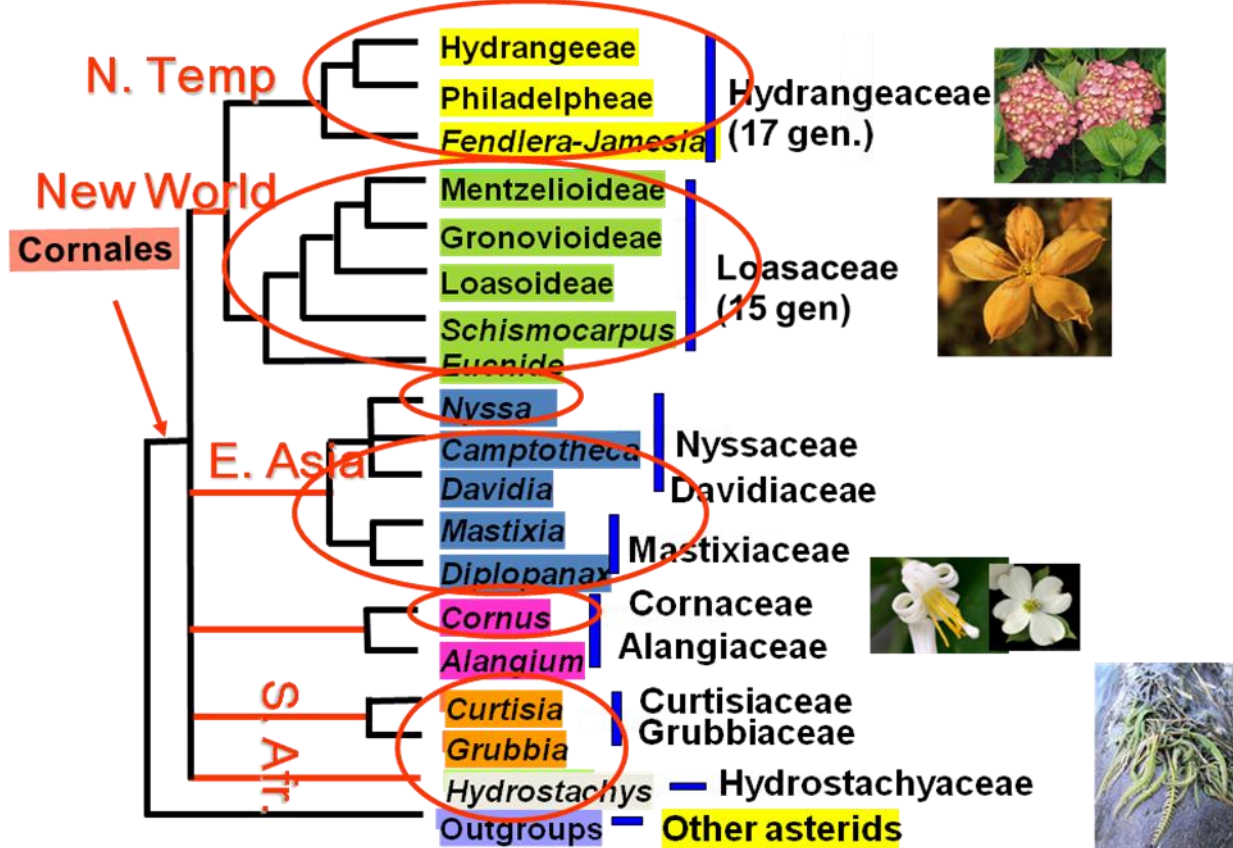


Major clades of Cornales – modified from Fan & Xiang 2003



Xiang et al. 2011.

Resolving and dating the phylogeny of Cornales – Effects of taxon sampling, data partitions, and fossil calibrations

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a b s t r a c t

The order Cornales descends from the earliest split in the Asterid clade of flowering plants. Despite a few phylogenetic studies, relationships among families within Cornales remain unclear. In the present study, we increased taxon and character sampling to further resolve the relationships and to date the early diversification events of the order.

We conducted phylogenetic analyses of sequence data from 26S rDNA and six chloroplast DNA (cpDNA) regions using parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods with different partition models and different data sets. We employed relaxed, uncorrelated molecular clocks on BEAST to date the phylogeny and examined the effects of different taxon sampling, fossil calibration, and data partitions. Our results from ML and BI analyses of the combined cpDNA sequences and combined cpDNA and 26S rDNA data suggested the monophyly of each family and the following familial relationships ((Cornaceae–Alangiaceae)–(Curtisiaceae–Grubbiaceae))–(((Nyssaceae–Davidiaceae)–Mastixiaceae)–((Hydrostachyaceae–(Hydrangeaceae–Loasaceae)))). These relationships were strongly supported by posterior probability and bootstrap values, except for the sister relationship between the N–D–M and H–H–L clades. The 26S rDNA data and some MP trees from cpDNA and total evidence suggested some alternative alignments for Hydrostachyaceae within Cornales, but results of SH tests indicated that these trees were significantly worse explanations of the total data. Phylogenetic dating with simultaneous calibration of multiple nodes suggested that the crown group of Cornales originated around the middle Cretaceous and rapidly radiated into several major clades. The origins of most families dated back to the late Cretaceous except for Curtisiaceae and Grubbiaceae which may have diverged in the very early Tertiary. We found that reducing sampling density within families and analyzing partitioned data sets from coding and noncoding cpDNA, 26S rDNA, and combined data sets produced congruent estimation of divergence times, but reducing the number and changing positions of calibration points resulted in very different estimations.

Research highlights

- Relationships among families of Cornales were resolved as ((Cornaceae–Alangiaceae)–(Curtisiaceae–Grubbiaceae))–(((Nyssaceae–Davidiaceae)–Mastixiaceae)–((Hydrostachyaceae–(Hydrangeaceae–Loasaceae)))).
- Cornales was estimated to originate around the middle Cretaceous and rapidly radiated into several major clades. The origins of most families dated back to the late Cretaceous.

Feng et al. 2009

Phylogeny and biogeography of Alangiaceae (Cornales) inferred from DNA sequences, morphology, and fossils

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a b s t r a c t

Alangiaceae, in the basal Asterid clade Cornales, consists of only one genus, *Alangium*. The genus has approximately 24 species distributed mainly in tropical and subtropical regions of the Old World and is well represented in the Tertiary fossil record of the northern hemisphere. We conducted phylogenetic and biogeographic analyses for *Alangium* by integrating data from DNA sequences, morphology, and fossils to evaluate systematic and biogeographic hypotheses. The results largely agree with the traditional classification of four sections within the genus, and suggest sects. *Conostigma* and *Rhytidandra* are successive sister taxa to a clade containing sects. *Marlea* and *Alangium*. Our results also indicate that the widespread species *A. chinense* consists of at least two lineages meriting recognition as distinct species.

Biogeographic analysis using DIVA and divergence time dating with the Bayesian method (MULTIDIVTIME) resolved the ancestor of *Alangium* as being in S.E. Asia in the Late Cretaceous. Several intercontinental migrations involving the margin of the Tethys seaway (TESW), the North Atlantic land bridge (NALB) or the Bering land bridge (BLB), and long-distance dispersals are suggested. The results support TESW for plant migration of thermophilic (including evergreen) taxa in the early Tertiary.

abstract

Identifying causes of genetic divergence is a central goal in evolutionary biology. Although rates of nucleotide substitution vary among taxa and among genes, the causes of this variation tend to be poorly understood. In the present study, we examined the rate and pattern of molecular evolution for five DNA regions over a phylogeny of *Cornus*, the single genus of Cornaceae. To identify evolutionary mechanisms underlying the molecular variation, we employed Bayesian methods to estimate divergence times and to infer how absolute rates of synonymous and nonsynonymous substitutions and their ratios change over time. We found that the rates vary among genes, lineages, and through time, and differences in mutation rates, selection type and intensity, and possibly genetic drift all contributed to the variation of substitution rates observed among the major lineages of *Cornus*. We applied independent contrast analysis to explore whether speciation rates are linked to rates of molecular evolution. The results showed no relationships for individual genes, but suggested a possible localized link between species richness and rate of nonsynonymous nucleotide substitution for the combined cpDNA regions. Furthermore, we detected a positive correlation between rates of molecular evolution and morphological change in *Cornus*. This was particularly pronounced in the dwarf dogwood lineage, in which genome-wide acceleration in both molecular and morphological evolution has likely occurred.

Manchester et al. 2007

***Curtisia* (Cornales) from the Eocene of Europe and its phytogeographical significance**

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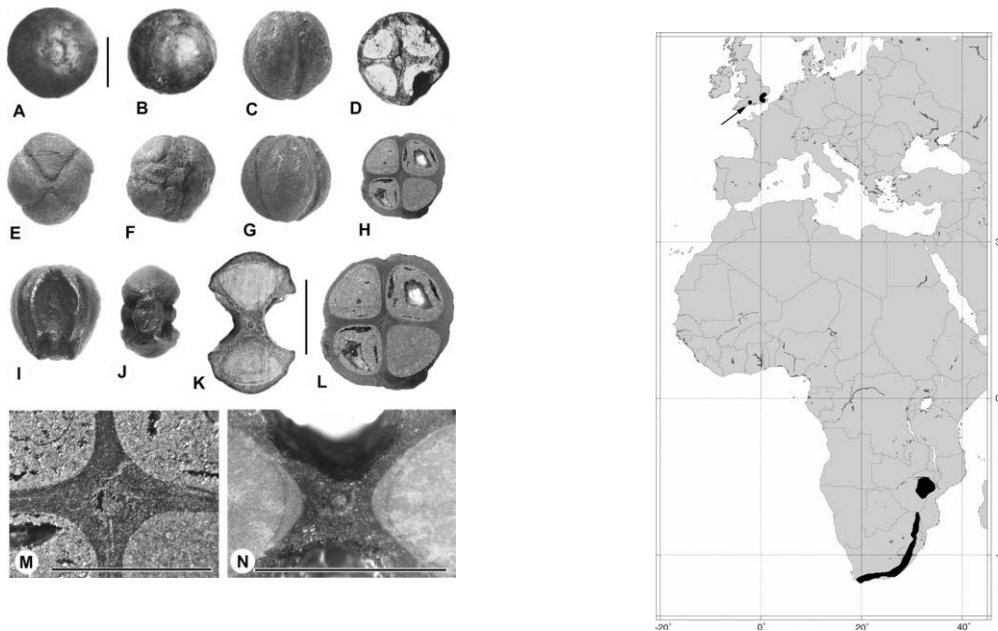


Figure 1. Map showing the geographical distribution of *Curtisia* with extant *C. dentata* in southern Africa (as mapped by Palgrave, 2002) and Eocene *C. quadrilocularis* in southern England (arrow). Base map from Online Map Creation

Manchester et al. 2010

FRUITS OF CORNELIAN CHERRIES (CORNACEAE: CORNUS SUBG. CORNUS) IN THE PALEOCENE AND EOCENE OF THE NORTHERN HEMISPHERE

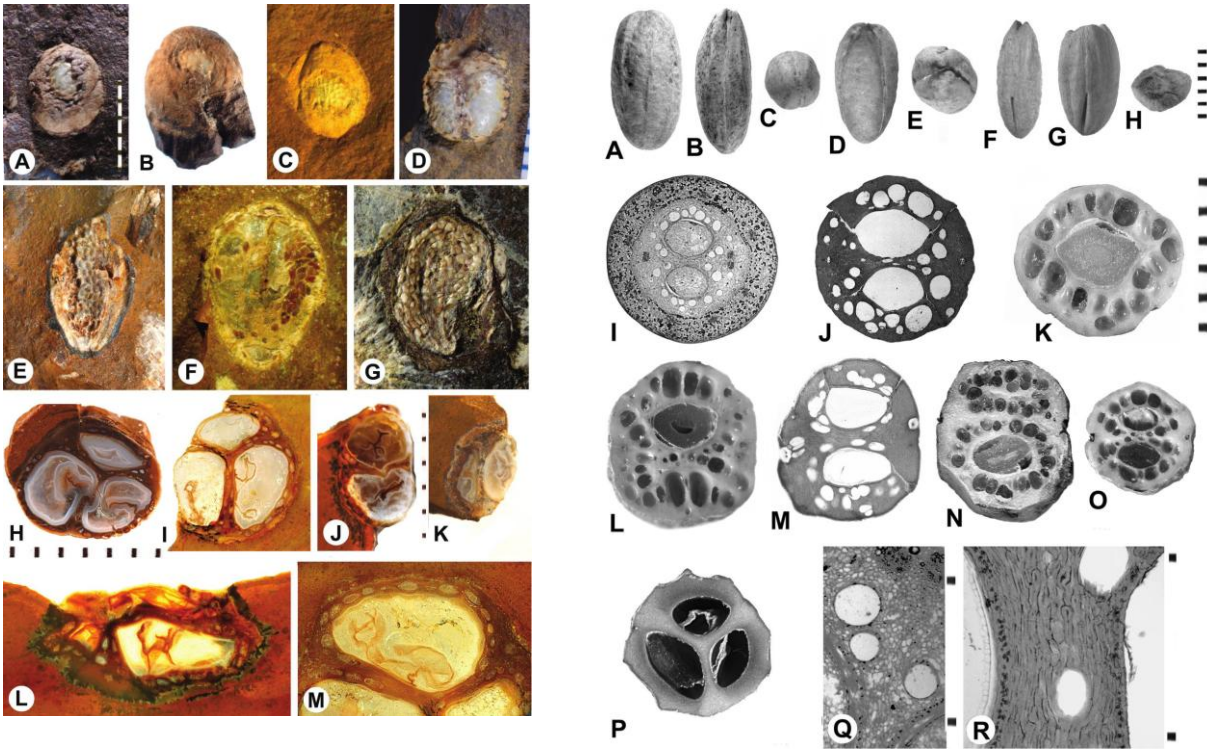
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Int. J. Plant Sci. 171(8):882–891. 2010.

Fossil fruits confirm that cornelian cherries (*Cornus*, subgenus *Cornus*) were established in the Northern Hemisphere in the Early Tertiary. We describe the oldest known member of the subgenus, *Cornus piggae* sp. n. on the basis of well-preserved silicified endocarps from the late Paleocene of North Dakota. The endocarps are ellipsoidal, thin walled, and two to three locular, and they lack an axial longitudinal bundle. The septa and external walls of the fruit stone are riddled with cavities, a feature diagnostic of extant subgenus *Cornus*. For comparison, we sectioned fruits of each of the extant species and reexamined fossil fruits from the Early Eocene

London Clay of southern England. These London Clay fossils differ from *C. piggae* by much thicker external walls (*Cornus ettingshausenii* [Gardner] Eyde) and higher locule number (up to 6 in *Cornus multilocularis* [Gardner] Eyde). Comparison with fruits of extant cornelian cherries indicates that the morphological range among the modern species is narrower than that seen in the Paleogene.



Manchester et al. 2009

LEAVES OF CORNUS (CORNACEAE) FROM THE PALEOCENE OF NORTH AMERICA AND ASIA CONFIRMED BY TRICHOME CHARACTERS

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Int. J. Plant Sci. 170(1):132–142. 2009.

The identification of *Cornus* foliage in the fossil record previously has relied primarily on similarities in venation, particularly the eucamptodromous secondary veins and widely spaced, transversely oriented tertiary veins. These features, while consistent with *Cornus*, are not by themselves diagnostic for the genus. Doublearmed, acicular

trichomes mineralized with calcium carbonate are an additional characteristic feature found in all extant species of the genus. The presence of such trichomes provides a means of confirming leaf impression fossils attributed to *Cornus*. Reexamination of previously described *Cornus* leaves from the Paleocene of the Rocky Mountains and Great Plains region leads us to reject *Cornus nebrascensis* Schimper ($\frac{1}{4}$ *Cornus newberryi* Hollick) from the genus. Another species, *Cornus hyperborea* Heer, is provisionally accepted as *Cornus* based on its venation, although we were unable to confirm the trichomes in the type material from Greenland or in the assigned specimens from North Dakota. We also review other Eurasian Paleocene *Cornus*-like leaf remains, including *Cornus platyphylla* Saporta and *Cornophyllum hebridicum* (Johnson) Boulter and Kvaček. We recognize two new Paleocene species, whose identity as *Cornus* is confirmed by the presence of characteristic trichomes and venation: *Cornus swingii* sp. n., from the Paleocene of Wyoming, Montana, and North Dakota, and *Cornus krassilovii* sp. n., from the Paleocene Tsagayan flora of Russia. These occurrences, along with fruit records, indicate that the extant genus was well established in the Northern Hemisphere early in the Tertiary.

