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Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Morphometric analysis of some Cretaceous angiosperm woods and their extant structural and phylogenetic analogues: Implications for systematics

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ARTICLE INFO

Article history:

Received 14 March 2009

Received in revised form 4 June 2009

Accepted 30 June 2009

Available online 8 July 2009

Keywords:

Cretaceous

fossil wood

early angiosperm evolution

morphometric analysis

systematics

Principal Component Analysis

ABSTRACT

Cretaceous fossil wood assemblages provide important evidence about the early evolution of angiosperms. However, the utility of these fossils is limited by two systematic problems: morphotaxa are generally over-split and in many cases cannot be securely assigned to extant families or orders. To address these problems we employed a 16-character Principal Component Analysis (PCA) to critically assess fossil wood systematics and investigate family/order affinity. In the first part of our study, we analyzed a large dataset of woods from extant trees. This served as a test of the PCA method, demonstrating a capability for clustering specimens into natural groups at species, genus, and to a more limited extent, family/order level. Having confirmed the validity of our approach, we then applied it to mid-Cretaceous fossil woods of icacinoid/platanoid and phyllanthoid types. Our PCAs support the distinctiveness of these groups, and most morphogeneric concepts contained therein, but raise significant questions about the uniqueness of many morphospecies. In particular, analyses highlight intra-specific variability as a major problem in delineating morphospecies and confirm suspicions that many taxa are over-split. Comparison of fossil specimens with extant structural and phylogenetic analogues also allows the probable affinity of morphotaxa to be assessed. Among the taxa analyzed, Cretaceous icacinoid/platanoid woods are similar to members of the Icacinaceae and Platanaceae, respectively, but an affinity with the Chloranthaceae or some other basal groups cannot be ruled out. In contrast, phyllanthoid fossil woods may be associated with magnoliid stem of the Laurales and Magnoliales. We argue that our PCA methodology offers a more rigorous and repeatable approach to fossil angiosperm wood systematics compared to those used in earlier studies.

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1. Introduction

Unequivocal angiosperm fossils (pollen, flowers) do not occur until the earliest Cretaceous (Berriasian–Valanginian, 145–136 Ma). For the next 15 myr, megafossil remains are extremely rare (Crane et al., 1995) and limited data imply that early angiosperms were either small shrubs within dark and disturbed forest floor niches (Feild et al., 2004) or herbs adapted to aquatic settings (Feild and Arens 2007). During the Aptian–Albian (120–99 Ma), the group underwent its first major radiation, diversity exploded, many extant families emerged (Heimhofer et al., 2005) and the tree-habit was adopted (Wheeler and Baas, 1991).

The oldest angiosperm fossil woods date from the mid-Cretaceous. In the Albian–Turonian interval (112–89 Ma) there are 11 securely dated records of angiosperm wood (Fliche, 1905; Serlin, 1982; Thayn et al., 1983, 1985; Wheeler et al., 1987; Herendeen, 1991a,b; Wheeler, 1991; Giraud et al., 1992; Takahashi and Suzuki, 2003; Oakley and

Falcon-Lang, 2009). These comprise two morphotypes, the icacinoid/platanoid type represented by *Icacinoxylon* and *Plataninium* and the phyllanthoid type represented by *Paraphyllanthoxylon* and the very similar taxa, *Bridelioxylon* and *Glochidioxylon* (Thayn and Tidwell, 1984; Wheeler et al., 1995). Understanding the taxonomy of these woods is important for analyzing angiosperm phylogeny and the early spread of trees and shrubs in particular.

However, the conservative evolutionary trajectory of angiosperm wood anatomy, coupled with high levels of ontogenetic variability, poses major challenges for fossil wood systematics (Bailey, 1924). This is well illustrated by the Inside Wood Database (<http://insidewood.lib.ncsu.edu>; accessed 20 January 2009), which lists 264 records of angiosperm wood of Cretaceous age representing 188 morphospecies in 113 morphogenera. This high diversity relative to the number of records is anomalous and implies that taxa have been over-split based on insignificant characters or ontogenetic variants (Falcon-Lang, 2005). Furthermore, 42% of Cretaceous morphospecies ($n=112$) listed in the Inside Wood Database cannot be assigned to extant families. This may reflect the existence of a high proportion of stem-taxa, which share characters with one or more extant families, or that the character suites they exhibited no longer occur in extant families.

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Table 1
Anatomical characters of the modern woods used in the Principal Component Analysis. Specimens with pre-fix Kw are wood samples from the Economic Botany Collections held in the Banks Building, Royal Botanic Gardens, Kew, UK. Those with the pre-fix KJw are the microscope slides in the Micromorphology Reference Collection in the Jodrell Laboratory, Royal Botanic Gardens, Kew, UK. Unknown values denoted by "?".

Number	Kew number	Family	Species	(1) Vessel diameter (µm)	(2) Vessel number per mm ²	(3) perforation plate type (scalariform/simple)	(4) Vessel distribution (>90% solitary or not)	(5) Intervessel pit diameter (µm)	(6) Ray number per linear mm	(7) Maximum ray width in cells	(8) Maximum ray height (less or greater than 1 mm)	(9) Ray cell composition (homocellular/heterocellular)	(10) Rays of two distinct sizes (absent/present)	(11) Septate fibres (absent/present)	(12) Growth rings (absent/distinct)	(13) Porosity (diffuse/ring)	(14) Tyloses (absent/present)	(15) Paratracheal axial parenchyma (absent/present)	(16) Apotracheal axial parenchyma (absent/present)
W1	KJw18510	Icacinaeae	<i>Apodytes dimidiata</i>	61	40	0	0	4.4	6.0	3	1	1	0	0	0	0	0	0	1
W2	KJw18511	Icacinaeae	<i>Apodytes dimidiata</i>	85	42	0	0	7.1	6.5	3	1	1	0	0	0	0	0	0	1
W3	KJw18514	Icacinaeae	<i>Apodytes mauritiana</i>	92	17	0	1	3.7	9.6	4	1	1	0	0	0	0	0	0	1
W4	KW72251	Icacinaeae	<i>Apodytes benthamiana</i>	75	20	0	0	5.2	8.2	3	1	1	0	0	0	0	0	0	1
W5	N/A	Icacinaeae	<i>Cassinopsis tinifolia</i>	42	43	0	0	?	9.7	3	1	1	1	0	0	0	0	1	1
W6	KJw18518	Icacinaeae	<i>Emmotum nitens</i>	154	13	0	0	6.0	3.1	13	1	1	1	0	0	0	0	1	1
W7	KW79674	Icacinaeae	<i>Emmotum sp.</i>	65	9	0	0	4.8	10.8	8	1	1	1	0	0	0	0	1	1
W8	KW20718	Icacinaeae	<i>Emmotum fagifolium</i>	107	22	0	0	5.3	0.9	13	1	1	1	0	0	0	0	1	1
W9	KJw18531	Pennantiaceae	<i>Pennantia corymbosa</i>	42	190	0	0	3.6	2.8	6	1	1	1	0	0	0	0	0	1
W10	KJw18530	Pennantiaceae	<i>Pennantia cunninghamii</i>	61	54	0	0	4.9	2.0	9	1	1	1	0	0	0	0	0	1
W11	KJw18532	Pennantiaceae	<i>Pennantia cunninghamii</i>	64	48	0	0	3.7	2.6	9	1	1	1	0	0	0	0	0	1
W12	KJw23178	Platanaceae	<i>Platanus kerrii</i>	78	29	0	0	4.8	2.3	25	1	1	0	0	0	0	0	0	1
W13	KJw23177	Platanaceae	<i>Platanus occidentalis</i>	67	49	0	1	4.8	2.9	9	1	1	1	0	1	0	0	0	1
W14	KJw23175	Platanaceae	<i>Platanus occidentalis</i>	82	53	0	1	7.2	2.3	9	1	1	1	0	1	0	0	0	1
W15	KJw23179	Platanaceae	<i>Platanus orientalis</i>	60	106	0	1	4.8	2.8	11	1	1	1	0	1	0	0	0	1
W16	KJw23180	Platanaceae	<i>Platanus wrightii</i>	58	145	0	1	7.3	2.0	10	1	1	1	0	1	0	0	0	1
W17	KJw23174	Platanaceae	<i>Platanus acerifolia</i>	50	100	0	1	4.8	2.6	9	1	1	0	0	1	0	0	0	1
W18	KJw18879	Lauraceae	<i>Laurus nobilis</i>	43	28	1	1	5.3	7.9	4	0	1	0	0	1	0	0	1	0
W19	KJw18875	Lauraceae	<i>Laurus camphora</i>	112	8	1	1	5.5	4.0	4	0	1	0	0	1	0	0	1	0
W20	KJw18876	Lauraceae	<i>Laurus canariensis</i>	92	21	1	1	5.6	6.2	2	0	1	0	1	1	0	0	1	0
W21	KJw18877	Lauraceae	<i>Laurus nobilis</i>	57	27	1	1	4.2	6.5	4	0	1	0	0	1	0	0	1	0
W22	KJw 15904	Calycanthaceae	<i>Calycanthus occidentalis</i>	31	277	1	1	9.8	8.0	5	0	1	0	0	1	1	0	1	0
W23	KJw15904	Calycanthaceae	<i>Calycanthus occidentalis</i>	35	211	1	1	7.3	6.8	6	0	1	0	0	1	1	0	1	0
W24	KJw15905	Calycanthaceae	<i>Chimonanthus fragrans</i>	34	228	1	1	?	6.3	5	0	1	0	0	1	1	0	1	1
W25	KJw15906	Calycanthaceae	<i>Idiospermum australiense</i>	121	9	1	1	?	6.3	1	0	1	0	0	0	0	1	1	1
W26	KJw15907	Calycanthaceae	<i>Idiospermum australiense</i>	113	10	1	1	12.2	8.7	1	0	1	0	0	0	0	1	1	1
W27	KJw17756	Phyllanthaceae	<i>Phyllanthus flexuosus</i>	41	109	1	1	6.1	11.0	4	1	1	0	1	1	1	0	1	0
W28	KJw17757	Phyllanthaceae	<i>Phyllanthus flexuosus</i>	48	28	1	1	4.8	11.5	3	1	1	0	1	1	1	0	1	0
W29	KJw17755	Phyllanthaceae	<i>Phyllanthus ferdinandi</i>	132	14	1	1	4.9	6.3	4	1	1	0	1	1	0	0	1	0
W30	KJw17760	Phyllanthaceae	<i>Phyllanthus nobilis</i>	54	19	1	1	4.9	11.4	3	0	1	0	1	0	0	0	0	0

W31	KJw17752	Phyllanthaceae	<i>Phyllanthus acidus</i>	68	30	1	1	3.7	6.4	5	1	1	0	1	0	0	0	0
W32	KJw17754	Phyllanthaceae	<i>Phyllanthus discordus</i>	89	14	1	1	4.9	9.8	4	1	1	0	1	0	0	0	0
W33	KJw17609	Phyllanthaceae	<i>Bridelia monoica</i>	110	14	1	1	3.9	8.2	4	1	1	0	1	0	0	1	1
W34	KJw17611	Phyllanthaceae	<i>Bridelia montana</i>	105	15	1	1	4.9	4.5	5	1	1	0	1	0	0	1	1
W35	KJw17608	Phyllanthaceae	<i>Bridelia micrantha</i>	124	18	1	1	5.1	7.9	3	1	1	0	1	0	0	1	1
W36	KJw17613	Phyllanthaceae	<i>Bridelia retusa</i>	109	10	1	1	4.4	6.2	3	1	1	0	1	0	0	0	1
W37	KJw17612	Phyllanthaceae	<i>Bridelia ndellensis</i>	107	14	1	1	5.4	3.8	3	1	1	0	1	0	0	0	1
W38	KJw17606	Phyllanthaceae	<i>Bridelia ferruginea</i>	77	10	1	1	4.6	10.2	4	1	1	0	1	0	0	0	1
W39	KJw14586	Annonaceae	<i>Guatteria cestrifolia</i>	184	3	1	1	7.9	2.1	8	1	1	0	0	0	0	0	1
W40	KJw14586	Annonaceae	<i>Guatteria cestrifolia</i>	219	3	1	1	5.8	2.7	8	1	1	0	0	0	0	0	1
W41	KJw14581	Annonaceae	<i>Guatteria amplifolia</i>	77	13	1	1	2.8	3.2	7	1	1	0	0	0	0	0	1
W42	KJw14587	Annonaceae	<i>Guatteria lucens</i>	124	4	1	1	5.2	2.5	6	1	1	0	0	0	0	0	1
W43	KJw14582	Annonaceae	<i>Guatteria boyacana</i>	75	11	1	1	2.7	6.0	5	1	1	0	0	0	0	0	1
W44	KJw21803	Magnoliaceae	<i>Magnolia acuminata</i>	64	98	1	1	11.2	4.6	2	0	0	0	0	1	0	1	0
W45	KJw21816	Magnoliaceae	<i>Magnolia grandiflora</i>	53	110	0	1	?	4.5	4	0	1	0	0	1	0	0	0
W46	KJw21817	Magnoliaceae	<i>Magnolia grandiflora</i>	59	78	0	1	15.1	5.4	4	0	1	0	0	1	0	0	0
W47	KJw21820	Magnoliaceae	<i>Magnolia grandiflora</i>	59	177	0	1	?	6.0	3	0	1	0	0	1	0	0	0
W48	KJw21806	Magnoliaceae	<i>Magnolia acuminata</i>	55	44	1	1	12.3	6.2	2	0	0	0	0	1	0	1	0
W49	KJw21805	Magnoliaceae	<i>Magnolia acuminata</i>	43	219	1	1	4.8	4.0	2	0	0	0	0	1	0	1	0
W50	KJw22557	Myristicaceae	<i>Myristica attenuata</i>	129	5	0	1	7.3	8.0	2	0	1	0	0	0	0	0	1
W51	KJw22557	Myristicaceae	<i>Myristica attenuata</i>	104	10	0	1	?	9.1	1	0	1	0	0	0	0	0	1
W52	KJw22558	Myristicaceae	<i>Myristica castaneifolia</i>	129	60	0	1	7.3	7.4	2	0	1	0	0	0	0	0	1
W53	KJw22559	Myristicaceae	<i>Myristica castaneifolia</i>	123	6	0	1	11.0	11.4	2	0	1	0	0	0	0	0	1
W54	KJw22566	Myristicaceae	<i>Myristica fragrans</i>	52	14	0	1	4.9	9.7	2	0	1	0	0	0	0	0	1
W55	KJw22567	Myristicaceae	<i>Myristica laurina</i>	91	3	0	1	4.9	9.1	1	1	1	0	0	0	0	0	1
W56	KJw14935	Aristolochiaceae	<i>Aristolochia manshuriensis</i>	41	132	1	1	7.3	1.1	24	1	1	0	0	1	1	0	1
W57	KJw14935	Aristolochiaceae	<i>Aristolochia manshuriensis</i>	41	84	1	1	7.3	1.7	30	1	1	0	0	1	1	0	1
W58	KJw16281	Chloranthaceae	<i>Ascarina maheshwarii</i>	60	32	0	1	6.1	3.6	8	1	1	1	0	0	0	0	0
W59	KJw16282	Chloranthaceae	<i>Ascarina philippensis</i>	68	13	0	1	6.1	3.4	6	1	1	1	0	0	0	0	0
W60	KJw19287	Chloranthaceae	<i>Hedyosmum scabrum</i>	85	12	0	1	10.5	2.3	17	1	0	0	0	0	0	0	1
W61	KJw16284	Chloranthaceae	<i>Hedyosmum arborescens</i>	55	36	0	1	4.4	2.4	9	1	0	0	0	0	0	0	1
W62	KJw16283	Chloranthaceae	<i>Hedyosmum arborescens</i>	60	19	0	1	8.2	1.7	7	1	0	0	0	0	0	0	1
W63	KJw16285	Chloranthaceae	<i>Hedyosmum domingense</i>	57	50	0	1	?	2.3	8	1	1	0	1	0	0	0	1
W64	N/A	Austrobaileyaceae	<i>Austrobaileya scandens</i>	119	25	0	1	11.0	?	17	1	1	1	1	0	0	0	1

Table 2
Anatomical characters of the icacinoid/platanoid and phyllanthoid morphospecies used in the Principal Component Analysis. The sources of the data are given on the table. Unknown values denoted by "?".

Number	Kew number	Reference	Age	(1) Vessel diameter (μm)	(2) vessel number per mm^2	(3) perforation plate type (scalariform/ simple)	(4) Vessel distribution (>90% solitary or not)	(5) Intervessel pit diameter (μm)	(6) Ray number per linear mm	(7) Maximum ray width in cells	(8) Maximum ray height (less or greater than 1 mm)	(9) Ray cell composition (homocellular/ heterocellular)	(10) Rays of two distinct sizes (absent/ present)	(11) Septate fibres (absent/ present)	(12) Growth rings (absent/ distinct)	(13) Porosity (diffuse/ ring)	(14) Tyloses (absent/ present)	(15) Paratracheal axial parenchyma (absent/ present)	(16) Apotracheal axial parenchyma (absent/ present)
<i>Icacinoide/platanoid group</i>																			
W65	<i>icacinoxylon citronelloides</i>	Shilkina (1956)	Miocene	57	49	0	0	?	1	23	1	1	?	1	0	0	1	1	1
W66	<i>icacinoxylon pittense</i>	Thayn et al. (1985)	Cretaceous	90	24	0	0	?	3.5	12	1	1	0	0	0	0	1	0	1
W67	<i>icacinoxylon alternipunctata</i>	Wheeler et al. (1987)	Maastrichtian	163	13	0	0	7.5	7	10	1	1	1	1	0	0	0	0	1
W68	<i>icacinoxylon kokubunii</i>	Takahashi and Suzuki (2003)	Turonian	93	7	0	0	6	?	35	1	1	1	0	0	0	0	0	1
W69	<i>icacinoxylon nishidae</i>	Takahashi and Suzuki (2003)	Coniacian–Santonian	93	21	0	1	?	2	17	1	1	1	0	0	0	0	0	1
W70	<i>icacinoxylon species 1</i>	Herendeen (1991b)	Cretaceous	54	18	0	0	?	2	10	?	1	1	0	0	0	0	0	1
W71	<i>icacinoxylon species 2</i>	Herendeen (1991b)	Santonian–Campanian	44	80	0	0	?	?	?	?	1	1	1	0	0	0	0	1
W72	<i>icacinoxylon pecinovense</i>	Oakley and Falcon-Lang (2009)	Cenomanian	52	67	0	0	0	6	8	1	1	1	0	0	0	0	0	1
W73	<i>Plataninium jezoensis</i>	Takahashi and Suzuki (2003)	Cenomanian	83	51	0	1	3	?	30	1	0	0	0	0	0	0	0	1
W74	<i>Plataninium ogasawarae</i>	Takahashi and Suzuki (2003)	Coniacian–Santonian	63	59	0	1	15	?	27	1	0	0	0	0	0	0	0	1
W75	<i>Plataninium platanoides</i>	Page (1968)	Cretaceous	65	?	0	0	?	?	15	1	1	0	0	0	0	0	1	1
W76	<i>Plataninium californicum</i>	Page (1968)	Cretaceous	130	8	0	0	?	?	20	1	1	0	0	0	0	0	1	1
W77	<i>Plataninium decipiens</i>	Brett (1972)	Eocene	80	30	0	0	?	3	18	1	1	0	0	0	0	0	0	1
W78	<i>Plataninium decipiens</i>	Meijer (2000)	Santonian	65	55	0	0	15	?	30	1	1	0	0	1	0	1	1	1
W79	<i>Plataninium decipiens</i>	Poole et al. (2002)	Eocene	81	65	0	0	22	3.5	20	1	1	0	0	0	0	1	?	?
W80	<i>Plataninium brettii</i>	Crawley (1989)	Palaeocene	35	50	0	0	?	3.5	9	1	1	1	0	1	0	1	0	1
W81	<i>Plataninium decipiens</i>	Crawley (1989)	Palaeocene	75	16	0	0	?	1.5	30	1	1	0	0	0	0	0	0	1
W82	<i>Plataninium pierci</i>	Wheeler et al. (1995)	Maastrichtian	48	64	0	0	?	?	25	1	1	0	0	0	0	0	0	1
W83	<i>Plataninium haydani</i>	Wheeler (1991)	Palaeocene	88	59	0	1	0	2.3	22	1	1	1	0	0	0	0	0	1
<i>Phyllanthoid group</i>																			
W84	<i>Paraphyllanthoxylon arizonense</i>	Bailey (1924)	Cretaceous	175	11	1	1	?	4	7	?	1	0	1	0	0	1	1	0
W85	<i>Paraphyllanthoxylon cenomaniana</i>	Takahashi and Suzuki (2003)	Cenomanian	201	11	1	1	13	?	5	1	1	0	1	0	0	1	1	0
W86	<i>Paraphyllanthoxylon obiraense</i>	Takahashi and Suzuki (2003)	Santonian	96	27	1	1	10	?	3	1	1	0	1	0	0	1	1	0
W87	<i>Paraphyllanthoxylon illinoense</i>	Wheeler et al. (1987)	Maastrichtian	118	20	1	1	11	4	6	0	1	1	1	0	0	1	0	0
W88	<i>Paraphyllanthoxylon anazasii</i>	Wheeler et al. (1995)	Maastrichtian	84	25	1	1	9.5	?	3	0	1	0	1	0	0	1	1	0
W89	<i>Paraphyllanthoxylon anazasii</i>	Wheeler and Lehman (2000)	Campanian–Maastrichtian	107	15	1	1	9.5	8.5	3	0	1	0	1	0	0	1	1	0
W90	<i>Paraphyllanthoxylon marylandense</i>	Herendeen (1991a)	Cenomanian	122	21	1	1	6	?	4	0	1	0	1	0	0	1	0	0

W91	<i>Paraphyllanthoxylon cf. marylandense</i>	Meijer (2000)	Santonian	100	37	1	1	8	10.5	4	1	1	0	1	0	0	1	1	1
W92	<i>Paraphyllanthoxylon alabamense</i>	Cahoon (1972)	Cenomanian–Turonian	150	10	1	1	10	?	5	1	1	0	1	0	0	1	1	0
W93	<i>Paraphyllanthoxylon idahoense</i>	Spackman (1948)	Cretaceous	100	?	1	1	11	?	2	?	1	0	1	0	0	1	1	0
W94	<i>Paraphyllanthoxylon utahense</i>	Thayn et al. (1983)	Cretaceous	105	6	1	1	9	?	5	1	1	0	1	0	0	1	1	1
W95	<i>Paraphyllanthoxylon capense</i>	Mädel (1962)	Cretaceous	74	39	1	1	10	7.5	5	1	1	0	1	0	0	1	1	0
W96	<i>Paraphyllanthoxylon marylandense</i>	Oakley and Falcon-Lang (2009)	Cenomanian	132	11	1	1	6	8	3	0	1	0	1	0	0	1	0	0
W97	<i>Paraphyllanthoxylon kobense</i>	Suzuki (1984)	Miocene	120	60	1	1	9	9.5	4	1	1	0	1	0	0	1	1	0
W98	<i>Paraphyllanthoxylon lewisii</i>	Crawley (2001)	Palaeocene	147	11	1	1	11.5	7	6	0	1	0	1	0	0	1	0	0
W99	<i>Paraphyllanthoxylon yvardi</i>	Koeniguer (1967)	Neogene	73	53	1	1	?	7	7	1	1	?	1	0	0	?	1	0
W100	<i>Paraphyllanthoxylon kerienne</i>	Dayal (1967)	Cretaceous–Eocene	98	10	1	1	?	9	4	0	?	?	1	0	0	1	0	0
W101	<i>Paraphyllanthoxylon abbottii</i>	Wheeler (1991)	Palaeocene	188	9	1	1	11	7.5	4	0	1	0	1	0	0	1	1	0
W102	<i>Paraphyllanthoxylon mennegae</i>	Martinez-Cabrera et al. (2006)	Miocene	71	46	1	1	7	7.5	4	1	1	0	1	0	0	0	0	0
W103	<i>Paraphyllanthoxylon coloradensis</i>	Martinez-Cabrera et al. (2006)	Miocene	129	24	1	1	9.5	8.1	3	1	1	0	1	0	0	1	0	0
W104	<i>Paraphyllanthoxylon pfefferi</i>	Mädel (1962)	Neogene	86	30	1	1	8.75	?	5	0	1	?	1	0	0	?	0	0
W105	<i>Paraphyllanthoxylon teldense</i>	Privé (1970)	Oligocene	74	12	1	0	9	6.5	6	1	1	?	1	0	0	0	1	0
W106	<i>Glochidioxylon sahnii</i>	Prakash (1958)	Tertiary	74	37	1	1	?	14	7	1	1	1	1	0	0	1	1	1
W107	<i>Glochidioxylon tertiarum</i>	Ramanujam (1956)	Tertiary	103	23	1	1	?	8.5	4	1	1	0	1	0	0	0	0	1
W108	<i>Paraphyllanthoxylon pseudonobashirashi</i>	Ogura (1932)	Tertiary	140	27	1	1	9.5	6	4	?	?	?	1	0	0	1	1	0
W109	<i>Bridelioxylon cuddalorese</i>	Ramanujam (1956)	Tertiary	59	55	1	1	?	10	3	0	1	0	1	1	0	0	1	1
W110	<i>Bridelioxylon bohemicum</i>	Prakash and Brezina (1969–1970)	Turonian	128	17	1	1	8.5	6.75	3	0	1	0	1	0	0	1	1	1
W111	<i>Bridelioxylon fibrosum</i>	Mädel (1962)	Cretaceous	87	57	1	1	?	13	5	0	1	0	1	0	0	1	1	0

Table 3
Anatomical characters of the Czech specimens of *Icacinoxylon pecinovense* and *Paraphyllanthoxylon marylandense* (after Oakley and Falcon-Lang, 2009). Unknown values denoted by "?". BRSUG denotes Geology Museum, University of Bristol.

Number	Specimen number	(1) Vessel diameter (µm)	(2) Vessel number per mm ²	(3) Perforation plate type (scalariform/simple)	(4) Vessel distribution (>90% solitary or not)	(5) Intervessel pit diameter (µm)	(6) Ray number per linear mm	(7) Maximum ray width in cells	(8) Maximum ray height (less or greater than 1 mm)	(9) Ray cell composition (homocellular/heterocellular)	(10) Rays of two distinct sizes (absent/present)	(11) Septate fibres (absent/present)	(12) Growth rings (absent/distinct)	(13) Porosity (diffuse/ring)	(14) Tyloses (absent/present)	(15) Paratracheal axial parenchyma (absent/present)	(16) Apotracheal axial parenchyma (absent/present)
<i>Icacinoxylon pecinovense</i>																	
W112	BRSUG28792	49	72	0	0	?	?	2	0	1	1	0	0	0	0	0	?
W113	BRSUG28793	69	90	0	0	?	?	8	1	1	1	0	0	0	0	0	?
W114	BRSUG28796	75	71	0	1	?	3.9	4	1	1	1	0	0	0	0	0	1
W115	BRSUG28797	61	59	0	0	?	2.1	3	1	1	1	0	0	0	0	0	1
W116	BRSUG28798	76	100	0	1	6	6.3	5	1	1	1	0	0	0	0	0	1
W117	BRSUG28799	49	82	0	0	9	?	4	1	1	1	0	0	0	0	0	1
W118	BRSUG28800	74	66	0	1	?	?	2	0	1	1	0	0	0	0	0	?
W119	BRSUG28812	51	66	0	0	?	2.4	4	1	1	1	0	0	0	0	0	1
W120	BRSUG28818	25	59	0	1	?	?	5	1	1	1	0	0	0	0	0	1
W121	BRSUG28822	38	50	0	0	5	2.8	1	0	1	1	0	0	0	0	0	?
W122	BRSUG28824	51	41	0	0	7	?	1	0	1	1	0	0	0	0	0	?
W123	BRSUG28826	38	58	0	0	?	4	1	1	1	1	0	0	0	0	0	?
W124	BRSUG28828	23	61	0	0	?	?	3	0	1	1	0	0	0	0	0	?
<i>Paraphyllanthoxylon marylandense</i>																	
W125	BRSUG28790	92	8	1	0	11	5.4	1	0	1	0	0	0	0	?	0	0
W126	BRSUG28791	97	8	1	0	?	?	1	0	1	0	0	0	0	1	0	0
W127	BRSUG28794	164	4	1	0	8	?	3	0	1	0	1	0	0	1	0	0
W128	BRSUG28795	91	18	1	1	11	?	3	0	1	0	1	0	0	1	0	0
W129	BRSUG28801	71	23	1	0	?	3.7	1	0	1	0	1	0	0	?	0	0
W130	BRSUG28802	153	10	1	1	10	?	1	1	1	0	1	0	0	1	0	0
W131	BRSUG28803	117	21	1	1	?	?	3	0	1	0	0	0	0	1	0	0
W132	BRSUG28804	92	14	1	1	?	?	3	0	1	0	1	0	0	1	0	0
W133	BRSUG28805	119	6	1	1	6	?	3	0	1	0	1	0	0	1	0	0
W134	BRSUG28806	97	16	1	0	?	?	3	0	1	0	1	0	0	1	0	0
W135	BRSUG28807	139	15	1	0	?	?	1	1	1	0	?	0	0	1	0	0
W136	BRSUG28808	105	9	1	1	9	3.8	3	0	1	0	1	0	0	1	0	0
W137	BRSUG28809	101	8	1	0	?	6.9	1	0	1	0	1	0	0	0	0	0
W138	BRSUG28810	101	11	1	0	5	7.4	2	0	1	0	0	0	0	1	0	0
W139	BRSUG28811	101	11	1	0	5	5.2	2	0	1	0	1	0	0	1	0	0
W140	BRSUG28813	173	8	1	1	?	5.3	2	0	1	0	1	0	0	1	0	0
W141	BRSUG28814	132	7	1	1	13	5.7	1	1	1	0	1	0	0	1	0	0
W142	BRSUG28815	173	8	1	0	14	3.6	2	0	1	0	0	0	0	1	0	0
W143	BRSUG28816	149	8	1	1	?	?	2	1	1	0	0	0	0	1	0	0
W144	BRSUG28817	218	8	1	1	?	?	1	1	1	0	?	0	0	1	0	0
W145	BRSUG28819	172	11	1	1	3	5.6	1	0	1	0	1	0	0	1	0	0
W146	BRSUG28820	117	31	1	0	8	2.3	2	0	1	0	1	0	0	1	0	0
W147	BRSUG28821	153	9	1	0	?	4.7	1	1	1	0	1	0	0	1	0	0
W148	BRSUG28823	212	11	1	0	?	4.6	3	1	1	0	?	0	0	1	0	0
W149	BRSUG28825	150	3	1	0	?	?	3	1	1	0	?	0	0	1	0	0
W150	BRSUG28827	85	12	1	0	7	7.6	2	0	1	0	1	0	0	0	0	0

This situation has led some palaeobotanists “to despair” and devise an alternative taxonomic system based solely on anatomical properties, without reference to phylogeny (Page, 1979, 1980, 1981). While this morphological emphasis is entirely proper, it does limit the utility of fossil woods for the study of early angiosperm evolution.

In this paper we test the reliability of morphotaxon concepts for some Cretaceous angiosperm woods and propose a new method for rigorously assessing family/order affinity. Specifically we conduct morphometric analysis of Cretaceous icacinoid/platanoid and phyllanthoid woods and compare them with extant structural and phylogenetic analogues, *i.e.*, basal angiosperms whose wood anatomy resembles our fossil material, or who belong to families thought to be allied to extinct morphotaxa based on independent evidence. In doing so, we address the following key questions: Do morphotaxa occupy unique positions in morphospace and to what extent are taxa over-split? Can interspecific differences be distinguished from ontogenetic variability within a morphospecies? Can morphotaxa be reliably assigned to extant families? In addressing that final question, we emphasize that an obvious pitfall of our approach is that extant basal angiosperms are morphologically derived compared with their Cretaceous ancestors. Nevertheless, we argue that our study allows a more rigorous and reliable taxonomy of angiosperm fossil woods.

2. Anatomical character analysis

We analyzed the morphology of extant and fossil angiosperm wood using Principal Component Analysis (PCA). PCA is an ordination technique in which a multivariate dataset – in our case, a set of wood anatomical characters – is projected onto few, usually two, dimensions defined by the axes of maximal variance (Hammer and Harper, 2006). It represents a useful way of analyzing multivariate data and identifying clusters. In recent years, PCA has been successfully applied to systematic studies of extant angiosperm woods with increasing frequency (Hellberg and Carcaillet, 2003; Wickremasinghe and Heart, 2006; Oskolski et al., 2007), and once to studies of fossil wood (Oakley and Falcon-Lang 2009).

In our present study, each wood-type was characterized in terms of a suite of key quantitative and qualitative properties selected from the International Association of Wood Anatomist's hardwood character list (IAWA Hardwood Committee, 1989). As many key fossil woods used in our analysis are preserved as charcoal, the product of wildfire, an effort was made to correct quantitative data for the differential contraction that occurs during charring (as discussed in Oakley and Falcon-Lang, 2009) in order to make direct comparisons between permineralized and charcoaled woods feasible. The contraction factors used for charred specimens were as follows: tangential (33%), radial (25%) and longitudinal (15%). Whilst recognizing that charcoal contraction factors vary according to wood structure and fire temperature (McGinnes et al., 1971), an attempt to correct data is essential if charred and uncharred taxa are to be compared in a consistent manner.

The sixteen characters used in our study were as follows: (1) vessel diameter, (2) vessel number per mm² in transverse section, (3) vessel perforation plate type, scalariform or simple, (4) vessel distribution, less or greater than 90% solitary, (5) intervessel pit diameter, (6) ray number per linear mm in tangential section, (7) maximum ray width in cells, (8) maximum ray height, less or greater than 1 mm, (9) ray cell composition, homocellular or heterocellular, (10) rays of two distinct sizes, absent or present, (11) septate fibres, absent or present, (12) growth rings, absent or present, (13) porosity, diffuse porous or ring porous, (14) tyloses, absent or present, (15) paratracheal axial parenchyma, absent or present, and (16) apotracheal axial parenchyma, absent or present.

The sixteen characters were selected from the range of possible characters in the IAWA hardwood character list because (1) they encompassed most of the key characters used in the taxonomy of extant woods and (2) could be recognized in both extant woods and

fossil woods of moderate to good preservation. Characters such as the vasocentric, aliform and confluent distributions seen in paratracheal parenchyma were not included because, while we recognize that systematic value of these features, characters with multiple intergrading states cannot be easily included in Principal Component Analysis without biasing results. Two other important characters, intervessel pit type and vessel-ray parenchyma pit type, were also excluded because they were not sufficiently preserved in some of the fossil woods in our dataset and therefore did not meet our second criterion. We recognize that the exclusion of these characters limits, to a degree, the ability of our PCA to discriminate morphotaxa.

The sixteen characters selected comprised either quantitative or qualitative states. For quantitative characters, up to 50 measurements were taken, and average values were normalised with respect to variance by dividing by the standard deviation for each character in each data set. As explained further in Oakley and Falcon-Lang (2009), this type of standardization prevents the first principal component from being dominated by characters with large variances and is preferable when dealing with characters with differing units (Hammer and Harper, 2006; Möller et al., 2007). For the qualitative characters, a coding system of 0 and 1 was employed. We only allowed two states for each character, as multiple states would impose an actual quantitative level of difference between the various states. As characters with mixed/no units were being used correlation based PCAs were run on the data. This meant that for each PCA any characters for which no variance was seen (*i.e.* if all individuals had the same coding for a character) were removed from the data used. Data obtained are shown in Tables 1–3 and were analyzed using PAST (PAleontological STatistics) version 1.62 (Hammer et al., 2001).

3. Results

We conducted PCA analysis on three datasets of extant and fossil angiosperm woods. Our aims were (1) to test whether our 16-character PCA approach was an adequate tool for assessing wood taxonomy, (2) to test the general validity of fossil morphotaxon concepts, (3) to examine intra-specific variation in fossil morphotaxa and consider its systematic implications, and (4) to rigorously assess botanical affinities of fossil morphotaxa through comparison with modern analogues. For each dataset, PCAs were also run with various subsets of the data to check that relationships were stable. These analyses demonstrated that large-scale patterns were highly stable although the relationship of individual taxa in morphospace proved to be somewhat variable depending on which subset of the dataset was used. To improve clarity and cross-referencing in the following report, every record of modern and fossil wood analysed was assigned a unique identification number (W1–150).

3.1. Analysis of modern woods

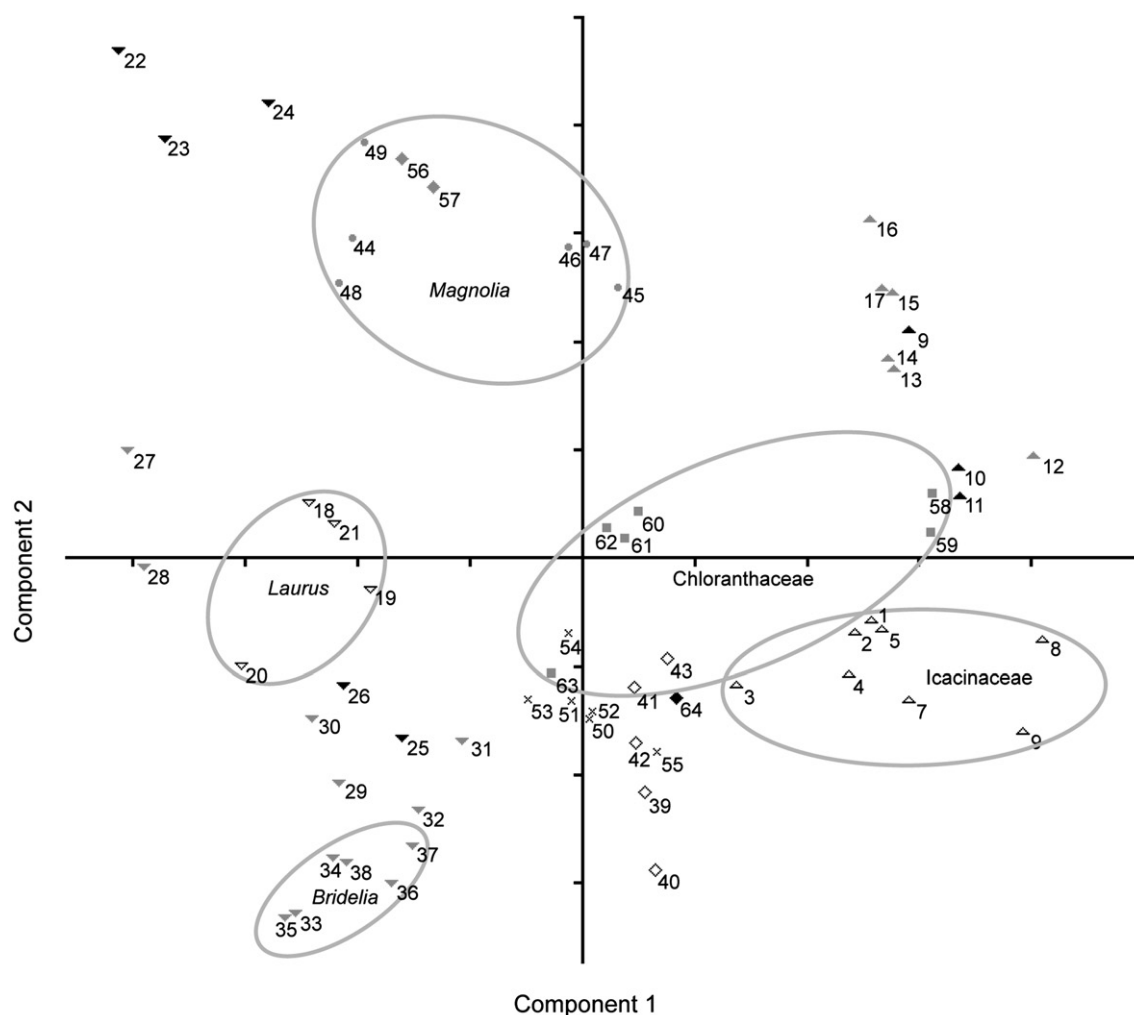
In the first part of our study, we conducted morphometric analysis of several extant structural and/or phylogenetic analogues for our mid-Cretaceous fossil woods (W1–64). The modern woods, comprising three groups, were studied in the collections of the Jodrell Laboratory, Royal Botanic Gardens, Kew, except for the *Austrobaileya* specimen. Mature wood of this lone genus was not available in the Kew collection so information was obtained from Carlquist (2001a). The first group (W1–17) comprised analogues for the icacinoid/platanoid fossil group and included members of the Icacinaceae (*Apodytes*, *Cassinopsis*, *Emmotum*), Pennantiaceae (*Pennantia*), and Platanaceae (*Platanus*). The second group (W18–38) comprised analogues for the phyllanthoid fossil group and included members of the Calycanthaceae (*Calycanthus*, *Chimonanthus*, *Idiospermum*), Lauraceae (*Laurus*), and Phyllanthaceae (*Bridelia*, *Phyllanthus*). The third group (W39–64) comprised woody angiosperms with vessels near the base of the phylogenetic tree (Soltis et al., 2005), which were not used in the other groups. These included *Austrobaileya*, and members of the Annonaceae (*Gutteria*),

Aristolochiaceae (*Aristolochia*), Chloranthaceae (*Ascarina*, *Heydyosmum*), Magnoliaceae (*Magnolia*), and Myristicaceae (*Myristica*). Despite this large dataset, we recognize that our census is far from comprehensive with many potentially important taxa having been omitted – a limitation imposed by time constraints and the availability of specimens in the Jodrell collection. Nevertheless, the selected taxa comprise a wide cross-section of trees that share similarities with our Cretaceous woods.

Analysis of all modern wood data (Fig. 1) tends to support the use of our 16-character PCA as a systematic tool because multiple occurrences of the same species and genera plot very closely together in morphospace. For example, at the generic level, the six occurrences of *Magnolia* (W44–49) cluster together and within that group the three occurrences of *Magnolia grandiflora* form a particularly tight cluster (W45–47). Similarly, the six different species of *Bridelia* (W33–38) also cluster. Even at the family level, some groups such as

the Icacinaceae (W1–8) show morphological coherence as indicated by the loose cluster formed by *Apodytes*, *Cassinopsis*, and *Emmotum*. At a still higher taxonomic level, the Lauraceae (W18–21) and Magnoliaceae (W44–49), related within the subclass Magnoliidae, also lie in the vicinity of each other. However, within other families and family-groups, morphological divergence is somewhat greater, e.g. within the Calycanthaceae (W22–26), or the relationship of the Annonaceae (W39–43) to other magnoliids. Nevertheless, overall this study shows that PCA has the clear potential to correctly group specimens into species, genera, and to a more limited extent, families and family-groups.

However, it is worth noting that intrataxon variability caused by ontogeny creates certain problems for this kind of analysis. For example, two *Phyllanthus* specimens (W27–28) comprise juvenile wood found within twigs and plot some distance from the other specimens of this



Key to all figures

Symbol	Family/genus/species	Numbers	×	Myristicaceae	W50-W55
△	Icacinaceae	W1-W8	◆	Aristolochiaceae	W56-W57
▲	Pennantiaceae	W9-W11	■	Chloranthaceae	W58-W63
▲	Platanaceae	W12-W17	◆	Austrobaileyaceae	W64
▽	Lauraceae	W18-W21	●	<i>Icacinoxylon</i> sp.	W65-W72
▽	Calycanthaceae	W22-W26	+	<i>Plataninum</i> sp.	W73-W83
▽	Phyllanthaceae	W27-W38	■	Phyllanthoid sp.	W84-W111
◇	Annonaceae	W39-W43	○	<i>Icacinoxylon pecinovense</i>	W112-W124
●	Magnoliaceae	W44-W49	□	<i>Paraphyllanthoxylon marylandense</i>	W125-W150

Fig. 1. 16-character Principal Component Analysis of all modern woods, representing 39.1% of the original variance of the dataset (see Table 1 for dataset).

genus that comprise mature wood (W29–32). This suggests that ontogenetic variation can disrupt PCA results but is insufficient to obscure systematic associations within the taxa examined in this study.

3.2. Analysis of fossil morphotaxon concepts

In the second part of our study, we undertook morphometric analysis of all morphogenera found in mid-Cretaceous (Albian–Turonian) strata, as well as Tertiary occurrences of the same morphogenera, to assess the validity of these morphotaxa. As noted in the introduction, selected morphotaxa comprised two groups, these being icacinoid/platanoid morphospecies of *Icacinoxylon* ($n=8$) and *Plataninium* ($n=11$) and phyllanthoid morphospecies of *Paraphyllanthoxylon* ($n=23$), *Bridelioxylon* ($n=3$) and *Glochidioxylon* ($n=2$). Anatomical data for each morphospecies were acquired from published descriptions, photographic plates, and information available on the Inside Wood Database rather than re-examination of type material. Although the latter approach would have been preferable, it proved unfeasible due to the fact that type specimens are scattered through the world's museums, and some have been lost.

PCA shows that icacinoid/platanoid and phyllanthoid woods are clearly distinguished in morphospace (Fig. 2), primarily along the x -axis (Principal Component 1). The loadings for this component show that it is not dominated by any one character but comprises several characters in roughly equal proportions, especially ray width, perforation plate type, occurrence of septate fibres, vessel distribution and occurrence of apotracheal parenchyma. The difference between the icacinoid/platanoid and phyllanthoid types is confirmed by an Analysis of Similarity (ANOSIM) test using the Jaccard coefficient as the distance metric. ANOSIM compares within-group and between-group differences and assigns an R -value, which ranges from 0 (complete similarity) to 1 (complete dissimilarity) when all available data are included in the analysis. Comparison of the two wood types produces an R -value of 0.931 indicating a high level of dissimilarity.

However, at the morphogeneric level, discrimination is much more difficult. Within icacinoid/platanoid group, the two morphogenera of *Icacinoxylon* and *Plataninium* strongly intergrade, and have an ANOSIM R -value of 0.171, suggesting a low level of dissimilarity. According to Wheeler et al. (1995), the key difference between woods of *Icacinoxylon* (W65–72) and *Plataninium* (W73–83) is the presence

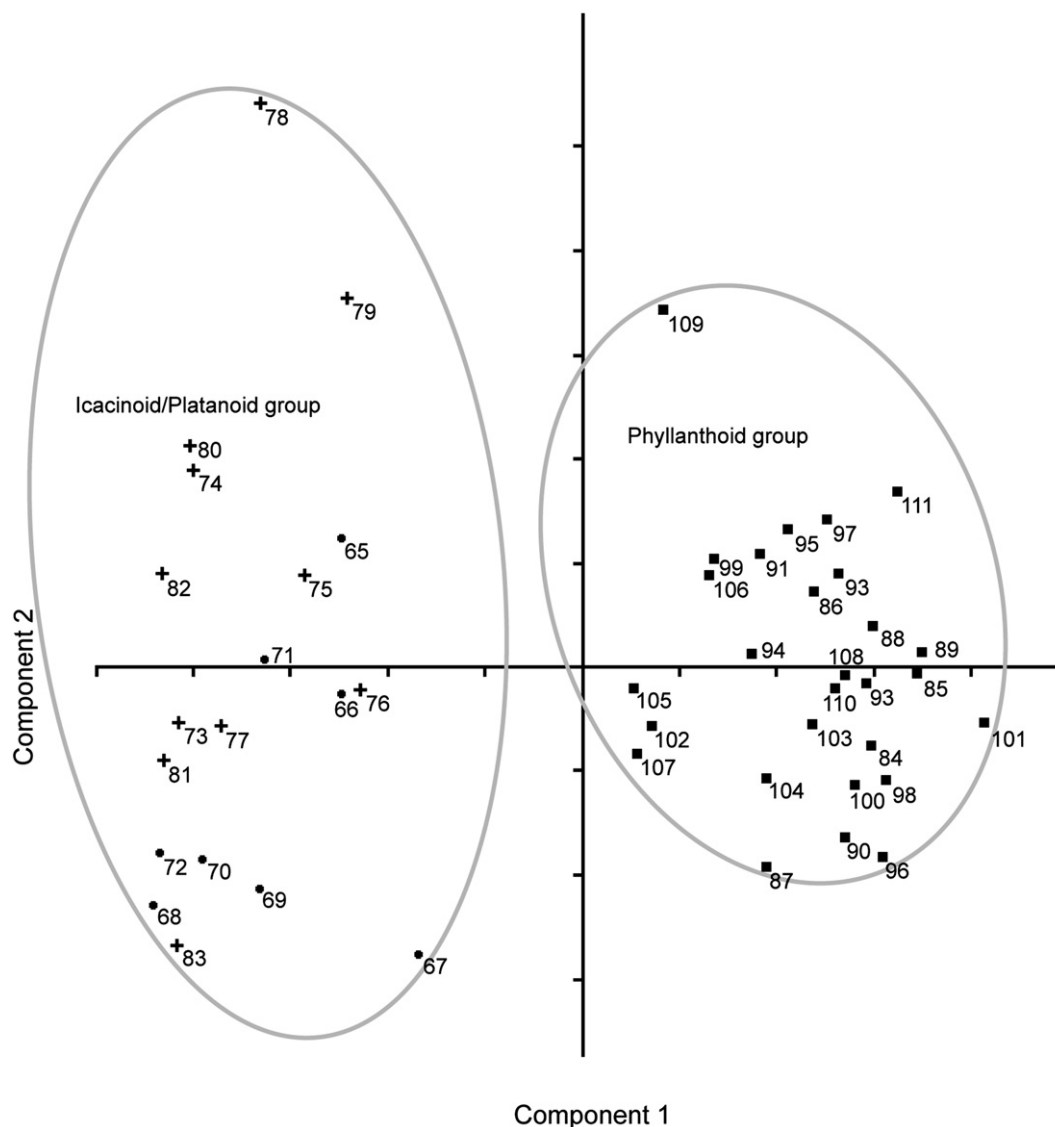


Fig. 2. 15-character Principal Component Analysis of fossil species of icacinoid/platanoid and phyllanthoid wood, representing 49.7% of the original variance of the dataset (see Table 2 for dataset).

of heterocellular rays in the former and homocellular rays in the later. However, most workers have not used this criterion, in some cases assigning specimens to *Plataninium* when heterocellular rays are present. A fairly high level of intergradation is also seen between the three phyllanthoid morphogenera, which show an average ANOSIM *R*-value of 0.316. It is unclear from this analysis whether *Paraphyllanthoxylon*, *Bridelioxylon* and *Glochidioxylon* warrant separate morphogeneric status at all based of this analysis.

Where multiple occurrences of the same morphospecies are known, the reliability of these concepts can also be evaluated. For example, there are four occurrences of *Plataninium decipiens* Brett in our dataset (Brett, 1972; Crawley, 1989; Meijer, 2000; Poole et al., 2002). PCA shows that these four occurrences do not cluster (Fig. 2). Although Crawley's (1989) occurrence (W81) lies close to Brett's (1972) type specimen (W77), the remaining occurrences plot a considerable distance away. The distal location of Poole et al.'s (2002) occurrence (W79) probably reflects that this was an ontogenetically juvenile specimen, but the even more distal location of Meijer's (2000) occurrence (W78) may simply imply incorrect assignment.

In a second example, we note that there are three occurrences of *Paraphyllanthoxylon marylandense* Herendeen (Herendeen, 1991a,b; Meijer, 2000; Oakley and Falcon-Lang, 2009) in our dataset. Again, these occurrences do not cluster on a PCA of all morphospecies (Fig. 2). Although Oakley and Falcon-Lang's (2009) occurrence (W96) plots near to Herendeen's (1991a,b) type specimen (W90), Meijer's

(2000) occurrence (W91) is a distal outlier from the type specimen (W90), perhaps again implying incorrect assignment. In a third example, the two occurrences of *Paraphyllanthoxylon anasasii* (W88 and W89) plot close together, as nearest neighbours (Fig. 2).

3.3. Assessment of intra-specific variability

In the third part of our study we investigated the intra-specific variability in fossil wood anatomy and its implications for the validity of morphospecies. Although ontogeny and environmental factors may result in a significant amount of intra-specific variability (Panshin and DeZeeuw, 1980; Carlquist, 2001b), this is rarely taken into account in studies of fossil wood systematics. To evaluate the significance of this issue, we compared the 8 occurrences of *Icacinoxylon* morphospecies (W65–72) with 13 specimens of *Icacinoxylon pecinovense* (W112–124) from the Cenomanian of the Czech Republic based on data published in Oakley and Falcon-Lang (2009). We also compared the 23 occurrences of *Paraphyllanthoxylon* morphospecies (W84–105 + 108) with 26 specimens of *Paraphyllanthoxylon marylandense* (W125–150) from the same Czech sites (Oakley and Falcon-Lang 2009).

PCA of the icacinoid dataset partly validates the *Icacinoxylon pecinovense* concept (Fig. 3). The 13 specimens of *I. pecinovense* (W112–124) form a loose cluster adjacent to the point that represents the centroid for that morphospecies (W72) and are weakly dissimilar from other morphospecies (W65–71) when intrataxon variability is

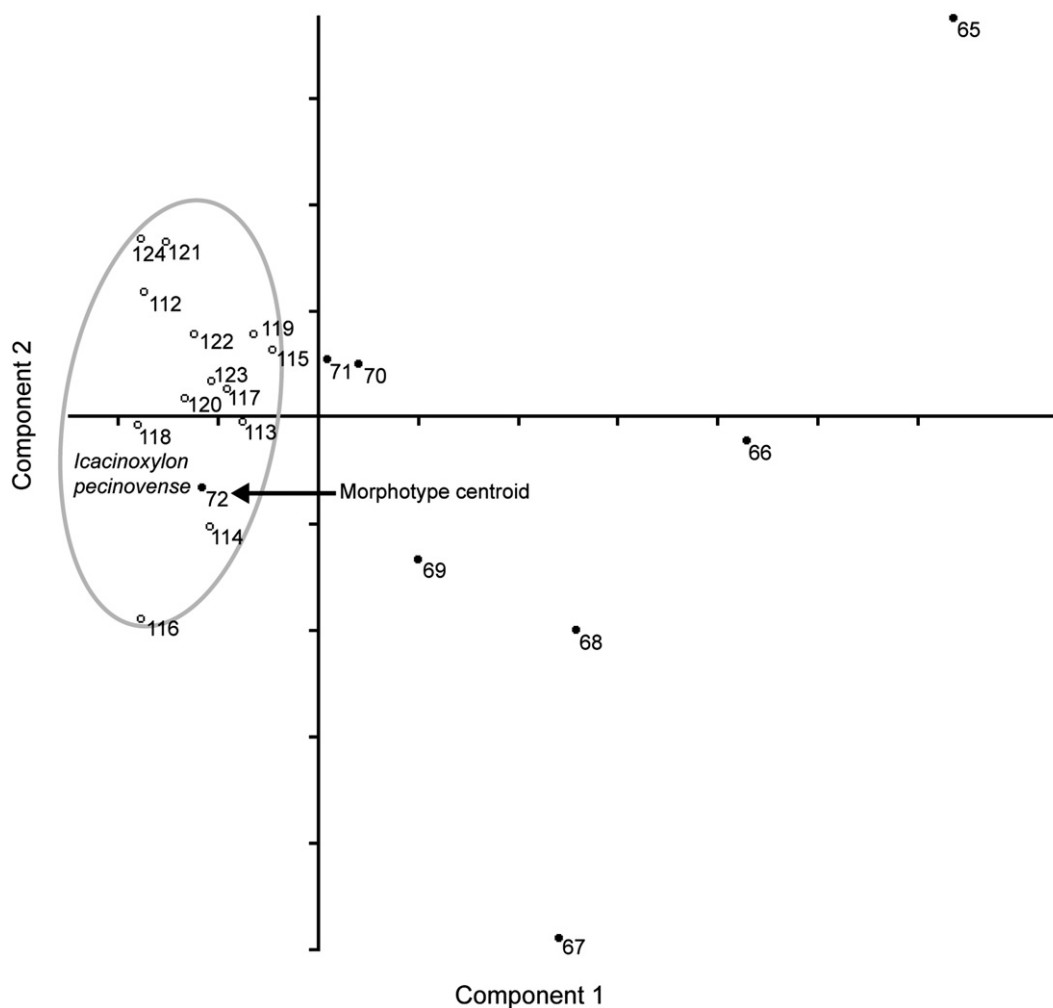


Fig. 3. 11-character Principal Component Analysis of *Icacinoxylon* morphospecies and Czech specimens of *Icacinoxylon pecinovense* (Oakley and Falcon-Lang, 2009) representing 45% of the original variance of the dataset (see Tables 2 and 3 for datasets).

taken into account. A PCA of the phyllanthoid dataset also, in part, validates the *Paraphyllanthoxylon marylandense* concept (Fig. 4). The 26 specimens of *P. marylandense* (W125–150) comprise a loose cluster adjacent to the point that represents the centroid for that occurrence (W96) and the centroid for the type specimen (W90), but adjacent to other morphospecies in the group. As already noted Meijer's (2000) occurrence (W91) plots as a distal outlier to the rest of the morphospecies. Discarding this anomalous record, an R -value of 0.372 indicates that *P. marylandense* is weakly dissimilar from other species in this morphogenus when intrataxon variability is taken into account.

However, there are good reasons to be concerned about the distinctiveness of some of these morphospecies. The size of the cluster formed by specimens of the two morphospecies studied represents the intra-specific variability. If similar levels of variation occur within all morphospecies then this would result in a high level of intergradation of types. At the very least, the close proximity of morphospecies to each other in the PCA plots implies that morphospecies have been over-split. This is especially true for the phyllanthoid material, whose morphospecies show a slightly clumped distribution in morphospace (Fig. 4). The overall coherence of these clumps is maintained even when phyllanthoid morphospecies are plotted alone (W84–111). Whether each of these clumps represents a group of

synonymous morphospecies is beyond the scope of this paper and would necessitate examination of type specimens, raising a systematic hypothesis to be tested in the future.

3.4. Assessment of botanical affinity of fossil woods

In the fourth part of our study, we compared our modern wood dataset with the icacinoid/platanoid and phyllanthoid fossil wood datasets to rigorously assess the family-affinity of these fossil morphotaxa. A PCA of icacinoid/platanoid fossil woods (W65–83) and modern analogues (W1–17) shows that the Icacinaceae forms a tight cluster within the very broad area occupied by the *Icacinoxylon*; however, there is no actual intergradation of these taxa. *Plataninium* occupies an area adjacent to the Platanaceae (Fig. 5); however again, the correspondence of these two groups is weak. Therefore, although *Plataninium* has previously been assigned to the Platanaceae and *Icacinoxylon* to the Icacinaceae/Platanaceae (Shilkina, 1956; Page, 1968; Brett, 1972; Poole et al., 2002; Oakley and Falcon-Lang, 2009) we consider this to be highly uncertain based on these analyses.

When a broader analysis is run, comparing the icacinoid/platanoid species to all modern woods used in this analysis, including many representatives of primitive angiosperms (W1–83), the *Icacinoxylon*

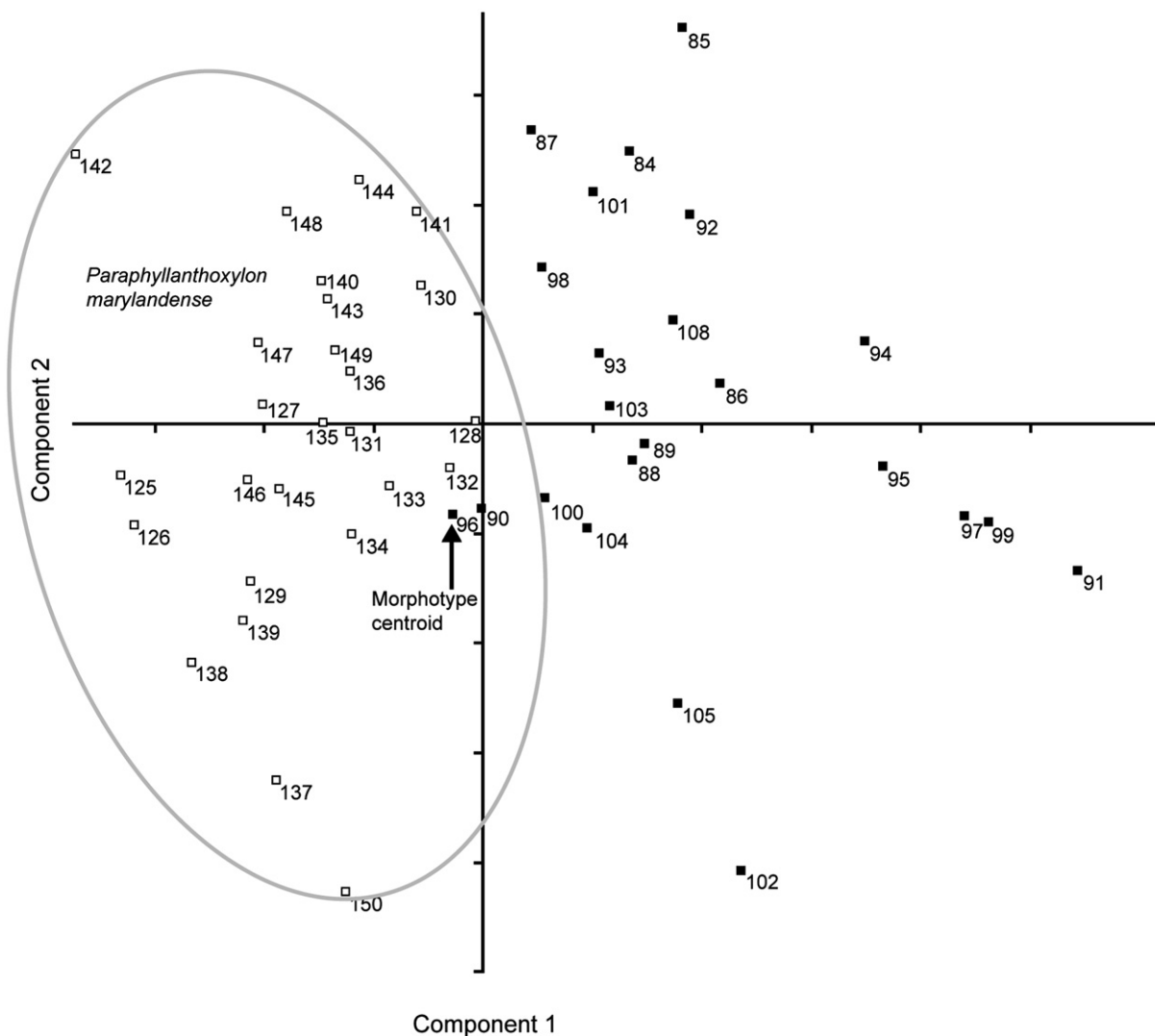


Fig. 4. 12-character Principal Component Analysis of *Paraphyllanthoxylon* morphospecies and Czech specimens of *Paraphyllanthoxylon marylandense* (Oakley and Falcon-Lang, 2009) representing 39.6% of the original variance of the dataset (see Tables 2 and 3 for dataset).

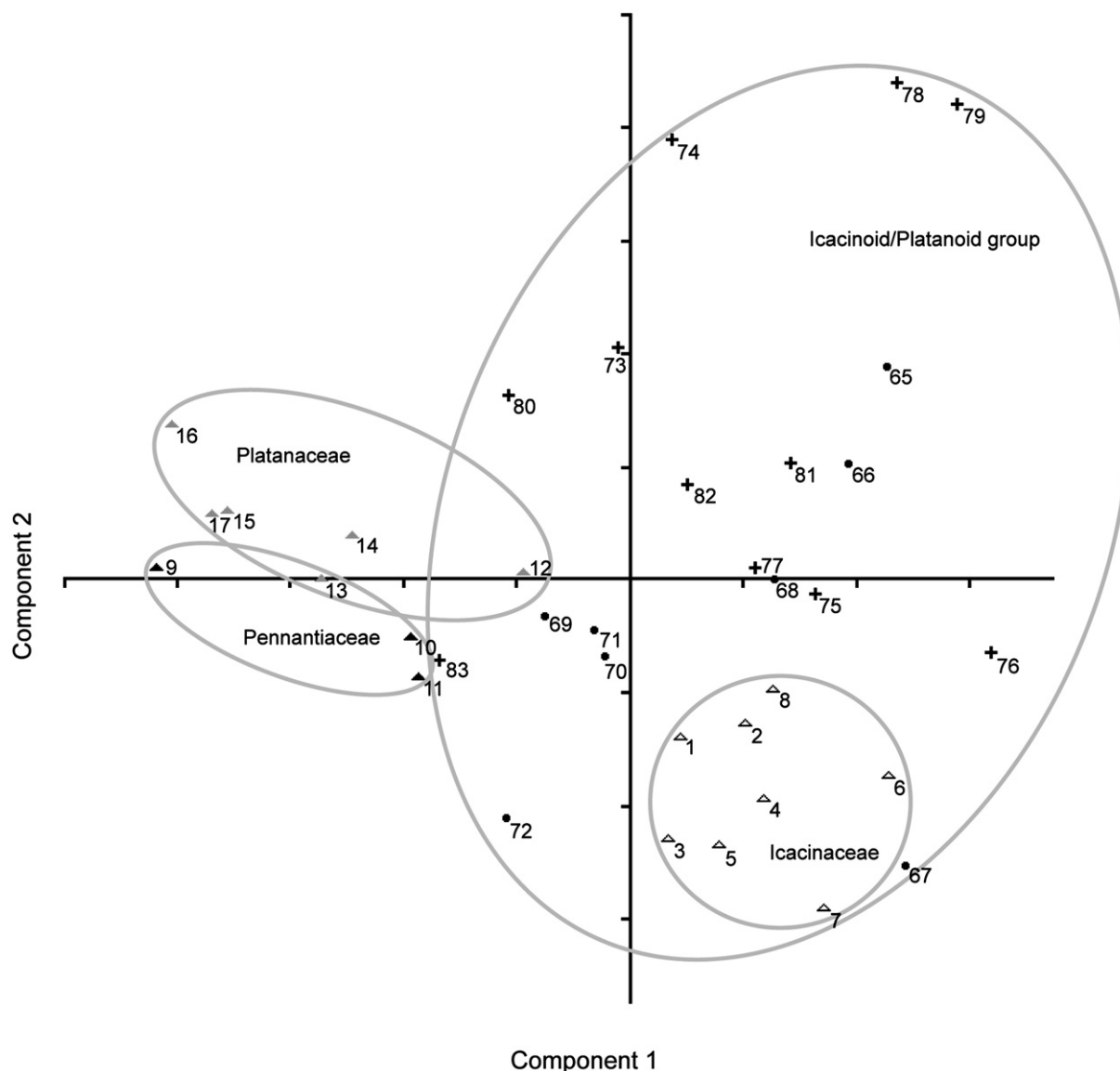


Fig. 5. 12-character Principal Component Analysis of icacinoid/platanoid morphospecies and extant analogues representing 39.5% of the original variance of the dataset (see Tables 1 and 2 for dataset).

and *Plataninium* morphospecies form a loose intergrading cluster (Fig. 6) and show correspondence with basal angiosperms across several major clades. As in the other analysis, *Icacinoxylon* records are scattered around the periphery of a tight cluster formed by the Icacinaceae. Modern representatives of the Chloranthaceae partially intergrade with *Icacinoxylon* while some members of the Annonaceae and Pennantiaceae comprise adjacent groups. The results of our analysis are therefore inconclusive implying some association of icacinoid woods with basal groups such as the Chloranthaceae and Annonaceae but also supporting an affinity with more derived members of the Icacinaceae and Pennantiaceae. However, we stress that members of the Cunoniaceae, Dilleniaceae, and Monimiaceae were not analyzed in this study and represent other possible candidates for family-affinity. With regards to the *Plataninium* morphospecies, modern representatives of the Platanaceae cluster very closely with this group, while the Pennantiaceae, Icacinaceae, and Chloranthaceae are adjacent groups. This supports a close association of *Plataninium* with the Platanaceae among the taxa used in this study.

A PCA of phyllanthoid fossil woods (W84–111) and modern analogues shows that some outliers of *Paraphyllanthoxylon* partially intergrades with members of the Phyllanthaceae (*Bridelia*, *Phyllanthus*;

W27–38) lending some limited support to Bailey's (1924) original assertion regarding affinity (Fig. 7); however correspondence is very weak. In contrast, members of the Lauraceae (W18–21) and Calycanthaceae (W22–26) plot as distinct groups, with the Lauraceae overlapping slightly with the periphery of the *Paraphyllanthoxylon* cluster. It is perhaps surprising that there is not a closer association seen here, given that some *Paraphyllanthoxylon* have been assigned to the Lauraceae based on attachment to inflorescences (Herendeen 1991a) although we stress that only one genus (*Laurus*) was analyzed in our study. Overall this analysis demonstrates that *Paraphyllanthoxylon* is mostly distinct from proposed structural and/or phylogenetic analogues.

When the phyllanthoid morphospecies (W84–111) are compared to all modern woods in our dataset (W1–64) predominant clustering with the Phyllanthaceae becomes more prominent (W27–38), but in this analysis *Idiospermum* samples (W25–26) are included within the group, while *Laurus* and *Myristica* (W50–55) form clusters that overlap with the phyllanthoid material (Fig. 8). *Idiospermum* is one of the most basal members of the Laurales while *Myristica* is one of the most basal members of the Magnoliales. Molecular studies indicate that the Laurales and Magnoliales form a distinct clade within the basal magnoliids (Soltis et al., 2005). The correspondence of

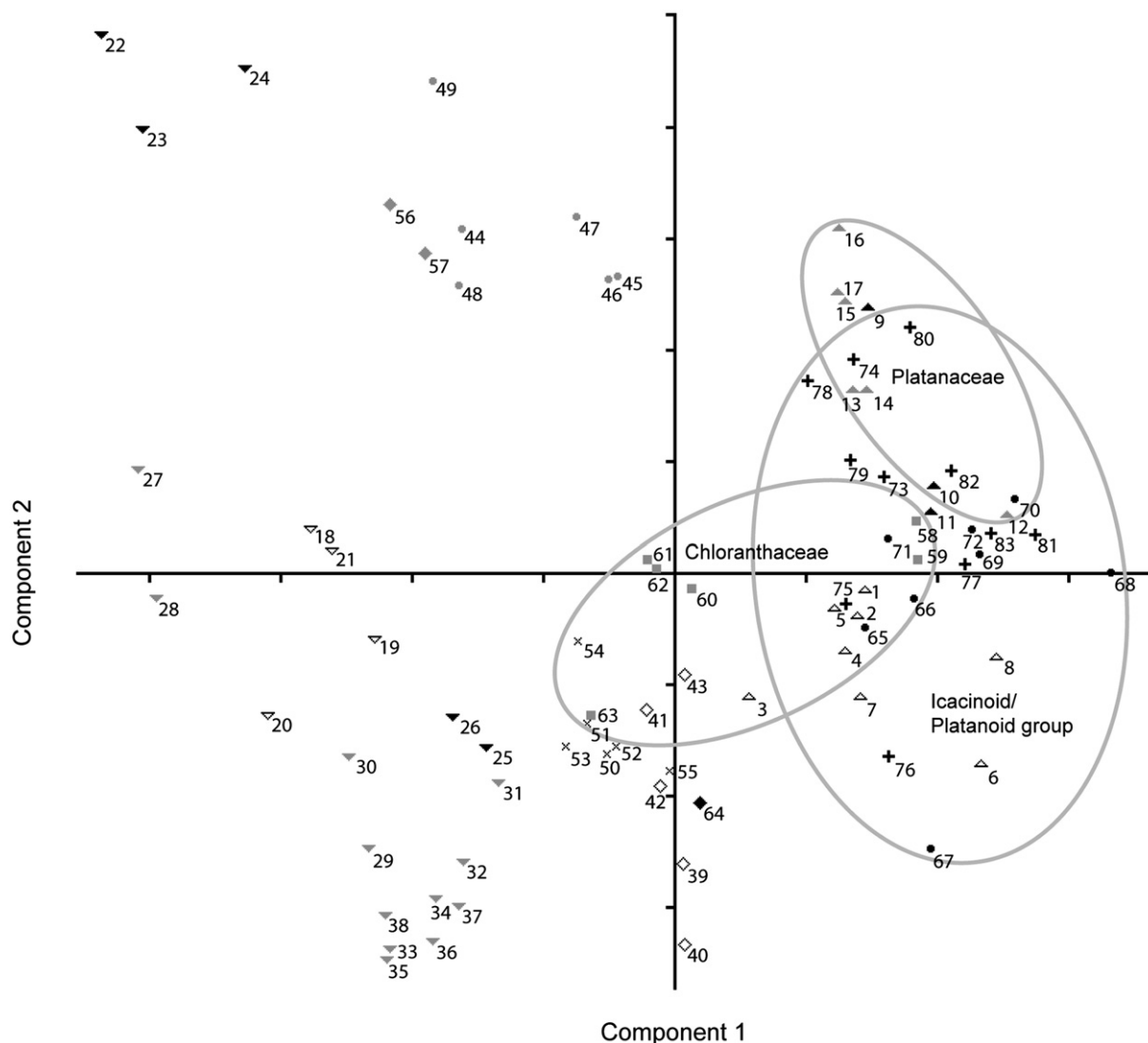


Fig. 6. 16-character Principal Component Analysis of icacinoid/platanoid morphospecies and all extant woods representing 39.4% of the original variance of the dataset (see Tables 1 and 2 for dataset).

phyllanthoid morphospecies with these extant taxa implies a position on the Laurales–Magnoliales stem rather than an association with the more derived Phyllanthaceae or Lauraceae. However, again we caution that this conclusion is based on a limited dataset of taxa.

4. Discussion

In this paper, we have investigated various aspects of fossil angiosperm wood systematics using Principal Component Analysis (PCA). The findings demonstrate the distinctiveness of certain basic divisions of morphotypes but raise questions about the morphological uniqueness of some morphogenera and morphospecies. This in turn implies high levels of synonymy in some taxa. The difficulty of segregating fossil material into morphospecies is compounded by intra-specific variability, which inevitably leads to significant intergradation between one taxon and its neighbours in morphospace.

Whilst our study reveals a consistent taxonomy in some morphospecies, in other cases, this is lacking. For example, two separately reported occurrences of *Paraphyllanthoxylon anzasii* (W88 and W89) are morphologically identical (Wheeler et al., 1995; Wheeler and Lehman, 2000). In contrast, specimens of *Paraphyllanthoxylon marylandense* reported by Meijer (2000) are significantly different from the type material with which it is compared. We therefore suggest our

PCA approach may be a useful guide for assessing taxonomic consistency in the literature and highlighting taxa that may be incorrectly assigned. That said, we do not propose that taxonomic revisions be undertaken based on this kind of analysis alone, but only after direct re-examination of the original fossils.

In order to avoid incorrect taxonomy in the future we make the following recommendations. First, taxa should not be based on a single specimen wherever possible. The degree of intra-specific variability seen in our material suggests that a minimum of 5–10 specimens is needed to capture morphological variability. Second, Principal Component Analysis, or some other method of ordination, should be applied to examine the distribution of specimens in morphospace and their relationship to pre-existing taxa. This will allow the uniqueness of material to be assessed and highlight potential morphospecies with which it needs to be compared. However, we stress the importance of examining PCAs of various subsets of the data to ascertain which patterns are stable and which are plastic. We also highlight the problem caused by juvenile material, which commonly plots away from the mature population and argue that ontogeny must be taken into account in systematic studies.

Our PCA also provides a more rigorous way of assessing the family/order affinity of certain fossil morphospecies. As their names suggest, *Plataninum*, *Icacinoxylon*, and *Paraphyllanthoxylon* were originally

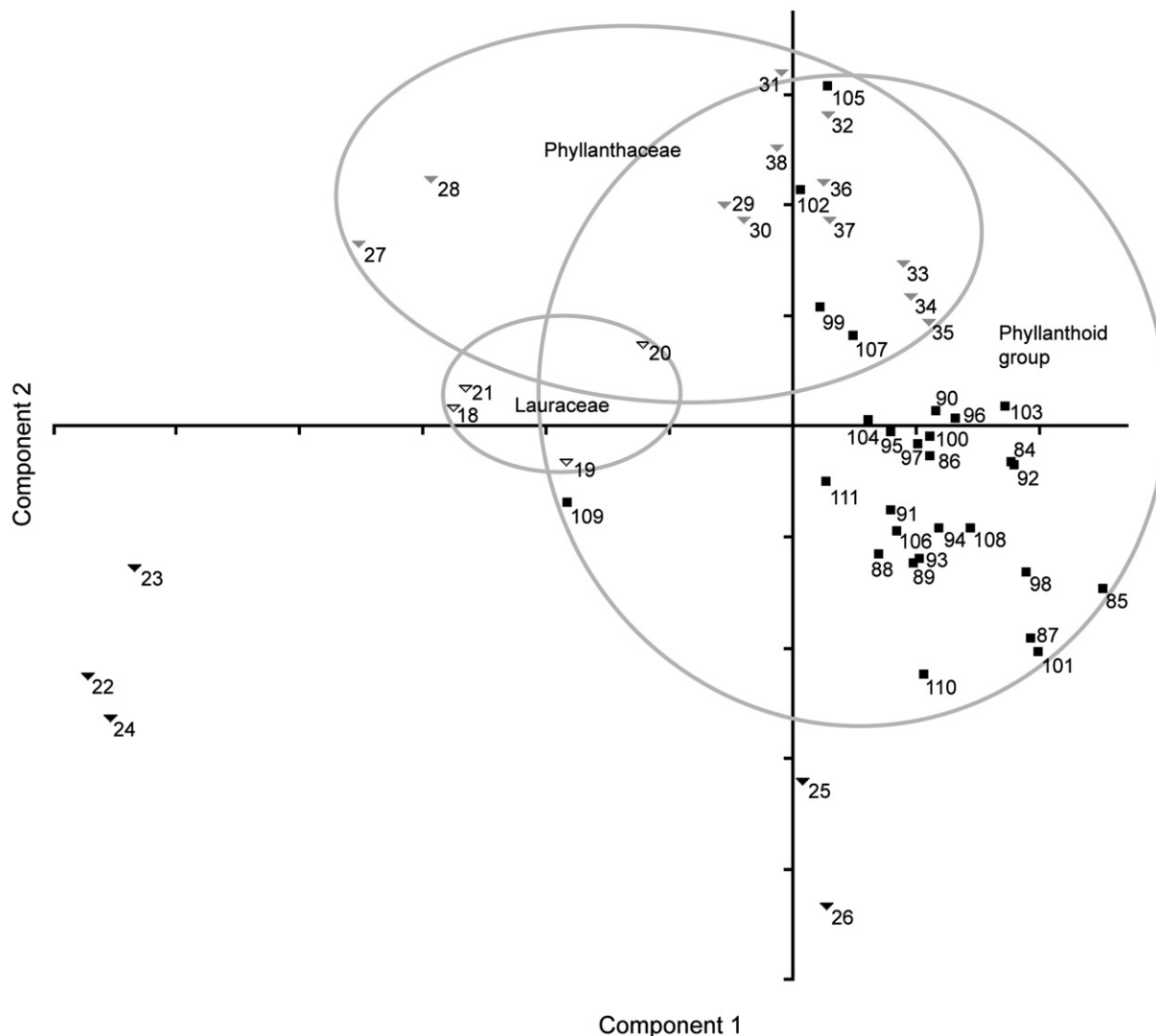


Fig. 7. 14-character Principal Component Analysis of phyllanthoid morphospecies and modern analogues representing 40.2% of the original variance of the dataset (see Tables 1 and 2 for dataset).

conceived as belonging to the Platanaceae, Icacinaceae, and Phyllanthaceae respectively. While our findings do show some correspondence between the fossil morphotaxa and these extant families, it also highlights several basal angiosperm groups that bear closer similarity. For example, *Paraphyllanthoxylon* shares a character suite with the stem of the Laurales–Magnoliales clade while *Icacinoxylon* and *Plataninium* are not only comparable to the Icacinaceae and Platanaceae respectively, but also share similarities with basal groups such as the Chloranthaceae. However, again we caution that these conclusions are based on a limited dataset of taxa. A further obvious pitfall is, of course, that even basal angiosperms are morphologically derived compared with their Cretaceous ancestors. Hence this kind of approach can only hint at relationships rather than unequivocally identify affinity.

5. Conclusions

We show that a Principal Component Analysis has the capability to cluster specimens of modern angiosperm wood into natural groups at the level of species, genera, and to a more limited extent, family.

Application of this technique to some fossil woods of icacinoid/platanoid and phyllanthoid types confirms these are distinctive groups but raised questions about the robustness of some morphogeneric and morphospecific concepts contained therein.

The robustness of morphospecific concepts is further questioned when intra-specific variability is analyzed, demonstrating that morphospecies represent large clouds in morphospace that finely intergrade with neighbouring morphospecies.

Analysis of modern and fossil woods allows rigorous assessment of the botanical affinity of fossil woods. Results suggest that the icacinoid/platanoid type is closest to modern Icacinaceae and Platanaceae, respectively, or the Chloranthaceae, while the phyllanthoid type is associated with Laurales–Magnoliales stem among the selected taxa used in our study. However, we note that analysis of a much larger dataset of modern woods is required to confirm these conclusions.

Acknowledgements

Dan Oakley thanks Paula Rudall (Royal Botanic Gardens, Kew) for generous access to equipment and resources in the Jodrell Laboratory. He also thanks Kasia Ziemska (RBGK) for help with slide preparation and Ian MacLachlan (RBGK) for discussions about methodology. Howard Falcon-Lang gratefully acknowledges a Leverhulme Early Career Fellowship held at the University of Bristol and a NERC Advanced Fellowship (NE/F014120/2) at Royal Holloway, University of London. We thank Elisabeth Wheeler and an anonymous reviewer for an exceptionally useful feedback on an earlier draft of this manuscript.

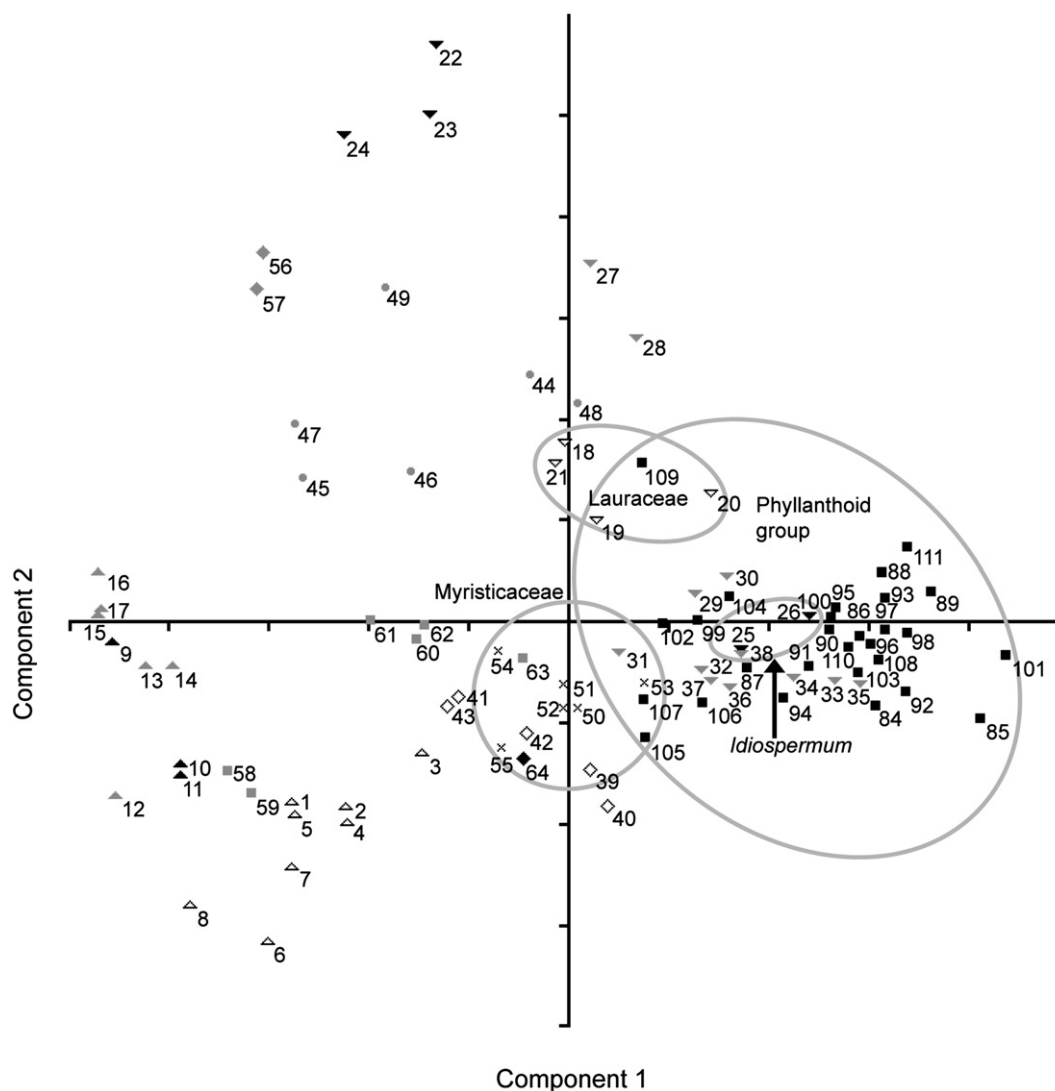


Fig. 8. 16-character Principal Component Analysis of phyllanthoid morphospecies and all extant woods representing 41.5% of the original variance of the dataset (see Tables 1 and 2 for dataset).

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