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Recent progress in the phylogenetics and classification of Araceae

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9.1 Introduction

The aim of this paper is to review progress in phylogenetic research of Araceae during the period since publication of the first major molecular study by French et al. (1995). This, the first cladogram of the whole family inferred from DNA molecular data (Fig 9.1), resulting from research by J.C. French, M. Chung and Y. Hur, was based on chloroplast restriction site data (RFLPs or restriction fragment length polymorphisms). Their paper was highly significant and marked the beginning of the modern era of molecular phylogenetics of Araceae, nowadays based on DNA sequence data (e.g. Cabrera et al., 2008; Cusimano et al., 2011; Nauheimer et al., 2012b). It was innovative for Araceae in other ways as well, being the first family-scale cladistic analysis using computer algorithms and the first published cladogram for the family as a whole using genera as the ultimate operational taxonomic units (OTUs).

No attempt has been made in the present chapter to discuss in detail the work of the previous 25 years during which many significant advances in systematic knowledge of the family were made, both in morphological taxonomy, but also in other fields such as cytology, palynology, phytochemistry, anatomy, fossil aroids, pollination biology and seedling morphology. Reviews of this literature have been provided by various authors, including Petersen (1989), Grayum (1990),

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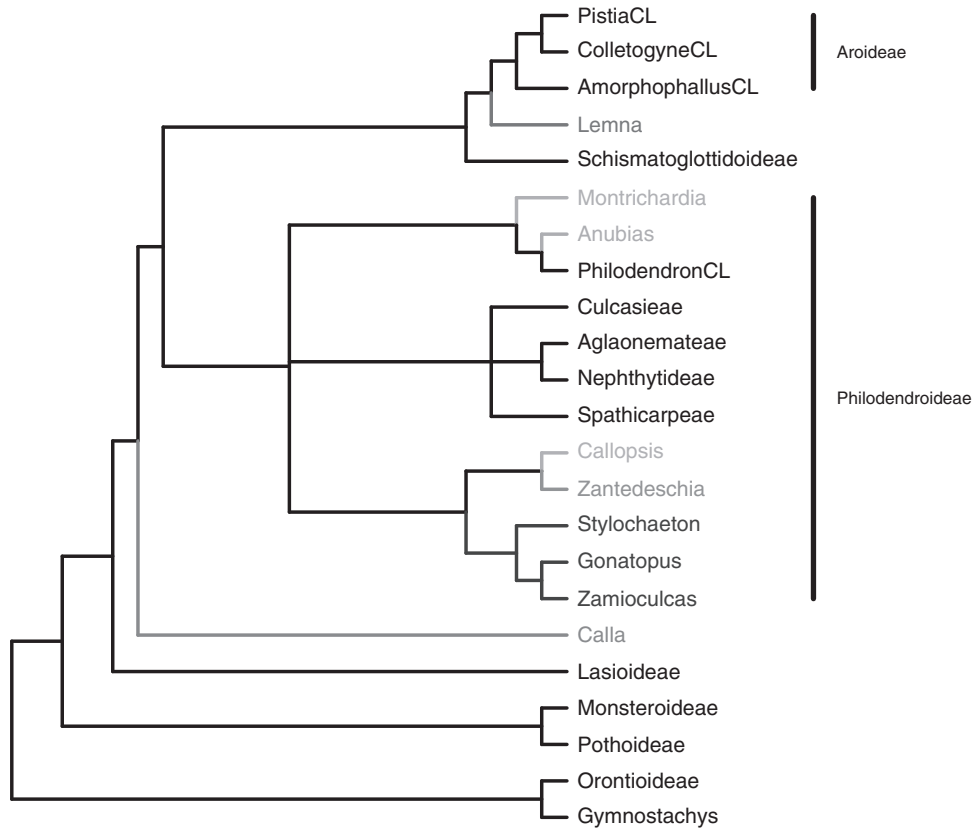


Fig 9.1 Cladogram simplified from French et al. (1995), showing circumscription of subfamilies Aroideae and Philodendroideae as circumscribed by Keating (2003). See Table 9.1 for details of circumscription of suprageneric taxon names. Names ending in ‘-CL’ are abbreviations for ‘... clade’, e.g. *Pistia*CL \equiv *Pistia* clade. Coloured clades show contrasting positions in Fig 9.2. Colour version to be found in colour plate section.

Mayo et al. (1997) and Keating (2003), and Nicolson (1960) and Croat (1990) summarized classifications published in this earlier period.

From the beginning of the 1980s, J.C. French, initially in collaboration with P.B. Tomlinson, produced a steady stream of anatomical studies (see review and references in French, 1997) that threw doubt on a number of aspects of the then-prevailing Englerian classification as exemplified by the synopsis published by Bogner (1979). A critical watershed then came with the doctoral thesis of M.H. Grayum (Grayum, 1984), a comprehensive survey of aroid systematic literature combined with the first family-wide SEM survey of pollen surface structure, which coincided with the more widespread use of cladistic methods in botanical taxonomy. Grayum’s powerfully argued case for the removal of *Acorus* from Araceae (Grayum, 1987) had a wide impact and set the scene for what was to

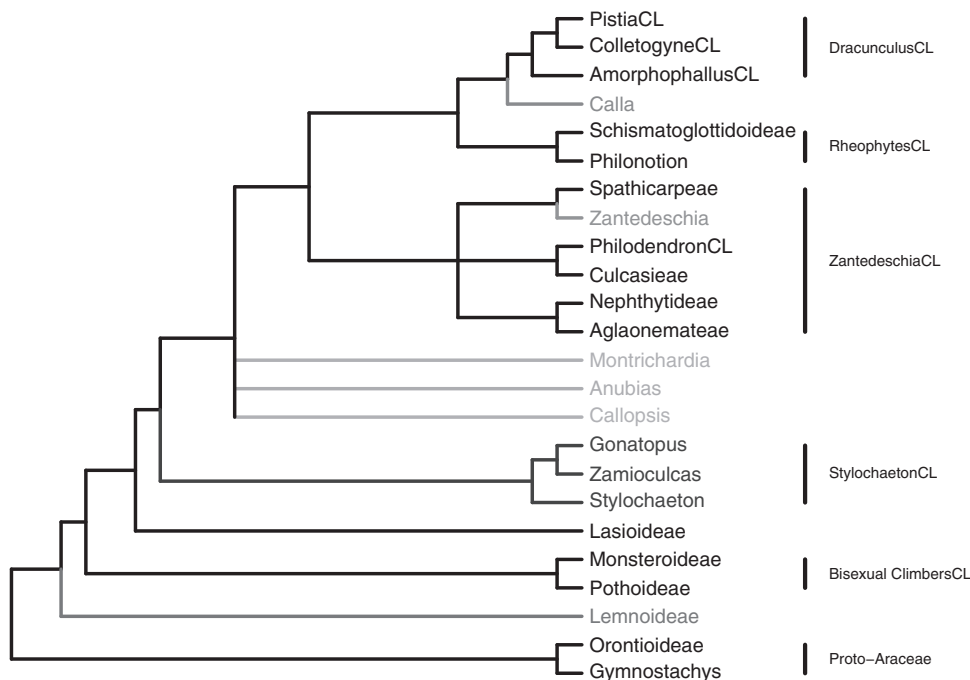


Fig 9.2 Cladogram simplified from Cusimano et al. (2011) showing major changes (coloured clades) from the cladogram in Fig 9.1 (French et al. 1995). See Table 9.1 for details of circumscription of suprageneric taxon names. Names ending in '-CL' are abbreviations for '... clade', e.g. *PistiaCL* ≡ *Pistia* clade. Colour version to be found in colour plate section.

come. A few years later, with his general papers on the evolution, phylogeny and SEM palynology of Araceae, Grayum (1990, 1992) effectively brought an end to the century-long pre-eminence of the Engler system, proposing a new classification in its place. In the meantime, J. Bogner and D.H. Nicolson had been collaborating over a number of years to update and modify Engler's system, incorporating results from French's anatomical work, and with the additional aim of producing a diagnostic key to all the genera; this work was eventually published in 1991 (Bogner and Nicolson, 1991) and represents the last version of the Englerian classification.

The comparison of new data between the Bogner and Nicolson, and Grayum systems then became a stimulus for new hypotheses by other workers and it was in this context that the cladogram of French et al. (1995) appeared. It presented many features that were substantially different from previous classifications but subsequent work has confirmed many of their novel results. The present review takes in turn the main clades of the French et al. (1995) cladogram (Fig 9.1) and discusses the results of more recent work (Fig 9.2) in relation to each. This shows that the

molecular view of Araceae phylogenetics is broadly consistent and that the basis for a new classification exists for which there is a reasonable expectation of stability in general outline, although much detailed work remains to be done and certain genera do not yet seem to have found a stable phylogenetic position.

Fossil Araceae have become an increasingly important focus for research in the past decade and apart from their intrinsic interest as direct evidence of ancient Araceae taxa, have a vital role to play in providing calibration for dating phylogenetic trees. Recent palaeobotanical work is here discussed in the context of the clades to which they have been ascribed. In particular, Nauheimer et al. (2012b) have published a comprehensive treatment of the global history of the family based on fossil dating and a new molecular analysis of all genera.

9.2 A note on names

The various classifications and phylogenetic analyses of recent decades have resulted in different taxon concepts for many suprageneric names. To deal with this, suprageneric names mentioned in the text, unless referenced otherwise, refer to the taxon concepts given here in alphabetical order as Table 9.1; this is based on the list of well-supported clades presented by Cusimano et al. (2011), with additional taxa referenced usually to the last formal synopsis published by Bogner and Petersen (2007). The informal term ‘lemnoid’ refers to the taxa of duckweeds, i.e. subfamily Lemnoideae (previously Lemnaceae). The informal term ‘aroid’ is today ambiguous in meaning, since it may refer to all Araceae (i.e. including lemnoids), Araceae minus lemnoids or just the taxa belonging to subfamily Aroideae; where used in this paper, it means Araceae minus lemnoids.

9.3 *Gymnostachys*

This highly distinctive Australian endemic was grouped with *Acorus* by Engler (1920). Bogner and Nicolson (1991) placed it at the beginning of their classification as the only genus of a new subfamily Gymnostachydoideae. Grayum (1990: 669) noted interesting phenotypic similarities between *Gymnostachys* and Orontioideae (assigned by Grayum, 1990: 688 to his subfamily Lasioideae), but despite this he placed the genus in his broadly circumscribed subfamily Pothoideae as the first taxon of his classification. French et al. (1995) found that *Gymnostachys* was indeed closely related to Orontioideae and that this well-supported clade was placed as the most basal branch of their cladogram. Duvall et al. (1993), using plastid *rbcL* sequence data, had previously recorded a sister-group relationship between *Gymnostachys* and *Symplocarpus* (Orontioideae) but the significance of this finding was not then apparent as their analysis included only nine genera of Araceae.

Table 9.1 Clades, clade numbers and clade names based on the circumscriptions of Cusimano et al. (2011).

Taxon	Reference	Clade number	Genera included
Aglaonemateae	Cusimano et al. 2011	9	<i>Aglaodorum</i> , <i>Aglaonema</i>
<i>Alocasia</i> clade	Cusimano et al. 2011	30	<i>Alocasia</i> , <i>Arisaema</i> , <i>Arum</i> , <i>Biarum</i> , <i>Dracunculus</i> , <i>Eminium</i> , <i>Helicodiceros</i> , <i>Lazarum</i> , <i>Pinellia</i> , <i>Sauromatum</i> , <i>Theriophonum</i> , <i>Typhonium</i>
<i>Ambrosina</i> clade	Cusimano et al. 2011	36	<i>Alocasia</i> , <i>Ambrosina</i> , <i>Ariopsis</i> , <i>Arisaema</i> , <i>Arisarum</i> , <i>Arophyton</i> , <i>Arum</i> , <i>Biarum</i> , <i>Carlephyton</i> , <i>Colletogyne</i> , <i>Colocasia</i> , <i>Dracunculus</i> , <i>Eminium</i> , <i>Helicodiceros</i> , <i>Lazarum</i> , <i>Peltandra</i> , <i>Pinellia</i> , <i>Pistia</i> , <i>Protarum</i> , <i>Remusatia</i> , <i>Sauromatum</i> , <i>Stuednera</i> , <i>Theriophonum</i> , <i>Typhonium</i> , <i>Typhonodorum</i>
<i>Amorphophallus</i> clade	Cusimano et al. 2011	35	<i>Amorphophallus</i> , <i>Caladium</i> , <i>Chlorospatha</i> , <i>Filarum</i> , <i>Hapaline</i> , <i>Jasarum</i> , <i>Pseudodracontium</i> , <i>Scaphispatha</i> , <i>Syngonium</i> , <i>Ulearum</i> , <i>Xanthosoma</i> , <i>Zomicarpa</i> , <i>Zomicarpella</i>
Anadendreae	Bogner and Petersen 2007		<i>Anadendrum</i>
<i>Anchomanes</i> clade	Cusimano et al. 2011	26	<i>Aglaodorum</i> , <i>Aglaonema</i> , <i>Anchomanes</i> , <i>Nepthytis</i> , <i>Pseudohydrosme</i>
Araceae	Cusimano et al. 2011	44	<i>Alloschemone</i> , <i>Alocasia</i> , <i>Ambrosina</i> , <i>Amorphophallus</i> , <i>Amydrium</i> , <i>Anadendrum</i> , <i>Anaphyllopsis</i> , <i>Anaphyllum</i> , <i>Anthurium</i> , <i>Apoballis</i> , <i>Aridarum</i> , <i>Ariopsis</i> , <i>Arisaema</i> , <i>Arisarum</i> , <i>Arophyton</i> , <i>Arum</i> , <i>Bakoa</i> , <i>Biarum</i> , <i>Bucephalandra</i> , <i>Caladium</i> , <i>Calla</i> , <i>Carlephyton</i> , <i>Chlorospatha</i> , <i>Colletogyne</i> , <i>Colocasia</i> , <i>Cryptocoryne</i> , <i>Cyrtosperma</i> , <i>Dracontioides</i> , <i>Dracontium</i> , <i>Dracunculus</i> , <i>Eminium</i> , <i>Epipremnum</i> , <i>Filarum</i> , <i>Gonatopus</i> , <i>Gymnostachys</i> , <i>Hapaline</i> , <i>Helicodiceros</i> , <i>Hestia</i> , <i>Heteropsis</i> , <i>Holochlamys</i> , <i>Jasarum</i> , <i>Lagenandra</i> , <i>Landoltia</i> , <i>Lasia</i> , <i>Lasimorpha</i> , <i>Lazarum</i> , <i>Lemna</i> , <i>Lysichiton</i> , <i>Monstera</i> , <i>Ooia</i> , <i>Orontium</i> , <i>Pedicellarum</i> , <i>Peltandra</i> , <i>Philonotion</i> , <i>Phymatarum</i> , <i>Pichinia</i> , <i>Pinellia</i> , <i>Piptospatha</i> , <i>Pistia</i> , <i>Podolasia</i> , <i>Pothoidium</i> , <i>Pothos</i> ,

			<i>Protarum, Pseudodracontium, Remusatia, Rhabdophora, Rhodospatha, Sauromatum, Scaphispatha, Schismatoglottis, Schottariella, Scindapsus, Spathiphyllum, Spirodela, Stenospermation, Steudnera, Stylochaeton, Symplocarpus, Syngonium, Theriophonum, Typhonium, Typhonodorum, Ulearum, Urospatha, Wolffia, Wolffia, Xanthosoma, Zamioculcas, Zomicarpa, Zomicarpella</i>
Areae	Cusimano et al. 2011	21	<i>Arum, Biarum, Dracunculus, Eminium, Helicodiceros, Lazarum, Sauromatum, Theriophonum, Typhonium</i>
Arisareae	Cusimano et al. 2011	18	<i>Ambrosina, Arisarum</i>
Aroideae	Cusimano et al. 2011	39	<i>Aglaodorum, Aglaonema, Alocasia, Ambrosina, Amorphophallus, Anchomanes, Anubias, Apoballis, Aridarum, Ariopsis, Arisaema, Arisarum, Arophyton, Arum, Asterostigma, Bakoa, Biarum, Bognera, Bucephalandra, Caladium, Calla, Calloopsis, Carlephyton, Cercestis, Chlorospatha, Colletogyne, Colocasia, Croatiella, Cryptocoryne, Culcasia, Dieffenbachia, Dracunculus, Eminium, Filarum, Furtadoa, Gearum, Gorgonidium, Hapaline, Helicodiceros, Hestia, Homalomena, Incarum, Jasarum, Lagenandra, Lazarum, Mangonia, Montrichardia, Nephthytis, Ooia, Peltandra, Philodendron, Philonotium, Phymatarum, Pichinia, Pinellia, Piptospatha, Pistia, Protarum, Pseudodracontium, Pseudohydrosme, Remusatia, Sauromatum, Scaphispatha, Schismatoglottis, Schottariella, Spathantheum, Spathicarpa, Steudnera, Synandropadix, Syngonium, Tacca, Theriophonum, Typhonium, Typhonodorum, Ulearum, Xanthosoma, Zantedeschia, Zomicarpa, Zomicarpella</i>
Arophyteae	Cusimano et al. 2011	19	<i>Arophyton, Carlephyton, Colletogyne</i>
Bisexual Climbers clade	Cusimano et al. 2011	31	<i>Alloschemone, Amydrium, Anadendrum, Anthurium, Epipremnum, Heteropsis, Holochlamys, Monstera, Pedicellarum, Pothoidium, Pothos, Rhabdophora, Rhodospatha, Scindapsus, Spathiphyllum, Stenospermation</i>

Table 9.1 (cont.)

Taxon	Reference	Clade number	Genera included
Caladieae	Cusimano et al. 2011	17	<i>Caladium</i> , <i>Chlorospatha</i> , <i>Filarum</i> , <i>Hapaline</i> , <i>Jasarum</i> , <i>Scaphispatha</i> , <i>Syngonium</i> , <i>Ulearum</i> , <i>Xanthosoma</i> , <i>Zomicarpa</i> , <i>Zomicarpella</i>
<i>Colletogyne</i> clade	Cusimano et al. 2011	33	<i>Ambrosina</i> , <i>Arisarum</i> , <i>Arophyton</i> , <i>Carlephyton</i> , <i>Colletogyne</i> , <i>Peltandra</i> , <i>Typhonodorum</i>
<i>Colocasia</i> clade	Cusimano et al. 2011	20	<i>Ariopsis</i> , <i>Colocasia</i> , <i>Remusatia</i> , <i>Stuednera</i>
Colocasieae	Bogner and Petersen 2007		<i>Alocasia</i> , <i>Ariopsis</i> , <i>Colocasia</i> , <i>Protarum</i> , <i>Remusatia</i> , <i>Stuednera</i>
Cryptocoryneae	Cusimano et al. 2011	14	<i>Cryptocoryne</i> , <i>Lagenandra</i>
Culcasieae	Cusimano et al. 2011	11	<i>Cercestis</i> , <i>Culcasia</i>
Dieffenbachieae	Bogner and Petersen 2007		<i>Bognera</i> , <i>Dieffenbachia</i>
<i>Dracunculus</i> clade	Cusimano et al. 2011	37	<i>Alocasia</i> , <i>Ambrosina</i> , <i>Amorphophallus</i> , <i>Ariopsis</i> , <i>Arisaema</i> , <i>Arisarum</i> , <i>Arophyton</i> , <i>Arum</i> , <i>Biarum</i> , <i>Caladium</i> , <i>Carlephyton</i> , <i>Chlorospatha</i> , <i>Colletogyne</i> , <i>Colocasia</i> , <i>Dracunculus</i> , <i>Eminium</i> , <i>Filarum</i> , <i>Hapaline</i> , <i>Helicodiceros</i> , <i>Jasarum</i> , <i>Lazarum</i> , <i>Peltandra</i> , <i>Pinellia</i> , <i>Pistia</i> , <i>Protarum</i> , <i>Pseudodracontium</i> , <i>Remusatia</i> , <i>Sauromatum</i> , <i>Scaphispatha</i> , <i>Stuednera</i> , <i>Syngonium</i> , <i>Theriophonum</i> , <i>Typhonium</i> , <i>Typhonodorum</i> , <i>Ulearum</i> , <i>Xanthosoma</i> , <i>Zomicarpa</i> , <i>Zomicarpella</i>
Gymnostachydoideae	Bogner and Petersen 2007		<i>Gymnostachys</i>

Heteropsideae	Bogner and Petersen 2007		<i>Heteropsis</i>
<i>Heteropsis</i> clade	Cusimano et al. 2011	4	<i>Alloschemone, Heteropsis, Rhodospatha, Stenospermatum</i>
<i>Homalomena</i> clade	Cusimano et al. 2011	27	<i>Cercestis, Culcasia, Furtadoa, Homalomena, Philodendron</i>
Homalomeneae	Bogner and Petersen 2007		<i>Furtadoa, Homalomena</i>
Lasioideae	Cusimano et al. 2011	7	<i>Anaphyllopsis, Anaphyllum, Cyrtosperma, Dracontioides, Dracontium, Lasia, Lasimorpha, Podolasia, Pycnospatha, Urospatha</i>
Lemnoideae	Cusimano et al. 2011	2	<i>Landoltia, Lemna, Spirodela, Wolffia, Wolffia</i>
Monstereae	Bogner and Petersen 2007		<i>Alloschemone, Amydrium, Epipremnum, Monstera, Rhabdophora, Rhodospatha, Scindapsus, Stenospermatum</i>
Monsteroideae	Cusimano et al. 2011	24	<i>Alloschemone, Amydrium, Anadendrum, Heteropsis, Holochlamys, Epipremnum, Monstera, Rhabdophora, Rhodospatha, Scindapsus, Spathiphyllum, Stenospermatum</i>
Nephtyideae	Cusimano et al. 2011	10	<i>Anchomanes, Nephtytis, Pseudohydrosme</i>
Orontioideae	Cusimano et al. 2011	1	<i>Lysichiton, Orontium, Symplocarpus</i>
Peltandreae	Bogner and Petersen 2007		<i>Peltandra, Typhonodorum</i>

Table 9.1 (cont.)

Taxon	Reference	Clade number	Genera included
Philodendreae	Bogner and Petersen 2007		<i>Philodendron</i>
<i>Philodendron</i> clade	Cusimano et al. 2011	12	<i>Furtadoa</i> , <i>Homalomena</i> , <i>Philodendron</i>
<i>Philonotium</i> clade	Cusimano et al. 2011	38	<i>Alocasia</i> , <i>Ambrosina</i> , <i>Amorphophallus</i> , <i>Apoballis</i> , <i>Aridarum</i> , <i>Ariopsis</i> , <i>Arisaema</i> , <i>Arisarum</i> , <i>Arophyton</i> , <i>Arum</i> , <i>Bakoa</i> , <i>Biarum</i> , <i>Bucephalandra</i> , <i>Caladium</i> , <i>Calla</i> , <i>Carlephyton</i> , <i>Chlorospatha</i> , <i>Colletogyne</i> , <i>Colocasia</i> , <i>Cryptocoryne</i> , <i>Dracunculus</i> , <i>Eminium</i> , <i>Filarum</i> , <i>Hapaline</i> , <i>Helicodiceros</i> , <i>Hestia</i> , <i>Jasarum</i> , <i>Lagenandra</i> , <i>Lazarum</i> , <i>Ooia</i> , <i>Peltandra</i> , <i>Philonotium</i> , <i>Phymatarum</i> , <i>Pichinia</i> , <i>Pinellia</i> , <i>Piptospatha</i> , <i>Pistia</i> , <i>Protarum</i> , <i>Pseudodracontium</i> , <i>Remusatia</i> , <i>Sauromatum</i> , <i>Scaphispatha</i> , <i>Schismatoglottis</i> , <i>Schottariella</i> , <i>Stuednera</i> , <i>Syngonium</i> , <i>Therophonum</i> , <i>Typhonium</i> , <i>Typhonodorum</i> , <i>Ulearum</i> , <i>Xanthosoma</i> , <i>Zomicarpa</i> , <i>Zomicarpella</i>
<i>Pistia</i> clade	Cusimano et al. 2011	34	<i>Alocasia</i> , <i>Ariopsis</i> , <i>Arisaema</i> , <i>Arum</i> , <i>Biarum</i> , <i>Colocasia</i> , <i>Dracunculus</i> , <i>Eminium</i> , <i>Helicodiceros</i> , <i>Lazarum</i> , <i>Pinellia</i> , <i>Pistia</i> , <i>Protarum</i> , <i>Remusatia</i> , <i>Sauromatum</i> , <i>Stuednera</i> , <i>Therophonum</i> , <i>Typhonium</i>
<i>Podolasia</i> clade	Cusimano et al. 2011	41	<i>Alocasia</i> , <i>Ambrosina</i> , <i>Amorphophallus</i> , <i>Anaphyllopsis</i> , <i>Anaphyllum</i> , <i>Apoballis</i> , <i>Aridarum</i> , <i>Ariopsis</i> , <i>Arisaema</i> , <i>Arisarum</i> , <i>Arophyton</i> , <i>Arum</i> , <i>Bakoa</i> , <i>Biarum</i> , <i>Bucephalandra</i> , <i>Caladium</i> , <i>Calla</i> , <i>Carlephyton</i> , <i>Chlorospatha</i> , <i>Colletogyne</i> , <i>Colocasia</i> , <i>Cryptocoryne</i> , <i>Cyrtosperma</i> , <i>Dracontioides</i> , <i>Dracontium</i> , <i>Dracunculus</i> , <i>Eminium</i> , <i>Filarum</i> , <i>Gonatopus</i> , <i>Hapaline</i> , <i>Helicodiceros</i> , <i>Hestia</i> , <i>Jasarum</i> , <i>Lagenandra</i> , <i>Lasia</i> , <i>Lasimorpha</i> , <i>Lazarum</i> , <i>Ooia</i> , <i>Peltandra</i> , <i>Philonotium</i> , <i>Phymatarum</i> , <i>Pichinia</i> , <i>Pinellia</i> , <i>Piptospatha</i> , <i>Pistia</i> , <i>Podolasia</i> , <i>Protarum</i> , <i>Pseudodracontium</i> , <i>Pycnospatha</i> , <i>Remusatia</i> , <i>Sauromatum</i> ,

			<i>Scaphispatha, Schismatoglottis, Schottariella, Steudnera, Stylochaeton, Syngonium, Theriophonum, Typhonium, Typhonodorum, Ulearum, Urospatha, Xanthosoma, Zamiculcas, Zomicarpa, Zomicarpella</i>
Potheae	Cusimano et al. 2011	3	<i>Pedicellarum, Pothoidium, Pothos</i>
Pothoideae	Cusimano et al. 2011	23	<i>Anthurium, Pedicellarum, Pothoidium, Pothos</i>
Proto-Araceae	Cusimano et al. 2011	22	<i>Gymnostachys, Lysichiton, Orontium, Symplocarpus</i>
<i>Rhaphidophora</i> clade	Cusimano et al. 2011	6	<i>Amydrium, Anadendrum, Epipremnum, Monstera, Rhaphidophora, Scindapsus</i>
Rheophytes clade	Cusimano et al. 2011	28	<i>Apoballis, Aridarum, Bakoa, Bucephalandra, Cryptocoryne, Hestia, Lagenandra, Ooia, Philonotion, Phymatarum, Pichinia, Piptospatha, Schismatoglottis, Schottariella</i>
Schismatoglottideae	Cusimano et al. 2011	15	<i>Apoballis, Aridarum, Bakoa, Bucephalandra, Hestia, Ooia, Phymatarum, Pichinia, Piptospatha, Schismatoglottis, Schottariella</i>
Spathicarpeae	Cusimano et al. 2011	13	<i>Asterostigma, Bognera, Croatiella, Dieffenbachia, Gearum, Gorgonidium, Incarum, Mangonia, Spathantheum, Spathicarpa, Synandropadix, Taccarum</i>
Spathiphyllaeae	Cusimano et al. 2011	5	<i>Holochlamys, Spathiphyllum</i>
<i>Spirodela</i> clade	Cusimano et al. 2011	43	<i>Alloschemone, Alocasia, Ambrosina, Amorphophallus, Amydrium, Anadendrum, Anaphyllopsis, Anaphyllum, Anthurium, Apoballis, Aridarum, Ariopsis, Arisaema, Arisarum, Arophyton, Arum, Bakoa, Biarum, Bucephalandra, Caladium, Calla, Carlephyton, Chlorospatha, Colletogyne,</i>

Table 9.1 (cont.)

Taxon	Reference	Clade number	Genera included
			<i>Colocasia, Cryptocoryne, Cyrtosperma, Dracontioides, Dracontium, Dracunculus, Eminium, Epipremnum, Filarum, Gonatopus, Hapaline, Helicodiceros, Hestia, Heteropsis, Holochlamys, Jasarum, Lagenandra, Landoltia, Lasia, Lasimorpha, Lazarum, Lemna, Monstera, Ooia, Pedicellarum, Peltandra, Philonotion, Phymatarum, Pichinia, Pinellia, Piptospatha, Pistia, Podolasia, Pothoidium, Pothos, Protarum, Pseudodracontium, Pycnospatha, Remusatia, Rhabdophora, Rhodospatha, Sauromatum, Scaphispatha, Schismatoglottis, Schottariella, Scindapsus, Spathiphyllum, Spirodela, Stenospermation, Steudnera, Stylochaeton, Syngonium, Theriophonum, Typhonium, Typhonodorum, Ulearum, Urospatha, Wolffia, Wolffia, Xanthosoma, Zamiculcas, Zomicarpa, Zomicarpella</i>
Stylochaeton clade	Cusimano et al. 2011	25	<i>Gonatopus, Stylochaeton, Zamiculcas</i>
Thomsonieae	Cusimano et al. 2011	16	<i>Amorphophallus, Pseudodracontium</i>
True Araceae clade	Cusimano et al. 2011	42	<i>Alloschemone, Alocasia, Ambrosina, Amorphophallus, Amydrium, Anadendrum, Anaphyllopsis, Anaphyllum, Anthurium, Apoballis, Aridarum, Ariopsis, Arisaema, Arisarum, Arophyton, Arum, Bakoa, Biarum, Bucephalandra, Caladium, Calla, Carlephyton, Chlorospatha, Colletogyne, Colocasia, Cryptocoryne, Cyrtosperma, Dracontioides, Dracontium, Dracunculus, Eminium, Epipremnum, Filarum, Gonatopus, Hapaline, Helicodiceros, Hestia, Heteropsis, Holochlamys, Jasarum, Lagenandra, Lasia, Lasimorpha, Lazarum, Monstera, Ooia, Pedicellarum, Peltandra, Philonotion, Phymatarum, Pichinia, Pinellia, Piptospatha, Pistia, Podolasia, Pothoidium, Pothos, Protarum, Pseudodracontium, Remusatia, Rhabdophora,</i>

			<i>Rhodospatha, Sauromatum, Scaphispatha, Schismatoglottis, Schottariella, Scindapsus, Spathiphyllum, Stenospermation, Steudnera, Stylochaeton, Syngonium, Theriophonum, Typhonium, Typhonodorum, Ulearum, Urospatha, Xanthosoma, Zamioculcas, Zomicarpa, Zomicarpella</i>
<i>Typhonodorum</i> clade	Cusimano et al. 2011	29	<i>Arophyton, Carlephyton, Colletogyne, Peltandra, Typhonodorum</i>
Unisexual Flowers clade	Cusimano et al. 2011	40	<i>Alocasia, Ambrosina, Amorphophallus, Apoballis, Aridarum, Ariopsis, Arisaema, Arisarum, Arophyton, Arum, Bakoa, Biarum, Bucephalandra, Caladium, Calla, Carlephyton, Chlorospatha, Colletogyne, Colocasia, Cryptocoryne, Dracunculus, Eminium, Filarum, Gonatopus, Hapaline, Helicodiceros, Hestia, Jasarum, Lagenandra, Lazarum, Ooia, Peltandra, Philodendron, Philonotion, Phymatarum, Pichinia, Pinellia, Piptospatha, Pistia, Protarum, Pseudodracontium, Remusatia, Sauromatum, Scaphispatha, Schismatoglottis, Schottariella, Steudnera, Stylochaeton, Syngonium, Theriophonum, Typhonium, Typhonodorum, Ulearum, Xanthosoma, Zamioculcas, Zomicarpa, Zomicarpella</i>
Zamioculcadoideae	Cusimano et al. 2011	8	<i>Gonatopus, Zamioculcas</i>
<i>Zantedeschia</i> clade	Cusimano et al. 2011	32	<i>Aglaodorum, Aglaonema, Anchomanes, Asterostigma, Bognera, Cercestis, Croatiella, Culcasia, Dieffenbachia, Furtadoa, Gearum, Gorgonidium, Homalomena, Incarum, Mangonia, Nephthytis, Philodendron, Pseudohydrosme, Spathantheum, Spathicarpa, Synandrospadix, Taccharum, Zantedeschia</i>
Zantedeschieae	Bogner and Petersen 2007		<i>Zantedeschia</i>

As noted by French et al. (1995), their demonstration of the cladistic association of *Gymnostachys* with Orontioideae was novel. Prior to their study the three genera of Orontioideae had a varied taxonomic history. Engler (1887–1889, 1920) grouped them with *Calla* in his subfamily Calloideae, but Grayum (1990), and Bogner and Nicolson (1991) grouped them instead in their respective circumscriptions of subfamily Lasioideae. Mayo et al. (1997), having also obtained the pairing of *Gymnostachys* with the Orontioideae in a morphological cladistic analysis, named the clade informally as ‘proto-Araceae’, but nevertheless recognized *Gymnostachydoideae* and Orontioideae as distinct subfamilies. Rothwell et al. (2004) found a sister-group relation between *Gymnostachys* and *Symplocarpus* in their analysis of 27 genera of Araceae. Tam et al. (2004), in a study of the DNA sequences of the plastid *trnL-F* spacer/intron region of 42 Araceae genera, confirmed that *Gymnostachys* and all three genera of Orontioideae formed a robust clade and advocated formal recognition of proto-Araceae as a subfamily. Cabrera et al. (2008), in a comprehensive and detailed study of 102 of the 110 genera then accepted, used sequences from five regions of coding and noncoding plastid DNA and their result provided further confirmation, as did Cusimano et al. (2011) more recently.

9.4 Orontioideae

This taxon has been the object of several specific phylogenetic studies in addition to those already mentioned in the wider context of family phylogenetics. An early cladistic paper was by Barabé and Forget (1987), who used morphological characters to show that the orontiods and *Calla* did not form a natural group when placed together in the Englerian subfamily Calloideae. Wen et al. (1996) reported on the biogeography of the genus *Symplocarpus*, using plastid DNA restriction site data, and this was followed by papers by Kitano et al. (2005) on *Symplocarpus* in Japan using plastid DNA sequences and Nie et al. (2006) on the Orontioideae as a whole. The last paper described a study based on DNA sequences from *trnL-F* and *ndhF* regions of the plastid genome which sampled six species of Orontioideae and eight other genera of Araceae, including *Gymnostachys* and *Calla*. In their cladograms, *Gymnostachys* grouped with the orontiods as found by other authors of molecular studies, whereas *Calla* paired with *Philodendron* within the Unisexual Flowers clade (Table 9.1).

Nie et al. (2006) made use of the recent discovery of a Cretaceous orontiod fossil, *Albertarum pueri* (Bogner et al., 2005) to date their tree. *Albertarum pueri* is a remarkable fossil infructescence from Late Cretaceous deposits of Alberta, Canada which Bogner et al. (2005) placed near *Symplocarpus* although it is distinct within the Orontioideae due to its trilocular ovary, uniovulate locules and seeds

with a ribbed testa. Leaf fossils of Orontioideae were reported by Bogner et al. (2007), comprising four species. The three North American species, from the Late Cretaceous and Paleogene, are new (*Orontium wolfei*, *O. mackii*, *Symplocarpus hoffmaniae*). *Lysichiton austriacus*, from the Late Cretaceous of Austria, was transferred from the fossil genus *Araciphyllites*.

Nauheimer et al. (2012b) report the existence of an orontoid fossil leaf from Ceará in Northeast Brazil.

9.5 Lemnoideae

The most recent cladistic analyses of Araceae (Cabrera et al., 2008; Cusimano et al., 2011; Nauheimer et al., 2012b) placed the five genera of Lemnoideae (*Spirodela*, *Lemna*, *Landoltia*, *Wolffia* and *Wolffiella*) near the base of the cladogram just above the proto-Araceae, but prior to these studies lemnooid relationships were not clear.

French et al. (1995) included a single species of Lemnoideae (duckweeds) in their analysis and found that it grouped within the unisexual Araceae — but not close to *Pistia* — as sister to Keating's (2003, 2004) subfamily Aroideae (curiously enough the same position occupied by *Calla* in the cladograms of Cabrera et al., 2008 and Cusimano et al., 2011). Duvall et al.'s (1993) early *rbcL* analysis also placed *Lemna* high up in the Araceae clade, but their sample of taxa was small (nine Araceae genera).

According to Mayo et al. (1995, 1997), the weight of evidence favoured inclusion of the lemnooid genera within Araceae, but these authors did not do so in their classification. Keating (2003), on the other hand, basing his classification on the cladogram of French et al. (1995), formally recognized subfamily Lemnoideae. Barabé et al. (2002), in a phylogenetic analysis of 34 Araceae genera including one lemnooid species (*Lemna* sp.) and using the plastid *trnL* and *trnL-F* DNA regions, were the first authors to place the lemnooids in their currently recognized near-basal position.

Because of a primary focus on ingroup topology, this result did not emerge in Les et al.'s (2002) comprehensive phylogenetic analysis of Lemnoideae (as Lemnaceae), which included all 38 accepted species and used five plastid genes (*rbcL*, *matK*, 5' *trnK* spacer, 3' *trnK* spacer, *rpl16* intron). Having reviewed the existing evidence, these authors concluded that the most probable position for Lemnaceae was sister to unisexual Araceae. This formed the basis for their choice of *Pistia* and seven other unspecified Araceae genera as outgroups.

The topology for lemnooids found by Barabé et al. (2002) emerged again in the study by Tam et al. (2004), which placed the single lemnooid taxon sampled (*Lemna* sp.) above the four genera of proto-Araceae and sister to the 37 sampled genera of the True Araceae clade (*sensu* Mayo et al. 1997: 70).

Rothwell et al. (2004), in an analysis of the *trnL-trnF* region of the plastid genome in 27 Araceae genera, showed the five lemnoide genera in a quite distinct position from *Pistia*, the latter associated with genera from Keating's (2003) subfamily Aroideae. This study built on an earlier paper by Stockey et al. (1997) on the Late Cretaceous lemnoide fossil genus *Limnobiophyllum*, in which, by contrast, *Pistia* had emerged as sister to the lemnoide in a morphological cladistic analysis of 11 Araceae genera. Kvaček (1995) had previously highlighted the importance of *Limnobiophyllum* for the relationship of Lemnoideae and Araceae. Rothwell et al. (2004) concluded that the floating habit had evolved twice independently in extant Araceae and if the fossil record were also considered then the floating habit would have evolved within the Araceae clade perhaps three times independently since the Cretaceous. Stockey et al. (2007) reinforced this by demonstrating that the Late Cretaceous fossil *Cobbania corrugata* may be related to Araceae, although its position within the family is unclear.

To settle the question of lemnoide relationships a general analysis of Araceae as a whole was needed, and this was presented by Cabrera et al. (2008). Unlike previous workers, these authors analysed not only all lemnoide genera but also most of the aroid genera (93%) recognized at that time as well. Their result confirmed the pattern reported by Barabé et al. (2002), but with a wider range of genes and a near-comprehensive generic sampling. Cusimano et al.'s (2011) analysis of an augmented version of the same molecular matrix added further support for the conclusion that lemnoide are an early (but not the earliest) branch of the Araceae clade. Bogner (2009) has provided a well-illustrated survey of the fossil and extant floating Araceae.

9.6 Pothoideae and Monsteroideae

French et al.'s (1995) cladogram grouped together into a single clade the genera of subfamilies Pothoideae and Monsteroideae, confirming the views of Hotta (1970) and Keating (2003), who grouped them together formally as the single subfamily Pothoideae. Carvell's detailed study of the floral anatomy of Pothoideae and Monsteroideae also supported this grouping (Carvell 1989). Grayum's (1990) cladogram and classification did not associate these two groups exclusively, but presented a wider concept of the Pothoideae, which also included Zamioculcadeae (our Zamioculcadoideae) and *Gymnostachys*. Bogner and Nicolson (1991) reduced Engler's Pothoideae to consist only of the three genera of tribe Potheae and recognized subfamily Monsteroideae as distinct with the four tribes Monstereae, Spathiphyllaeae, Anadendreae and Heteropsidaeae, the latter two transferred from Engler's Pothoideae. Mayo et al. (1997), and Bogner and Petersen (2007) maintained this position with the difference that they included *Anthurium* in Pothoideae.

In all later molecular analyses (Barabé et al., 2002; Tam et al., 2004; Cabrera et al., 2008; Cusimano et al., 2011) there is a single clade consisting of two major subclades corresponding respectively to Pothoideae (*Pothos*, *Pothodium*, *Pedicellarum*, *Anthurium*) and Monsteroideae (*Alloschemone*, *Amydrium*, *Anadendrum*, *Epipremnum*, *Heteropsis*, *Holochlamys*, *Monstera*, *Rhaphidophora*, *Rhodospatha*, *Scindapsus*, *Spathiphyllum*, *Stenospermation*).

The latter three studies, which have a complete representation of the monsterooid genera, reveal a new topology in which *Heteropsis* and *Anadendrum* are embedded in two different well-supported clades, but the position of tribe Spathiphyllae is less clear. Tam et al. (2004) first showed that the genera *Rhodospatha*, *Stenospermation*, *Alloschemone* and *Heteropsis* formed a clade, and this was confirmed with better support by Cabrera et al. (2008) and Cusimano et al. (2011). The last two studies also showed equally strong support for a clade formed by six other genera (*Monstera*, *Epipremnum*, *Scindapsus*, *Rhaphidophora*, *Anadendrum*, *Amydrium*), but in Tam et al.'s (2004) cladogram, with a much larger sampling of monsterooid species, this clade had no support greater than 50%.

The ambiguous position of Spathiphyllae vis-à-vis these other two internal clades of Monsteroideae (*Heteropsis* clade and *Rhaphidophora* clade) is interesting. Although Spathiphyllae have been regarded as phenotypically plesiomorphic in many respects (Grayum, 1990: 670), there is as yet little molecular support for its sister-group position to a clade of the other monsterooid genera, a topology which their morphology would suggest. Both Spathiphyllae and the *Rhaphidophora* clade have remarkable amphipacific geographical distributions (Grayum, 1990: 670–671; Mayo, 1993). Tarasevich (1988) discovered that the striate pollen of *Spathiphyllum*, hitherto thought to be inaperturate, was actually multiaperturate. Carvell (1989) discovered vestigial tepal-like structures in the flowers of species of *Alloschemone*, *Monstera*, *Rhaphidophora* and *Rhodospatha*, thus weakening still further the morphological distinction between these three clades.

At the population level, I.M. Andrade and colleagues studied species of *Anthurium* (Pothoideae) and *Monstera* (Monsteroideae) in northeastern Brazil (Andrade et al., 2007, 2009; Andrade and Mayo, 2010) using AFLP molecular markers to gather evidence of population and species differentiation in isolated humid forest fragments.

Fossil Monsteroideae have been studied by various workers. An early Cretaceous pollen fossil from Portugal, *Mayoa portugallica*, was discovered and identified as a member of the tribe Spathiphyllae by Friis et al. (2004), but doubt has been thrown on this assignment more recently by Hofmann and Zetter (2010). The tribe Monstereae is well established from the Late Cretaceous (Santonian?, Campanian to Maastrichtian) of Portugal by an *Epipremnum*-like inflorescence with stamens and pollen *in situ*, as well as seeds (E.-M. Friis, pers. comm.). A viny

axis, *Rhodospathodendron tomlinsonii*, from the Late Cretaceous (Late Maastrichtian) was described from India and assigned to Monstereae by Bonde (2000). Hesse and Zetter (2007) reinterpreted certain *Ephedripites* forms from the Late Cretaceous and Palaeogene as *Spathiphyllum* (*S. vanegensis*, *S. elsikii*). A zona-aperturate pollen fossil of *Monstera* or *Gonatopus* type has been reported from the Lower Eocene of Austria (Zetter et al., 2001; Hesse and Zetter, 2007), similar to the fossil *Proxapertites operculatus*. Wilde et al. (2005) described the leaf fossil *Araciphyllites tertarius* from the Middle Eocene Messel Formation of Germany and ascribed it to the tribe Monstereae. More recent are fossil seeds of *Epipremnites* and *Scindapsites* of tribe Monstereae (Gregor and Bogner, 1984, 1989) from European Tertiary deposits. *Teichosperma spadiciflorum* (Upper Eocene to Lower Oligocene) is known from infructescences, fruits and seeds resembling those of *Epipremnum* in the Monstereae (Renner, 1907; Kräusel and Stromer, 1924, Tiffney, pers. comm.).

In the Pothoideae, *Anthurium* has been the object of recent molecular studies by L. Temponi (2006) and M. Carlsen (pers. comm.). Temponi's study focussed mainly on Brazilian taxa and indicated that most Brazilian species belonged to a single clade which appears to have evolved independently of the rest of the genus in the eastern Atlantic forest of South America. Carlsen's study is a broader survey of this, the largest genus of Araceae (pers. comm.).

Herrera et al. (2008) described the fossil genus *Petrocardium* with two species from the Paleocene of Colombia and showed that this taxon is more similar in its leaf morphology to *Anthurium* than to any other genus. Wilde et al. (2005) emended the circumscription of the fossil leaf genus *Araceophyllum*, based on *A. engleri* Kräusel from the Neogene of Sumatra, and placed it in the tribe Potheae because of the leaf venation type.

9.7 Lasioideae

Lasioideae have been a problematic group since their first description by Engler (1876), and it was only with French et al.'s (1995) molecular cladogram that a clearer concept of this taxon was achieved. It was Grayum (1990: 672–673) who first clearly targeted the artificiality of Engler's Lasioideae, aided by new data on pollen structure and anatomy. In his original concept of the subfamily, Engler relied on vegetative characters to group the genera and in doing so brought together taxa with diverse reproductive structures, as discussed by Grayum (1990: 672–673). It seems likely that Engler was misled by a mistaken belief that the bisexual-flowered tribe Lasieae (\equiv our Lasioideae) possessed latificers (Mayo and Bogner, Chapter 10, this volume), a question that was only settled in recent times by French (1988) and Keating (2003).

Although he removed the genera of Engler's unisexual-flowered tribes Nephthytideae, Amorphophalleae (= Thomsonieae) and Montrichardieae to other subfamilies, Grayum (1990) introduced the three genera of Orontioideae and unisexual-flowered *Stylochaeton* into his Lasioideae, which makes its circumscription different from the current one. Bogner and Nicolson (1991) followed Grayum by including the Orontioideae and removing the genera of Thomsonieae, but they included bisexual-flowered *Anthurium* and various unisexual-flowered genera: *Montrichardia*, *Cercestis*, *Culcasia*, *Nephthytis*, *Anchomanes*, *Pseudohydrosme*, *Calloopsis* and the Zamioculcadeae (\equiv Zamioculcadoideae). In contrast, the morphological cladistic analysis of Mayo et al. (1997) obtained a result similar to that of French et al. (1995) in which the genera of the bisexual-flowered clade tribe Lasieae formed a group distinct from all the others with which they had previously been associated. The agreement of the two analyses on this point led Mayo et al. (1997) to formally recognize what is now the currently accepted circumscription for Lasioideae, corresponding to the Englerian tribe Lasieae (Engler 1920). The systematics of this group were studied in detail by Hay (1986, 1988, 1992). Hay and Mabberley (1991) published a wide-ranging essay on the phenotypic evolution of this group that included consideration of homoeotic saltation, a topic later taken up by Barabé et al. (2008).

Keating (2003, 2004), basing his classification on the molecular analysis by French et al. (1995), proposed the same concept of Lasioideae, and all subsequent molecular analyses have upheld its distinctness (Barabé et al., 2002; Tam et al., 2004; Cabrera et al., 2008; Cusimano et al., 2011). However, in the latest molecular analyses, the relationships of the Lasioideae clade to the rest of the family are still not secure. The studies of Cabrera et al. (2008) and Cusimano et al. (2011) agreed in placing Lasioideae above the Pothoideae–Monsteroideae clade, but the interrelationships of the main unisexual-flowered clade (Aroideae) to Lasioideae and the *Stylochaeton* clade are not well supported. Cabrera et al. (2008) showed two different topologies for these three clades, and in Cusimano et al. (2011) the position for Lasioideae below the *Stylochaeton* clade and Aroideae is only weakly supported by molecular data.

Lasioideae pollen fossils from the Upper Cretaceous Timerdakh Formation in Vilui Basin (Siberia, Russia) were recently described by Hofmann and Zetter (2010) as *Lasioideaeacidites hessei* and *L. bogneri* and represent the oldest evidence for the subfamily so far discovered. Smith and Stockey (2003) presented a detailed description of *Keratosperma allenbyense*, the seeds of a fossil genus of Lasioideae from the Middle Eocene of British Columbia in Canada. This study, based on earlier work by Cevallos-Ferriz and Stockey (1988), confirmed that *Keratosperma* is a distinct lasioid genus. More recent palaeobotanical evidence for Lasioideae is provided by the seed fossil taxon *Urospathites* from Eurasian mid-Tertiary (Gregor and Bogner, 1984, 1989).

9.8 Monoecious aroids form a monophyletic lineage

Perhaps the most striking of all the results presented by French et al.'s (1995) cladogram was the grouping together into a single large clade of all the unisexual-flowered genera. In proposing his phylogenetic classification of Araceae, Engler (1876, 1920) had explicitly rejected as artificial the primary division of the family into bisexual-flowered and unisexual-flowered taxa put forward by his predecessor H.W. Schott (1860), emphasizing instead patterns of vegetative anatomy and morphology. One result of this was the formation of two subfamilies, Pothoideae and Lasioideae, in which bisexual- and unisexual-flowered genera were brought together and within which Engler envisaged parallel evolution from the former to the latter condition. This unparsimonious idea persisted in most Araceae classifications (e.g. Grayum, 1990; Bogner and Nicolson, 1991; Hay and Mabberley, 1991) until the advent of molecular systematics.

Mayo et al.'s (1997) morphological analysis obtained a similar result to French et al. (1995) in this respect and they consequently formalized the unisexual clade as a new and much broader concept of subfamily Aroideae, since it represented a major new classificatory feature supported by congruence of independent data sets. Keating (2003), however, argued that the four distinct subclades within this large group shown by French et al.'s cladogram were supported by anatomical data and on this basis he recognized a formal division of the unisexual clade into subfamilies Philodendroideae, Schismatoglottidoideae, Lemnoideae and Aroideae.

Leaving aside the question of the circumscription of subfamilies, subsequent molecular analyses have in general tended to group the unisexual-flowered genera together. Barabé et al. (2002) grouped those they sampled into one subclade of a trichotomy with unisexual-flowered *Zamioculcas* and the bisexual-flowered Lasioideae. Tam et al. (2004) resolved the position of the *Zamioculcadoideae* as sister to a clade containing all other unisexual-flowered genera they sampled.

As discussed in the previous section, in the comprehensive analyses by Cabrera et al. (2008) and Cusimano et al. (2011) the validity of a single origin for the unisexual-flowered genera remains equivocal due to the lack of strong support for the sister-group relationship of the *Stylochaeton* clade to the other unisexual genera. This still leaves open the possibility that Lasioideae might be the sister group for the main Araceae clade and that unisexuality evolved independently in the *Stylochaeton* clade. Cusimano et al. (2011) provide strong support for the exclusion of the *Stylochaeton* clade from Aroideae, which is noteworthy since these three genera were included in the philodendroid clade by French et al. (1995) and Keating (2003, 2004).

A further complicating factor in the concept of the bisexual–unisexual transition as a strict synapomorphy in Araceae is provided by *Calla*, which in the most recent

and most complete molecular analyses (Cabrera et al., 2008; Cusimano et al., 2011) is embedded within the Aroideae. *Calla* flowers have bisexual morphology (although the upper part of the spadix is functionally male), and there are other important characters (particularly of the pollen) discussed in more detail by Cabrera et al. (2008) and Cusimano et al. (2011), which make its position within the unisexual Aroideae clade seemingly anomalous.

Friis et al. (2010) report fragments of an inflorescence interpreted as bearing staminate, naked flowers from the Early Cretaceous of Portugal ('Araceae fossil sp. A') noting that this fossil has aperturate, semi-tectate reticulate pollen. Other fossils that have been tentatively ascribed to the monoecious (unisexual-flowered) Araceae clade include *Cobbania corrugata* (see below) and *Cobbanicarpites amurensis* (Krassilov and Kodrul, 2009).

9.9 The *Stylochaeton* clade: Zamioculcadoideae + *Stylochaeton*

Engler's tribe Zamioculcadeae (*Zamioculcas*, *Gonatopus*) was raised to subfamily rank as Zamioculcadoideae by Bogner and Hesse (2005) and is currently treated as such by Bogner and Petersen (2007). The association of this group with *Stylochaeton* was yet another innovation of the French et al. (1995) analysis. Previous classifications had kept them separate. Grayum (1990) and Hay and Mabberley (1991) kept Zamioculcadeae in subfamily Pothoideae, where Engler had originally placed them, while *Stylochaeton* was transferred to the Lasioideae. Bogner and Nicolson (1991) on the other hand moved Zamioculcadeae into the Lasioideae, while keeping *Stylochaeton* in its own tribe in the Aroideae, as had Engler (1920).

French et al.'s (1995) analysis grouped the three genera as a distinct clade within the large unisexual Aroideae clade, with *Stylochaeton* as sister to the two zamioculcad genera. Mayo et al.'s (1997) morphological analysis placed Zamioculcadeae and then *Stylochaeton* as successive sister groups to Aroideae. The plesiomorphies of absence of laticifers and presence of a perigon in these three genera seemed to qualify them uniquely as transitional genera at the base of the unisexual Aroideae in a paraphyletic arrangement, and these authors dubbed them informally as the 'perigoniata Aroideae'. Keating (2003, 2004) maintained them as separate but adjacent tribes in his subfamily Philodendroideae following French et al.'s (1995) topology, pointing out the distinct morphology and anatomy of the two taxa.

Hesse et al. (2001) focussed on the palynology of the three genera of 'perigoniata Aroideae' and showed, among other things, that both Zamioculcadeae and *Stylochaeton* differed significantly from Aroideae in pollen structure, but also that each had peculiarities that mirrored their differences in macro-morphology. In a

later paper Bogner and Hesse (2005) separated the zamioiculcads as a subfamily and recommended that *Stylochaeton* be regarded as the basal element of the Aroideae clade, by virtue of its transitional pollen and floral characters.

Neither Barabé et al. (2002) nor Tam et al. (2004) sampled both taxa, and it was not until Cabrera et al.'s (2008) analysis that French et al.'s (1995) result was examined again with molecular data. Their result was unequivocal support for a monophyletic 'perigoniate Aroideae' and these authors argued that subfamily Zamioiculcadoideae should be expanded to include *Stylochaeton*, despite the clear phenotypic divergence. Cusimano et al.'s (2011, *Stylochaeton* clade) results lent further support to this view.

As noted by Cabrera et al. (2008), these three genera are African endemics and geophytes, each exhibiting peculiar morphology. The difficulties thus posed for phylogenetic interpretation based on the phenotype suggest that many pieces of this particular evolutionary jigsaw puzzle became extinct during the Tertiary aridification of Africa (Raven and Axelrod, 1974). As with the lemnooid genera, this is probably a case where molecular evidence has special value in providing insights.

9.10 Progress in establishing the internal structure of subfamily Aroideae

One of the great strengths of Engler's classification was its subfamily structure, i.e. the reduction of the complexity of Schott's many tribes into a small number of larger groups, most of which seemed to have a more-or-less recognizable 'facies'. In the words of Mayo et al. (1997: 73):

In a rough and ready manner subsequent specialists of the family learned to recognize subfamily *Pothoideae* by their complete lack of laticifers, subfamily *Monsteroideae* by their trichosclereids and mostly aperigoniate bisexual flowers, subfamily *Calloideae* by their temperate Northern hemisphere distribution and preference for swampy habitats, subfamily *Lasioideae* by their frequent possession of deeply sagittate or dracontiooid leaves, subfamily *Philodendroideae* by their unisexual flowers and parallel-pinnate leaf venation, subfamily *Colocasioideae* by their unisexual flowers, anastomosing laticifers and special type of leaf venation ('colocasiooid' ...) and subfamily *Aroideae* by their unisexual flowers, mostly geophytic habit and frequent possession of a smooth terminal spadix appendix.

All subsequent authors have maintained the classification of Araceae in subfamilies, and there is no doubt that this facilitates conceptual thinking about the classification. The formalization of the large unisexual clade as the subfamily Aroideae by Mayo et al. (1997) violated this tradition, since the Aroideae consequently contained well over half the genera. However, these authors were led to

this conclusion not only because of the striking and well-supported simplification thus introduced into the family classification and phylogenetic structure, but also because their morpho-anatomical analyses showed an inconsistent internal topology for Aroideae. Their cladistic results did not support the circumscription of any of the unisexual subfamilies of Engler (1920), Bogner and Nicolson (1991), Grayum (1990) or Hay and Mabberley (1991). Many tribal circumscriptions recognized by these authors were upheld, but the intertribal relationships advocated previously were mostly not supported. Mayo et al. (1997), seeking congruence between molecular and morphological patterns as the preferred basis for formal circumscriptions of supra-generic taxa, felt compelled to leave the classification of their large subfamily Aroideae largely unresolved above tribal rank: 'The internal topology of our subfamily *Aroideae* concept remains largely unresolved above the tribal level and this is a problem to which future phylogenetic studies should be devoted.' (Mayo et al., 1997: 70).

In contrast, as is now easier to see, French et al.'s (1995) large unisexual clade (Aroideae of Mayo et al., 1997) revealed three major clades in its internal topology if the positions of Lemnoideae, Zamioculcadoideae and *Stylochaeton* are ignored (see previous sections). These have turned out to be the foundation for a more consistent view of this part of the family's phylogenetic relationships. Keating (2003) presented a major new study of vegetative anatomical data that fitted this topology and on this basis he formalized the three clades as subfamilies Philodendroideae, Schismatoglottidoideae and Aroideae. This structure has been largely confirmed by later studies, which together represent substantial progress towards a better understanding of the phylogeny of this complex group.

The studies of Cabrera et al. (2008) and Cusimano et al. (2011), based largely on the same data but using somewhat different methods of analysis, both yielded the same three main aroid clades, if *Calla*, *Calloopsis*, *Montrichardia* and *Anubias* are ignored (see below).

9.10.1 The *Zantedeschia* clade ('philodendroids')

This clade, still the least robust of the three major unisexual subclades, brings together the genera of tribes Aglaonemateae, Culcasieae, Dieffenbachieae, Homalomenae, Nephthytideae, Philodendreae, Spathicarpeae and Zantedeschieae, as circumscribed in Bogner and Petersen (2007). It largely mirrors the earlier Philodendroideae clade of French et al. (1995) and Keating (2003). French et al.'s (1995) cladogram did not present bootstrap support, and even cautious recognition of the clade had to be tempered at that time by the lack of agreement with Mayo et al.'s (1997) morphological analyses and inconsistency of subsequent sequence analyses. In the earlier DNA sequence studies of Barabé et al. (2002) and Tam et al. (2004) this clade did not emerge, instead the various components sampled by them formed polytomies. It was not until the comprehensive analyses

by Cabrera et al. (2008) and Cusimano et al. (2011) that this clade was revealed as a well-supported unit.

The most important phylogenetic studies undertaken within this clade to date are those of Gonçalves (2002) and Gonçalves et al. (2007) on Spathicarpeae, and Gauthier et al. (2008) on *Philodendron*. French et al.'s (1995) molecular cladogram resuscitated a relationship between *Dieffenbachia* and the genera of the Spathicarpeae (in the older, narrower sense of Bogner and Petersen, 2007), which had been proposed much earlier by Schott (1860) on the basis of similarity in floral characters. Eduardo Gonçalves (Gonçalves, 2002; Gonçalves et al., 2007) tested this with a comprehensive analysis of the genera of Spathicarpeae that included the rare genera *Mangonia*, *Bognera* and *Gearum*. He used as outgroups genera (*Aglaonema*, *Cercestis*) representing the two sister groups present in French et al.'s polytomous topology and confirmed that tribe Spathicarpeae should be augmented to include both *Dieffenbachia* and *Bognera*, using both plastid DNA sequences (*matK*, *trnL-F*) and phenotypic data.

Gauthier et al. (2008) focussed on an investigation of the phylogeny of the large Neotropical genus *Philodendron*, using DNA sequences of two nuclear genes (ITS, ETS) and one plastid intron (*rpl16*) and a sample of 72 species of *Philodendron*, nine species of *Homalomena* and two outgroup genera, *Anchomanes* and *Culcasia*. Their choice of outgroups was guided by the earlier molecular study of Barabé et al. (2002), but is even better justified in the more recent cladogram of Cusimano et al. (2011). Their results showed, amongst other things, that the subgenera of *Philodendron* are monophyletic and confirmed the close relationship between (at least the Neotropical species of) *Homalomena* and *Philodendron*, which had been recognized since Engler (1920) and highlighted by French et al. (1995) and unpublished molecular studies by Cassia Sakuragui (1998 and pers. comm.).

Studies of population genetics and fingerprinting have been carried out in this clade. Cuartas-Hernández and Núñez-Farfán (2006) studied genetic variability in fragmented populations of *Dieffenbachia seguine* in Mexico using allozymes. Molecular fingerprinting of horticultural cultivars has been studied in several genera, which has provided important information for future studies of wild populations: *Aglaonema* (Chen et al., 2004a), *Dieffenbachia* (Chen et al., 2001) and *Philodendron* (Devanand et al., 2004).

Wilde et al. (2005) described the leaf fossil *Araciphyllites schaarschmidtii* and ascribed it to either tribe Homalomeneae (*Philodendron* clade) or tribe Aglaonemateae, i.e. from the *Zantedeschia* clade.

9.10.2 The rheophytes clade

French et al. (1995) found a close sister-group relationship between the two tribes Schismatoglottideae and Cryptocoryneae, which had previously been placed widely apart in different subfamilies by Engler (1920), Grayum (1990), Bogner

and Nicolson (1991) and Hay and Mabberley (1991). Mayo et al. (1997) recognized this group informally as the *Schismatoglottis* alliance, based on French et al.'s result, and later Keating formalized it as subfamily Schismatoglottidoideae. The more recent global analyses of Cabrera et al. (2008) and Cusimano et al. (2011) have confirmed this clade as robust; the latter authors have provided it with the informal name 'rheophytes clade' now that the genus *Philonotion* has been resurrected (see below).

Taxa of the rheophytes clade have long been an especially interesting focus of taxonomic attention. The work of N. Jacobsen and colleagues (e.g. Jacobsen, 1977; Othman et al., 2009; Bastmeijer et al., 2010) has made the tribe Cryptocoryneae cytologically and taxonomically one of the best-studied genera of Araceae. Othman (1997) carried out a detailed molecular study of 25 species of *Cryptocoryne*, using *Lagenandra* as outgroup. This study is notable for its wide-ranging methodological approach, which tested a variety of molecular markers, including nuclear (ITS), plastid (RFLP and sequenced *trnK* and *matK*) and RAPDs. This study provided insights into the historical biogeography of the species. Ipor et al. (2010) used DNA fingerprinting with M13 universal primer to investigate hybrids in *Cryptocoryne purpurea*.

Peter Boyce, S.Y. Wong and colleagues are currently carrying out wide-ranging phylogenetic, taxonomic and ecological studies of the Schismatoglottidoideae (e.g. Boyce and Wong, 2008, 2009; Wong and Boyce, 2010a, 2010b, 2010c). Wong et al. (2010) published a major phylogenetic study of the whole clade with 77 taxa, using plastid markers (*matK*, *trnK*, *trnL-F*) and the genera *Aglaonema*, *Anchomanes*, *Dieffenbachia*, *Hapaline* and *Homalomena* as outgroups. This revealed an unexpected phylogenetic insight in that the American species previously regarded as *Schismatoglottis americana* came out as sister to the two tribes combined. On this basis these authors resurrected the Schottian genus *Philonotion* and described a new tribe Philonotieae. The new phylogenetic tree also showed that the concept of an amphi-Pacific distribution for *Schismatoglottis* (e.g. Mayo, 1993) no longer held and sheds a sceptical light on the comparable distributions of *Homalomena* and the Spathiphyllaeae, the former now under active investigation by P. Boyce (pers. comm.).

9.10.3 The *Dracunculus* clade (Aroideae sensu Keating 2002)

This clade was first identified by French et al.'s (1995) RFLP study and has recently been confirmed by the DNA sequence analyses of Cabrera et al. (2008) and Cusimano et al. (2011). The earlier and less comprehensive sequence studies of Barabé et al. (2002) and Tam et al. (2004) each showed a clade that is compatible with this group.

In comparison to earlier classifications, the key new features of this part of the French et al. topology were: (1) a clade (*Amorphophallus* clade) consisting of the

Thomsonieae and Caladieae, the latter augmented by its merging with the Zomicarpeae, (2) a clade (*Colletogyne* clade) consisting of the pairing of *Ambrosina* and *Arisarum* and their association with a subclade consisting of *Peltandra*, *Typhonodorum* and the endemic Madagascan tribe Arophyteae and (3) a clade (*Pistia* clade) in which *Pistia* and *Protarum* attach to the basal nodes of a subclade grouping the *Colocasia* clade (including *Ariopsis*), *Alocasia* (a separate branch), *Arisaema*, *Pinellia* and the Areae. This radically different pattern represented a new understanding of the relationships of the most derived groups of the family. Previously Thomsonieae had not been associated with Caladieae, and the latter had been grouped with Colocasieae (in the sense of Bogner and Petersen, 2007) by almost all authors as subfamily Colocasioideae. The positions of *Pistia*, *Ambrosina* and *Protarum* had never been clear. *Pistia*, in particular, because of uniquely reduced floral structures and unusual vegetative morphology, had been treated by most previous authors as a separate tribe or subfamily. This was further reinforced by H.-D. Behnke's detailed survey of Araceae sieve element plastid ultrastructure (Behnke, 1995), which found that *Pistia*, uniquely in the family, has S-type plastids.

Molecular sequence studies have been carried out in the *Amorphophallus* clade by Grob et al. (2002) using 48 species from Thomsonieae with outgroups from six genera, *Filarum*, *Hapaline*, *Anchomanes*, *Arisaema*, *Sauromatum* and *Gonatopus*, based on plastid markers *matK* and *trnL*. This work was aimed primarily at testing the generic and sectional subdivision of Thomsonieae and resulted in the recognition of five major clades that represent a new understanding of the phylogeny and classification of the group, including the monophyly of the large group of African species and the reduction of *Pseudodracontium* to a subclade of *Amorphophallus*.

Loh et al. (2000), following an earlier fingerprinting study of *Caladium* cultivars (Loh et al., 1999), applied the technique of AFLP marker analysis to investigate relationships between five species of *Caladium* and three species of *Xanthosoma* and showed that these two genera could thus be distinguished.

The topology of the the *Colletogyne* clade, the second subclade of the *Dracunculus* clade, has since been confirmed by Cabrera et al. (2008), Mansion et al. (2008) and Cusimano et al. (2010). These results differ in whether *Peltandra* and *Typhonodorum* form their own subclade (corresponding to tribe Peltandreae in the sense of Bogner and Petersen, 2007) or whether they are successively sister to the three genera of Arophyteae. This is of biogeographic interest because of the fact that *Typhonodorum* and Arophyteae are Madagascan, whereas *Peltandra* occurs in eastern North America. However, the pairing of *Ambrosina*-*Arisarum* and their sister-group status to the clade comprising the former genera is well supported in all these studies.

Cobbania corrugata (Stockey et al., 2007) is a fossil from the Late Cretaceous of Alberta, Canada and the Amur region in the Russian Far East that as yet cannot be

ruled out of consideration as a unisexual-flowered aroid, though this remains highly speculative. The Palaeocene-Eocene leaf fossils of *Nitophyllites*, on the other hand, are more certainly ascribable to the *Dracunculus* clade. Wilde et al. (2005) have given a recent survey of this genus, which includes three species (*N. zaisanicus*, *N. limnestis*, *N. bohemicus*). These authors place *Nitophyllites* in this clade, relating it either to tribe Peltandreae or tribe Arophyteae.

The most intensively studied of the groups found by French et al. (1995) is the third and most derived, the *Pistia* clade (*sensu* Cusimano et al., 2011). Renner and Zhang (2004), who first dubbed the clade with this informal name, carried out a study of 37 species from 16 genera of the *Pistia* clade, with outgroup species from the genera *Caladium*, *Peltandra*, *Typhonodorum* and *Xanthosoma*, representing the other two subclades of the *Dracunculus* clade. These authors used DNA sequence data from three plastid regions (*trnL-trnF*, *rpl20-rps12*, *trnL*) and one mitochondrial region (*nad1* b/c) both to test earlier phylogenetic results and investigate the historical biogeography of *Pistia* with the help of fossils. This study was important in confirming the phylogenetic relationships of *Pistia*, previously never clear, but also reinforced the robustness of the *Pistia* clade and established its internal topology as consisting of five components above the basal nodes with *Pistia* and *Protarum*, successively the *Colocasia* clade (with *Ariopsis* and without *Alocasia*), *Alocasia* and finally a trichotomy of the tribe Areae, *Arisaema* and *Pinellia*, the last two genera not forming a monophyletic group as previously supposed by all authors, including French et al. (1995).

Chen et al. (2004b) used AFLP fingerprinting of 23 cultivars from 17 species of *Alocasia*, but did not include other genera of the *Pistia* clade in their study, which was aimed at investigating the potential for horticultural hybrid development. Nauheimer et al. (2012a) published an important study of 71 species of *Alocasia* and 25 species of other genera from the *Pistia* clade, based on plastid and nuclear DNA sequence data. They confirmed that *Alocasia* is a monophyletic group and showed that its sister group is *Colocasia gigantea* (Blume) Hook.f., which cannot now be considered to belong to the genus *Colocasia*. This study used extensive data to investigate the historical biogeography of the genus since the Miocene and was able to trace the origin of domesticated *Alocasia macrorrhizos* (Giant Taro) to the Philippines.

Mansion et al. (2008) used a phylogenetic tree of genera from the *Colletogyne* and *Pistia* clades to make a detailed and fascinating study of the historical biogeography of the western Mediterranean region. They sampled 54 species as 88 OTUs, including as outgroups *Amorphophallus*, *Caladium* and *Xanthosoma* from the *Amorphophallus* clade and the genus *Calla*, which is sister to the entire clade (*Dracunculus* clade) sampled. They used data from six regions of the plastid genome (*trnL* intron, *trnL-trnF* spacer, part of the *trnK* intron, *matK*, *rbcL* and *rps16*) and obtained a result which is compatible

with the topologies of Cusimano et al. (2010, 2011); some species of *Typhonium* are now species of *Sauromatum*. The only significant disagreement is the grouping of *Colocasia esculenta* with *Alocasia* in a clade apart from that of *Ariopsis*, *Remusatia* and *Stuednera*. *Arisaema* groups with the Areae rather than *Pinellia*, but this sister relationship has only weak support and may be considered equivalent to the polytomy found between these three groups by Renner and Zhang (2004) and Cusimano et al. (2011).

Renner and Zhang's (2004) result indicated that *Typhonium* was paraphyletic, and this has been further investigated in two more recent studies. Cusimano et al. (2010), in a study of 86 of the total 153 species of the Areae, including 53 species of *Typhonium* (in the broad sense), used both plastid (*rpl20-rps12*, *trnK*) and nuclear (*PhyC*) genome regions to analyse all relevant genera, using *Arisaema* as outgroup. Their results confirmed that the taxon concept of *Typhonium* hitherto used was paraphyletic, but showed that if *Sauromatum* were resurrected and the Australian species recognized as a distinct genus, all other current genera would then emerge as well-supported groups.

Ohi-Toma et al. (2010) used six plastid genome regions (3' *trnL-trnF*, *rpl20-5' rps12*, *psbB-psbH*, *trnG* intron, *rpoC2-rps2* and *trnK* 3' intron) to analyse 17 species of *Typhonium* and 8 species from other genera of Areae (*Arum*, *Biarum*, *Helicodicerus*, *Theriotophonum*), using outgroup taxa from *Alocasia*, *Colocasia*, *Remusatia*, *Arisaema* and *Pinellia*. Their study originated from a pioneer molecular (RFLP) paper by Sriboonma et al. (1993), one of the first to be specifically aimed at Araceae systematics. The differences between this study and that of Cusimano et al. (2010) appear to concern mainly the topology above *Theriotophonum*. Cusimano et al. (2010) obtained two main clades in this part of the cladogram, one corresponding to *Sauromatum* and the other to the Mediterranean clade (*Arum*, *Biarum*, *Dracunculus*, *Eminium*, *Helicodicerus*). Ohi-Toma et al. (2010), with a much smaller number of species from Areae and from *Typhonium* s.l. (five species), obtained a polytomy of four monophyletic elements, one of which corresponds to the Mediterranean clade. From the other branches they described three new monospecific genera, *Hirsutiarum*, *Diversiarum* and *Pedatyphonium*. A consequence of both papers was the resurrection of *Sauromatum*.

Renner et al. (2004) studied 77 species of the large and widespread genus *Arisaema* using plastid DNA regions *trnL* intron, *trnL-trnF* spacer and *rpl20-rps12* spacer, with outgroups *Pinellia* and *Typhonium* s.l. (including *Sauromatum giganteum*, *S. hirsutum*, *S. horsfieldii*, *S. venosum*). Their aim was to test the monophyly of the genus and to elucidate the historical biogeography of the genus, which is represented today in Africa, Asia and North America. They found that the sister-group relationships of the North American species involved East Asian species in patterns comparable to those revealed in Orontioideae by Nie et al. (2006), discussed earlier. They also did not find a sister-group relation with

Pinellia, which had been the general view of taxonomists hitherto. Genetic structure studies of *Arisaema* using allozymes have been carried out by Boles (1996) and Maki and Murata (2001).

Mansion et al. (2008) sampled 20 of the 30 currently recognized species of *Arum*, but two yet more recent studies focussed exclusively on the genus *Arum*. Espínola et al. (2010) sampled 28 species of *Arum*, using *Dracunculus* and *Biarum* as outgroups using DNA sequences from the four plastid regions 3'*rps16*-5'*trnK*, *ndhA* intron, *psbD-trnT* and *rpl32-trnL*. These authors traced selected phenotypic characters, such as ploidy, tuber morphology, flower type and ratio of spadix length to spathe length, and carried out a historical biogeographic analysis, including dating and dispersal-vicariance analysis. Their molecular cladogram only agreed partially with the infrageneric classification proposed by Boyce (1993, 2006); the two subgenera *Arum* and *Gymnomesium* (the latter consisting of just *Arum pictum*) emerged, but these authors recommended replacing the current two sections of subgenera *Arum* by five sections corresponding to the main subclades obtained in their analysis.

Linz et al. (2010) analysed the species of *Arum* with molecular data from three plastid (*matK*, *rbcL*, *trnL*) regions, one nuclear (ITS1, 5.8S, ITS2) region and AFLPs to produce a cladogram of 24 species, with *Dracunculus* as outgroup. Besides the elucidation of a robust and well-resolved cladogram of the genus, their objective also included the establishment of a phylogenetic framework for interpreting the evolution of pollination syndromes within the genus. The cladistic result was in broad agreement with the classification of Boyce (1993, 2006) and allowed these authors to hypothesize that dung mimicry and hence pollination by coprophilous flies and beetles is the oldest pollination syndrome in the genus.

There are a number of fossils known from the *Pistia* clade. Wilde et al. (2005) placed the leaf fossil genus *Caladiosoma* possibly in Colocasieae or near to *Alocasia*, but also with equal probability in the Caladieae (*Amorphophallus* clade). Their assignment was based especially on the leaf venation of their new species (*C. messelense*) from the Middle Eocene Messel deposits of Germany. *Pistia* fruits and seeds are known from Siberia (*P. sibirica*, Oligocene, Kvaček and Bogner, 2008).

As discussed by Cabrera et al. (2008) and Cusimano et al. (2011), phylogenetic studies have so far not been able to establish stable positions for the genera *Zantedeschia*, *Montrichardia*, *Anubias* and *Calloopsis*. These taxa have always been considered isolated taxonomically and biogeographically, and many authors have placed them individually in monogeneric tribes. Recent molecular studies (Cabrera et al., 2008; Cusimano et al., 2011; Nauheimer et al., 2012b) have grouped *Calla* within the unisexual Araceae clade, despite some major phenotypic differences, as previously discussed; this placement requires further testing by future phylogenetic analyses. Herrera et al. (2008) have reported the first reliably authenticated fossil of *Montrichardia* from the Palaeocene of Colombia, *M. aquatica*.

9.11 Conclusions

There has been substantial progress in the phylogenetic understanding of Araceae since 1995, not only with the aid of molecular cladistics but also through palaeobotanical studies. It is becoming increasingly clear that further comparative morphological studies are needed to link these two data fields. Although it is surely now indisputable that comparative morphology has been largely superseded by molecular studies for establishing the phylogenetic framework of extant taxa, at least above species level, the same cannot be said when it comes to finding the optimal phylogenetic placement for the increasingly abundant and carefully worked fossil taxa. To make this procedure more precise it is indispensable to establish more reliable and easily accessible data from the morphological data fields most commonly represented in fossils (e.g. pollen, seeds and leaves) and to optimize the distributions of these characters on molecular cladograms to serve as a more reliable basis for palaeobotanical interpretations. Excellent contributions have been made in recent times in relevant fields, e.g. M. Hesse and colleagues for pollen (Hesse and Zetter, 2007), E. Seubert for seed structure (Seubert, 1993, 1997a, 1997b) and V. Wilde and colleagues for leaf venation (Wilde et al., 2005). The further development of such studies will help the dating of phylogenetic trees and the further progress of historical biogeographical studies, such as the important recent review with new analyses by Nauheimer et al. (2012b).

9.12 References

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