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Eastern Asia as a Living Museum for Archaic Angiosperms and Other Seed Plants

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ABSTRACT: Asia, even excluding Malaysia, has the richest family and subfamily flora of angiosperms in the world, 478 of 755 total families and additional subfamilies recognized in my system of classification. Eastern and southeastern Asia are especially rich in conifers (6 of 7 families plus *Agathis* of the seventh family, Araucariaceae, in Malaya) and those angiospermous families and subfamilies retaining many primitive features, 27 of 41 families of Magnoliidae (Magnolianae, Nymphaeanae, and Rafflesianae) and Ranunculidae (Ranunculanae) (with 7 more families in Malesia and northeastern Australia that might have migrated from southeastern Asia since the junction of the Asiatic and Australian tectonic plates, possibly 15 million years before the present). Also represented in eastern and southeastern Asia are 9 of 9 families and additional subfamilies of Hamamelidales (Rosidae) and 26 of 32 families of Alismatidae (Triuridanae, Acoranae, Aranae, Alismatanae), and Liliales (Liliidae), which seem to be the least specialized monocots. The much studied close floristic relationships between eastern Asia and eastern North America were much stronger in Cretaceous and Tertiary time. Indeed, many of the archaic genera of seed plants now restricted to eastern Asia once were widely distributed in North America and other parts of the northern hemisphere. Hence, one can state that eastern and southeastern Asia are indeed a living museum of archaic vascular plants, but fossil evidence is presently inadequate to prove that the region is the major birthplace of the conifers and flowering plants. It is probable, however, that some of the gymnosperms and archaic angiosperms did evolve in eastern and southeastern Asia, and especially in the Sino-Japanese Region.

KEY WORDS: Archaic seed plants, Conifers, Magnoliidae, Ranunculidae, Alismatidae, Liliales, Asia as living museum.

INTRODUCTION

Southeastern Asia and its adjacent archipelagoes have often been suggested by plant geographers to be the most important center of preservation and also possibly the "cradle" of the Angiospermae (Takhtajan, 1957, 1969; Thorne, 1963; Smith, 1970, 1973). However, our rapidly increasing paleobotanical knowledge and the general acceptance of the theory of tectonic plate movement have caused one of us (Thorne, 1976, 1978) to reconsider Asia as the possible major birthplace of the seed plants. Other biogeographers (Schuster, 1972, 1976; Raven and Axelrod, 1974) with some justification favor Gondwanaland, especially the present South America and Africa, as the area from which the initial radiation of the flowering plants took place. It is therefore desirable to reexamine Asia as a probable center of preservation and as a possible center of origin of the seed plants.

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RESULTS AND DISCUSSION

Eastern Asia as a "living museum" of the seed plants

Asia, even excluding Malesia, has the richest family and subfamily flora of flowering plants in the world, 478 of 755 total families and additional subfamilies recognized in my latest system of classification (Thorne, 1999). The Eastern Asiatic Region alone, according to Takhtajan (1986) has an "extremely rich and distinctive" flora that includes "more than 20 endemic families and over 300 endemic genera, not to mention the huge number of endemic species". For his Indo-Chinese Region, Takhtajan (1986) lists another 250 endemic genera, and one endemic family, Plagiopteraceae, and his Indian Region adds another 120 endemic genera, a total of 21 endemic families and 670 endemic genera for eastern and southeastern Asia, not counting those families and genera that are endemic to two or all three of these asiatic regions.

Eastern and southeastern Asia are especially rich in conifers, including six of seven families (plus *Agathis* Salisb. of the seventh family, Araucariaceae, in Malesian Malaya). Among other representative Asian coniferous genera are *Cephalotaxus* Sieb. and Zucc. (Cephalotaxaceae); *Cryptomeria* D. Don, *Cunninghamia* R. Br., *Fokienia* A. Henry and H. Thomas, *Glyptostrobus* Endl., *Metasequoia* Miki, *Taiwania* Hayata, and *Thujopsis* Sieb. and Zucc. (Taxodiaceae/Cupressaceae); *Cathaya* Chun and Kuang, *Keteleeria* Carriere, and *Pseudolarix* Gordon (Pinaceae); *Dacrycarpus* (Endl.) Laubenf, *Dacrydium* Lambert, *Podocarpus* L'Hérit., and *Prumnopitys* Philipps (Podocarpaceae); *Sciadopitys* Sieb. and Zucc. (Sciadopityaceae); and *Amentotaxus* Pilger, *Pseudotaxus W. C.* Cheng, and *Torreya* Arn. (Taxaceae). Other gymnospermous genera represented are *Cycas* L. (Cycadaceae); *Ginkgo* L. (Ginkgoaceae); *Ephedra* L. (Ephedraceae); and *Gnetum* L. (Gnetaceae). Many of these genera, and two families, Cephalotaxaceae and Sciadopityaceae, are currently restricted to eastern Asia.

Among the angiosperm families, those retaining numerous primitive features are especially well represented in eastern Asia. Twenty-seven of 41 families of my archaic Magnoliidae (Magnolianae, Nymphaeanae, and Rafflesianae) and Ranunculidae (Ranunculanae) (Thorne, 1992, 1996a, 1999) are there represented, and seven more families in Malesia and northeastern Australia may have migrated from southeastern Asia before or since the junction of the Asiatic and Australian tectonic plates, possibly 15 million years before the present. Of the former families the Illiciaceae, Schisandraceae, Myristicaceae, Magnoliaceae, Annonaceae, Aristolochiaceae, Chloranthaceae, Calycanthaceae, Lauraceae, Hernandiaceae, Saururaceae, Piperaceae, Paeoniaceae, Glaucidiaceae, Menispermaceae, Lardizabalaceae (including *Sargentodoxa* Rehder and E. Wilson), Berberidaceae, Ranunculaceae, Circaeasteraceae, Pteridophyllaceae, Papaveraceae, Cabombaceae, Nymphaeaceae, and Rafflesiaceae are well represented in Asia with several families or subfamilies nearly or entirely restricted to eastern and southeastern Asia, as Illiciaceae, Schisandraceae, Hortonioideae, Glaucidiaceae, Lardizabalaceae, Nandinoideae, Circaeasteraceae, Pteridophyllaceae, Barclayoideae, and Rafflesioideae.

Similarly represented in eastern and southeastern Asia are nine of nine families and additional subfamilies of the highly archaic Hamamelidales (Rosidae) (Thorne, 1996a, 1999) with *Trochodendron* Sieb. and Zucc., *Tetracentron* Oliver, *Euptelea* Sieb. and Zucc., *Cercidiphyllum* Sieb. and Zucc. and *Disanthus* Maxim., each the sole genus of a family or subfamily, restricted or nearly so today to eastern and southeastern Asia. Of the 30 genera of

Hamamelidaceae 22 are represented in Asia with 19 restricted or nearly so to Asia, a few ranging into Malesia (Endress, 1993). The least specialized *Platanus* L., *P. kerrii* Gagnepain, most similar to early fossil platanoids in various features (Crane *et al.*, 1986; Wheeler, 1995; Wheeler *et al.,* 1995), is restricted to Laos and southern China (Kubitzki, 1993). Some authors, as Schwarzwalder and Dilcher (1991), consider the Hamamelidales at least as primitive as the Magnoliidae.

Among the monocotyledons the Alismatidae with Triuridanae, Acoranae, Aranae, and Alismatanae, and the Liliales of the Liliidae, because of retained primitive features, appear to be the least specialized monocots (Thorne, 1996a, 1999, 2000). Twenty-five of the 32 families of these taxa, as represented in the current modification of my classification (Thorne, 2000), are represented in eastern and southeastern Asia. Among some of the genera restricted nearly or entirely to Asia are *Petrosavia* Becc. (Petrosaviaceae), *Japonolirion* Nakai (Tofieldiaceae), and *Cryptocoryne* Fischer, *Raphidophora* Hassk., *Scindapsis* Schott, *Epipremnum* Schott, *Lasia* Lour., *Aglaonema* Schott, and *Typhonium* Schott (Araceae), most of these aroid genera also ranging into Malesia (Mabberly, 1987). In the Liliales *Chionographis* Maxim., *Heloniopsis* A. Gray, *Metanarthecium* Maxim. (Melanthiaceae); *Tricyrtis* Wallich (Tricyrtidaceae); *Cardiocrinum* Endl. and *Nomocharis* Franchet (Liliaceae); and *Heterosmilax* Kunth (Smilacaceae) are likewise oriental.

In addition to taxa of groups mentioned above, a good many of the endemic or near endemic genera of eastern Asia can be considered in part archaic because of their retention of primitive features. A few of the more outstanding genera are *Actinidia* Lindl. and *Clematoclethra* (Franchet) Maxim. (Actinidiaceae); *Alniphyllum* Matsum., *Pterostyrax* Sieb. and Zucc., and *Rehderodendron* Hu (Styracaceae); *Aucuba* Thunb. (Aucubaceae); *Bretschneidera* Hemsley (Bretschneideraceae); *Camptotheca* Decne. and *Davidia* Baillon (Nyssaceae); *Cardiandra* Sieb. and Zucc., *Kirengeshoma* Yatabe, and *Schizophragma* Sieb. and Zucc. (Hydrangeaceae); *Chaenomeles* Lindley, *Kerria* DC., *Prinsepia* Royle *Rhaphiolepis* Lindley, and *Stephanandra* Sieb. And Zucc. (Rosaceae); *Craigia* W. W. Sm. And W. E. Evans (Malvaceae including Sterculiaceae); *Cyclocarya* Iljinsk., *Platycarya* Sieb. and Zucc., and *Pterocarya* Kunth (Juglandaceae); *Dipentodon* Dunn (Dipentodontaceae); *Diplarche* Hook. f. and Thompson; and *Enkianthus* Lour. (Ericaceae); *Dipteronia* Oliver (Aceroideae of Sapindaceae); *Eleutherococcus* Maxim. (Araliaceae); *Eucommia* Oliver (Eucommiaceae); *Euscaphis* Sieb. and Zucc. and *Tapiscia* Oliver (Staphyleaceae); *Formanodendron* Nixon and Crepet (Fagaceae); *Helwingia* Willd. (Helwingiaceae); *Hemiptelea* Planch. (Ulmaceae); *Hosta* Tratt. (Hesperocallidaceae); *Idesia* Maxim. (Flacourtiaceae); *Limacia* Lour. (Menispermaceae); *Ostryopsis* Decne. (Betulaceae); *Phellodendron* Rupr. and *Skimmia* Thunb. (Rutaceae); *Rhoiptelea* Diels and Hand.-Mazz. (Rhoipteleaceae); *Schima* Reinw. (Theaceae); *Schumacheria* Vahl (Dilleniaceae); *Stachyurus* Sieb. and Zucc. (Stachyuraceae); and *Toricellia* DC. (Toricelliaceae).

Other genera retaining some primitive features but more widely distributed in the Old World are even more numerous. A few especially worthy of mention are *Adiandra* Jacq. and *Camellia* L. (Theaceae); *Alangium* Lam. (Alangiaceae); *Daphniphyllum* Blume (Daphniphyllaceae); *Kandelia* (DC.) Wight and Arn. (Rhizophraceae); *Nypa* Steck (Arecaceae); *Phytocrene* Wallich and *Stemonurus* Bl. (Icacinaceae); *Ploiarium* Korth. (Bonnetiaceae); *Sabia* Colebr. (Sabiaceae); and *Zelkova* Spach (Ulmaceae). Other genera so wide ranging that they reach the New World will be mentioned below.

The taxa enumerated above are surely adequate proof that eastern and southeastern Asia are indeed major centers of preservation of less specialized seed plants, thus presenting us

with a living museum, or refugium, for the conservation of archaic angiosperms and other seed plants that have been able to survive great climatic changes and other catastrophic events. In this great natural museum we have available those taxa that are critical for the study of seed plant diversity and evolution.

Eastern Asian and American floristic relationships

The strong floristic relationship between eastern Asia and eastern North America has long been known and much studied (Boufford and Spongberg, 1983; Hara 1962; Lee *et al.*, 1996; Li, 1952). Asa Gray (1846, 1859) first brought to our attention this fascinating disjunction. Elsewhere (Thorne, 1972). I have counted 74 temperate genera largely restricted to eastern North America and Asia, mostly in eastern and southeastern Asia. Among the better known of these probable Tertiary or Cretaceous relicts are *Arisaema C.* Martius, *Buckleya* Torr., C*arya* Nutt., *Catalpa* Scop., *Caulophyllum* Michx., C*ladrastis* Raf., *Croomia* Torr., *Gordonia* Ellis, *Hamamelis* L., *Illicium* L., *Liquidambar* L., *Liriodendron* L., *Magnolia* L., *Menispermum* L., *Nyssa* L., *Osmanthus* Lour., *Panax* L., *Penthorurn* L., *Phryma* L., *Podophyllum* L., *Sassafras* Nees and Eberm., *Saururus* L., *Schisandra* Michx., *Shortia* Torr. and A. Gray, *Stewartia* L., *Symplocarpus* Salisb., *Wisteria* Nutt., and *Zizania* L. Eighty-six more genera have a wider distribution in Eurasia and North America or are more restricted to eastern Asia and western North America or to eastern Asia and the Mexican highlands.

I have treated another 50 genera more widespread in the tropics and that reach both southeastern tropical Asia and tropical America as Amphi-Pacific Tropical disjuncts (Thorne, 1972). A few of the more conspicuous genera in this category are *Clethra* L., *Clyera* Thunb., *Dendropanax* Dcne. & Planch., *Meliosma* Bl., *Mitrastema* Makino, *Nelumbo* Adans., *Passiflora* L., *Persea* Miller. *Saurauia* Willd, *Sloanea* L., S*ymplocos* Jacq., *Thalassia* Soland., *Turpinia* Vent., *Xylosma* Forst. f., and *Zanthoxylum* L. Many hundred more taxa, species, species-pairs, and genera, having Eurasian-North American distributions in the Arctic and boreal regions, are circum-north temperate, or range also into temperate South America. I have discussed them in some detail much earlier in my paper on major disjunctions (Thorne, 1972).

The current distribution of taxa is not necessarily indicative of their distribution in the past. Illustrative of this biogeographic principle (Thorne, 1966b) is our much increased knowledge of the fossil record, which indicates that eastern Asia and North America had much stronger floristic links in Cretaceous and Tertiary time. Such paleobotanists as Call and Dilcher (1993, 1994, 1995), Crepet (1981), Crepet and Nixon (1989), Daghlian (1981), Fields (1994), Florin (1963), Frederiksen (1989), Herendeen *et al.* (1993), Herendeen and Dilcher (1991), Hickey (1980), Jarzen and Dettmann (1989), Krutzsch (1989), Kvacek *et al.* (1991), Manchester (1987, 1989, 1994a, 1994b, 1999), Manchester *et al.* (1991), Manchester and Kress (1993), Manchester and Tiffney (1993), Muller (1981), Nixon and Crepet (1989), Taylor (1990), Tiffney (1985, 1993), Wolfe (1977, 1981, 1989), and Wolfe and Tanai (1987) have identified, documented, or reported in North American Cretaceous or Tertiary time the occurrence of many genera currently restricted to eastern and/or southeastern Asia. Among the gymnospermous genera formerly in North America are *Amentotaxus, Cunninghamia, Ginkgo, Glyptostrobus, Keteleeria, Metasequoia, Pseudolarix,* and *Sciadopitys.* Much more numerous are the currently Asian angiospermous genera, some represented in temperate America by now extinct close relatives, possibly congeneric, and a few only from suspect terranes in Alaska (Wolfe, 1977). Among them are *Actinidia, Alangium, Castanopsis* (D.

Don) Spach, *Cercidiphyllum, Clematoclethra, Cleyera, Corylopsis* Sieb. and Zucc., *Craigia, Cyclocarya, Dipelta* Maxim., *Diplopanax* Hand.-Mazz., *Dipteronia, Eleutherococcus, Emmenopterys* Oliver, *Engelhardia* Leschen., *Eucommia, Euptelea, Exbucklandia R.* W. Br., *Formanodendron, Fortunearia* Rehder and E. Wilson, *Idesia, Mastixia* Blume, *Ostryopsis, Phellodendron, Platycarya, Pterocarya, Rhoiptelea, Sarcococca* Lindl., *Sargentodoxa, Sinowilsonia* Hemsley, *Tapiscia, Tetracentron, Toricellia, Trigonobalanoidea* Crepet and Nixon, and *Trochodendron.*

More wide-ranging Old World genera with reported North American fossil representation include *Ailanthus* Desf., *Alangium, Altingia* Noronh., *Anamirta* Colebr., *Artocarpus* Forst. & Forst. L., *Barringtonia* J. R. and G. Forst., *Bombax* L., *Calamus* L., *Caldesia* Parl., *Cananga* (DC.) Hook.f. and Thoms., *Castanopsis, Chloranthus* Sw., *Cinnamomum* Schaef., *Daphne* L., *Diploclisia* Miers, *Distylium* Sieb. & Zucc., *Dracontomelon* Bl., *Elaeocarpus* L., *Ensete* Horan., *Euodia* J. R. and G. Forst., *Firmiana* Marsighli, *Gironniera* Gauditch., *Hemiptelea* Planch., *Iodes* Bl., *Kandelia, Knema* Lour., *Koelreuteria* Laxm., *Limacia, Macaranga* Thou., *Mallotus* Lour., *Mastixia, Melanorrhoea* Wall., *Mezonevron* Desf., *Myristica* Gronov., *Nypa, Olax* L., *Paliurus* Miller, *Pandanus* Olay Parkins., *Parashorea* Kurz, *Phoebe* Nees, *Photinia* Lindl., *Phytocrene* Wall., *Platea* Bl., *Pycnarrhena* Miers, *Pyrenacantha* Hook., *Sabia, Stemonurus* Bl., *Tetrastigma* (Miq.) Planch., *Trapa* L., and *Zelkova*

In addition to these extant genera, a considerable number of extinct genera, as listed by Manchester (1999), have representation in both Asia and North America. Among them are *Palaeocarpinus* Crane (Betulaceae), *Nyssidium* Heer (Cercidiphyllaceae), *Amersinia* Manchester, Crane and Golovneva (Cornaceae), *Fagopsiphyllum* Manchester (Fagaceae), *Palaeocarya* Saporta (Juglandaceae), *Limnobiophyllum* Krassilov emend. Kvacek (Lemnaceae), *Florissantia* Knowlton (Tiliaceae), *Syzygioides* Manchester, Dilger and Wing (Myrtaceae), *Macginitiea* Wolfe and Wehr (Platanaceae), *Nordenskioldia* Heer (Trochodendraceae), *Porosia* and *Quereuxia* Kryshtofovich ex Nevolina (incertae sedis).

Many of the above mentioned Asian genera, and some not apparently reaching America, also have reported fossil representation in western Asia and Europe. Likewise, some of the archaic North American endemic coniferous genera, such as *Sequoia* Endl., *Sequoiadendron* Buchholz and *Taxodium* Rich., have fossil representation in the Old World. And a number of extant American angiosperm genera have fossil representation in Asia, including *Comptonia* L'Hérit. (Myricaceae), *Decodon* Gemelin (Lythraceae), *Leitneria* Chapman (Simaroubaceae), and *Sabal* Adans. (Arecaceae). Thus a large number of the genera and families of seed plants that now have a much restricted range once had wide representation in the northern hemisphere, some even ranging into the southern continents.

CONCLUSION

Available fossil evidence is inadequate to warrant the designation of any one area, including eastern and southeastern Asia, as the primary center of origin of the seed plants. It does seem likely, however, that eastern Asia was an important center of evolution for some seed plant families, as especially the Cephalotaxaceae, Circaeasteraceae, Hamamelidaceae, Lardizabalaceae, and Magnoliaceae.

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東亞是古老被子植物及其他種子植物的現存博物館

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摘　　要

即使不含馬來西亞，亞洲仍然是世界上具有最多的被子植物科及亞科的地區，在本人的分類系統中（全部計 755 科及亞科），有 478 科及亞科分佈於亞洲。特別是東亞及東南亞地區含有最多的裸子植物（在馬來半島就有裸子植物 7 科中的 6 科，以及第 7 南洋杉科的貝殼杉屬）以及保留許多原始特徵的被子植物如木蘭亞綱（木蘭，睡蓮及大花草超目"介於亞綱及目之間的類階"）及毛茛亞綱（毛茛超目）41 科中的 27 科（另有亞洲及澳洲共有的 7 科可能在一千五百萬年前當亞洲及澳洲板塊仍然相連時自東南亞傳播至澳洲東北部）。另外東亞及東南亞還包含金縷梅目（薔薇亞綱）絕大部份的科及亞科，以及最原始的單子葉植物如（霉草、菖蒲、天南星及澤瀉超目）32 科中的 26 科，及百合目（百合亞綱）。另外經常被研究的東亞及北美東部的植物相關係以在白堊紀及第三紀期間最為密切，許多目前侷限於東亞的古老種子植物屬在過去曾經廣泛分佈於北美及其他北半球區域，因此東亞及東南亞可說是古老維管束植物的現存博物館。但就目前收集到的化石而言，仍不足以證明本區是裸子植物及被子植物的故鄉。雖然如此，極可能某些裸子植物及古老的被子植物確實是在東亞（特別是中國及日本區域）及東南亞演化及孕育出來。

關鍵詞： 古老種子植物， 松柏類植物，木蘭亞綱，毛茛亞綱，澤瀉亞綱，百合目，亞洲作為現存博物館。

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