* 80: 517–523.
- Tiffney BH, Haggard KK. 1996. Fruits of Mastixioideae (Cornaceae) from the Paleogene of western North America. *Review of Palaeobotany and Palynology* 92: 29–54.
- Tiffney BH, Manchester SR. 2001. The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. *International Journal of Plant Sciences* 162 (6, suppl.): S3–S17.
- Tralau H. 1963. Asiatic dicotyledonous affinities in the Cainozoic flora of Europe. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 9 (3): 1–87, 5 pls.
- Tralau H. 1964. The genus *Trapella* Oliver in the Tertiary of Europe. *Botaniska Notiser* 117: 119–123.
- Tralau H. 1965. New facts and new finds of fossil *Trapella* Oliver in Europe. *Botaniska Notiser* 118: 21–24.
- Tralau H. 1968. Evolutionary trends in the genus *Ginkgo*.

- Lethaia 1: 63–101
- Tsukagoshi M, Ono Y, Hashimoto T. 1997. Fossil endocarp of *Davidia* from the Early Pleistocene sediments of the Tokai Group in Gifu Prefecture, central Japan. Bulletin of the Osaka Museum of Natural History 51: 13–23.
- Uemura K. 1986. A note on Tertiary *Sciadopitys* (Coniferopsida) from Japan. Bulletin of the National Science Museum, Tokyo, Series C 12 (2): 53–59.
- Uemura K. 1991. Middle Miocene plant megafossil assemblages from Onnebetsu and Niupu in the Nayoro area, Hokkaido. Memoirs of the National Science Museum, Tokyo 24: 17–26, pls. 1–3. (In Japanese with English Summary)
- Uemura K. 1997. Cenozoic history of *Ginkgo* in East Asia. In: Hori T, Ridge RW, Tulecke W, Tredici PD, Tremouillaux-Guiller J, Tobe H eds. *Ginkgo biloba* — a global treasure. Tokyo: Springer-Verlag. 207–221.
- Uemura K, Doi E, Takahashi F. 1999. Plant megafossil assemblage from the Kiwado Formation (Oligocene) from Ouchiyama-kami in Yamaguchi Pref. western Honshu, Japan. Bulletin of the Mine City Museum 15: 1–59. (In Japanese)
- Walther H. 1989. *Cunninghamia miocenica* Ettingshausen, eine wichtige Taxodiaceae im Tertiär Mitteleuropas. Flora 182: 287–311.
- Walther H. 1999. Die Tertiärflora von Kleinsaubernitz bei Bautzen. Palaeontographica Abt. B. 249: 63–174.
- Walther H. 2002. The Neogene flora of Ottendorf-Okrilla (Saxony). Acta Universitatis Carolinae Geologica 46 (4): 107–111.
- Walther H, Kvaček Z. 2007. The Oligocene flora of Seifhennersdorf. Acta Musei Nationalis Pragae, Ser. B, Historia Naturalis 63 (2–4): 85–174.
- Wang H-S. 1988. A study on the distribution and origin of endemic genera of spermatophytes in China. In: Whyte P, Aigner JS, Jablonski NG, Taylor G, Walker D, Wang P-X, So C-L eds. The palaeoenvironment of east Asia from the mid-Tertiary. Proceedings of the 2nd conference. Vol. 1. Hong Kong: Centre of Asia Studies, University of Hong Kong. 605–620.
- Wang Y-F, Xiang Q-P, Ferguson DK, Zastawniak E, Yang J, Li C-S. 2006. A new species of *Keteleeria* (Pinaceae) in the Shanwang Miocene flora of China and its phytogeographic connection with North America. Taxon 55: 165–171.
- Wang Y-F, Li C-S, Collinson ME, Lin J, Sun Q-G. 2003. *Eucommia* (Eucommiaceae), a potential biothermometer for the reconstruction of paleoenvironments. American Journal of Botany 90: 1–7.
- Watari S. 1948. Studies on the fossil woods from the Tertiary of Japan. V. Fossil woods from the Lower Miocene of Hanenisi, Simane Prefecture. Japanese Journal of Botany 13: 503–518.
- Watari S. 1952. Dicotyledonous woods from the Miocene along the Japan-Sea side of Honshu. Journal of the Faculty of Science, University of Tokyo, Section III (Botany) 6: 97–134.
- Weyland H. 1937. Beiträge zur Kenntnis der Rheinischen Tertiärflora. II. Erste Ergänzungen und Berichtigungen zur Flora der Blatterkohle und des Polierschiefers von Rott im Siebengebirge. Palaeontographica, Abt. B 83: 67–122.
- Weyland H, Kilpper K, Berendt W. 1967. Kritische Untersuchungen zur Kutikularanalyse tertiärer Blätter VII. Palaeontographica Abt. B 120: 151–168.
- Wheeler EA, Manchester SR. 2002. Woods of the Eocene Nut Beds flora, Clarno Formation, Oregon, USA. International Association of Wood Anatomists Journal, Supplement 3.
- Wilde V. 1989. Untersuchungen zur Systematik der Blattreste aus dem Mitteleozän der Grube Messel bei Darmstadt (Hessen, Bundesrepublik Deutschland). Courier Forschungsinstitut Senckenberg 115: 1–213.
- Wilde V, Frankenhäuser H. 1998. The Middle Eocene plant taphocoenosis from Eckfeld (Eifel), Germany. Review of Palaeobotany and Palynology 101: 7–28.
- Wing SL, Hickey LJ. 1984. The *Platycarya* perplex and the evolution of the Juglandaceae. American Journal of Botany 71: 388–411.
- WGPC (Writing Group of Cenozoic Plants of China). 1978. Cenozoic Plants from China, Fossil Plants of China. Vol. 3. Beijing: Science Press.
- Wolfe JA. 1977. Paleogene floras from the Gulf of Alaska Region. U.S. Geological Survey Professional Paper 997: 1–107.
- Wolfe JA, Wehr WC. 1987. Middle Eocene dicotyledonous plants from Republic, Northeastern Washington. U.S. Geological Survey Bulletin 1597: 1–25.
- Wolfe JA, Schorn HE. 1990. Taxonomic revision of the Spermatopsida of the Oligocene Creede flora, southern Colorado. U.S. Geological Survey Bulletin 1923: 1–40, 13 pls.
- Wu C-Y. 1998. Delineation and unique features of the Sino-Japanese floristic region. In: Boufford DE, Ohba H eds. Sino-Japanese flora: its characteristics and diversification. Bulletin of the University Museum, The University of Tokyo 37: 1–35.
- Wu C-Y, Raven PH eds. 1999. Flora of China. Vol. 4. Cycadaceae through Fagaceae. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.
- Xie G-W. 1998. Phytogeographical affinities in the forest floras of eastern China and Japan. In: Boufford DE, Ohba H eds. Sino-Japanese flora: its characteristics and diversification. Bulletin of the University Museum, The University of Tokyo 37: 1–187.
- Yamakawa C. 2000. Fossil *Ginkgo biloba* leaves from the Plio-Pleistocene Kobiwako Group in Shiga Prefecture, southwestern Japan. Japanese Journal of Historical Botany 8: 33–38. (In Japanese)
- Ying T-S, Zhang Y-L, Boufford DE. 1993. The endemic genera of seed plants of China. Beijing: Science Press.
- Ying T-S, Zhang Z-S. 1984. Endemism in the flora of China—studies on the endemic genera. Acta Phytotaxonomica Sinica 22: 259–268.
- Zablocki J. 1930. Tertiäre Pflanzen des Salzlagers von Wieliczka I–II. Acta Societatis Botanicorum Poloniae 5: 174–208; 7: 139–150.
- Zhao L-C, Li D-Y. 2008. Anatomically preserved seeds of *Corylopsis* (Hamamelidaceae) from the Miocene of Yunnan, China and their phytogeographic implications. International Journal of Plant Sciences 169: 483–494.
- Zhou Z-K, Momohara A. 2005. Fossil history of some endemic seed plants of East Asia and its phytogeographical significance. Acta Botanica Yunnanica 27: 449–470.