

The Impact of Recent DNA Studies on the Classification of Section *Pæonia*

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Summary of Modern DNA Sequence Studies



Analysis of DNA sequences is an extremely powerful tool for reconstructing complex evolution patterns in plants

► Recent studies applied to Peonies have uncovered some surprising new results

- The majority of species in section *Pæonia* are of hybrid origin
- *P. tenuifolia*, *p. anomala*, *p. veitchi* and *p. lactiflora* are probably the only species in section *pæonia* not derived from natural hybridization



The Peony Guru

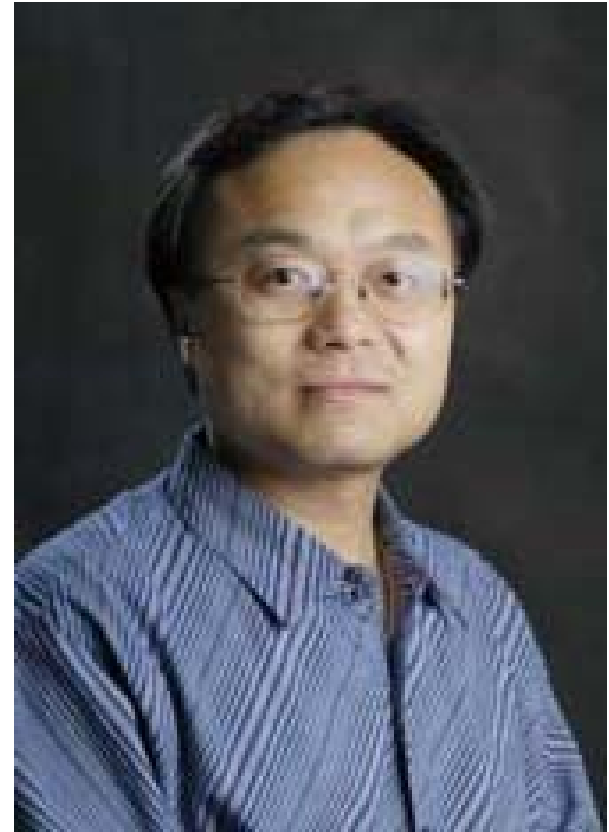


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Recent DNA Studies on Genus *Paeonia*



1. Sang, T., Crawford, D. J., & Stuessy, T.F. (1995) *Proc. Natl. Acad. Sci USA* 92, 6813-6817.
2. Sang, T., Crawford, D. J., & Stuessy, T.F. (1997) *Am. J. Bot.* 84, 1120-1136.
3. Sang, T. & Zhang, D. (1999) *Syst. Bot.* 24, 148-163.
4. Sang, T., Donoghue, M.J. & Zhang, D. (1997) *Mol. Biol. Evol.* 14, 994-1007.
5. Ferguson, D. & Sang, T., (2001) *Proc. Natl. Acad. Sci USA* 98, 3915-3919.
6. Sang, T. (1995) *Doctoral Dissertation, Ohio State University.*
7. Zhang, D. & Sang, T. (1999) *Am. J. Bot.* 86 (5), 735-740.
8. Zhang, D. & Sang, T. (1998) *Genome.* 41 (6), 848-853.
9. Tank, D.C. & Sang, T. (2001) *Mol. Phylogenet Evol.* 19 (3), 421-429.
10. Sang, T. (2002) *Critical Reviews in Biochemistry and Molecular Biology* 37: 121-147.
11. Sang, T. and Y. Zhong. (2000) *Systematic Biology* 49: 422-434.

Major Conclusions of Recent DNA Studies on Genus *Pæonia*



Various recent DNA sequence studies support the grouping of the genus into three (3) sections as proposed by Stern in 1946. These sections are:

Moutan

Onæpia

Pæonia

► Classification of the largest section (*Pæonia*) is complicated by the finding that significant natural hybridization has occurred within the section.

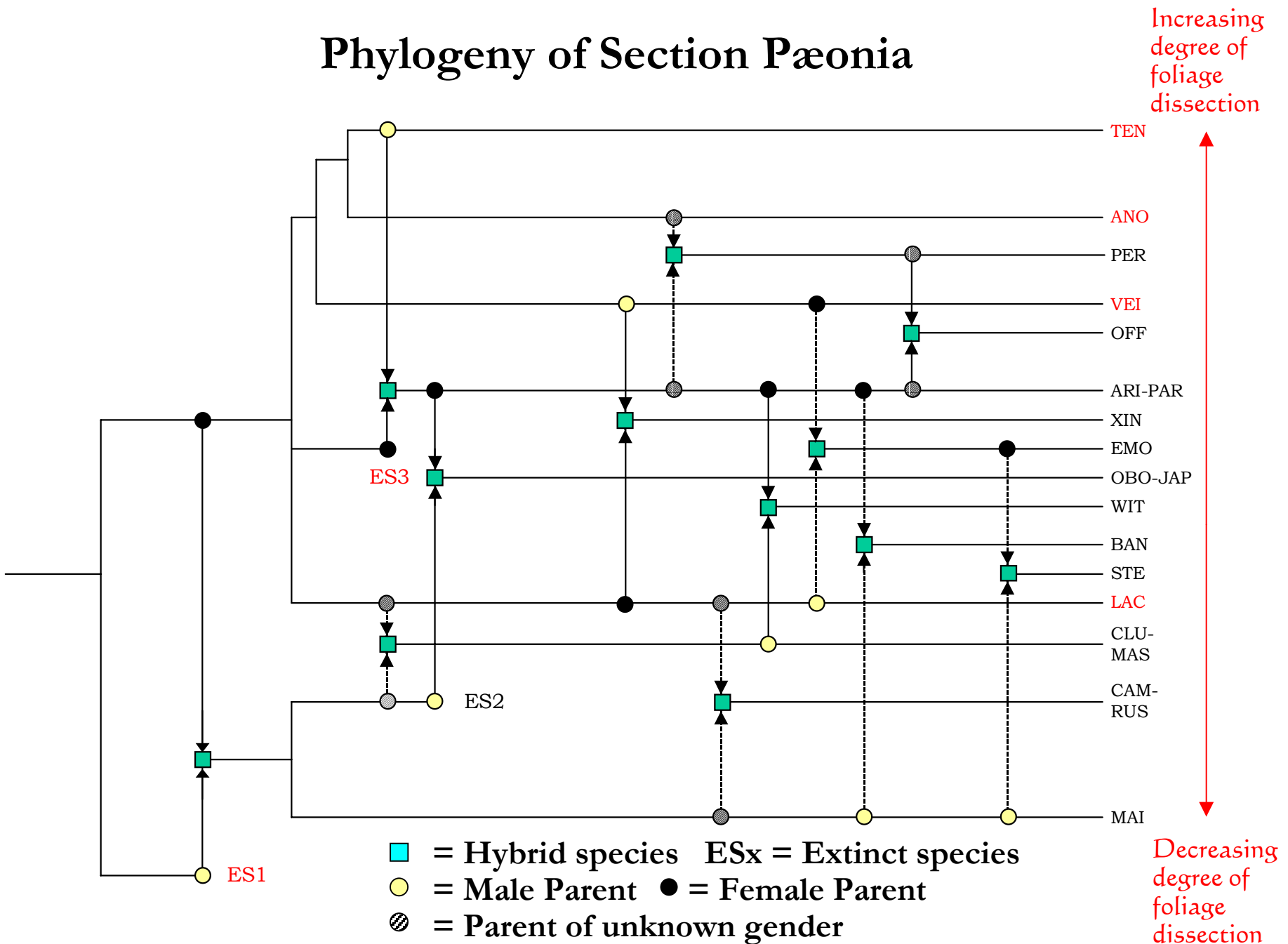


Key DNA Study on Genus Pæonia

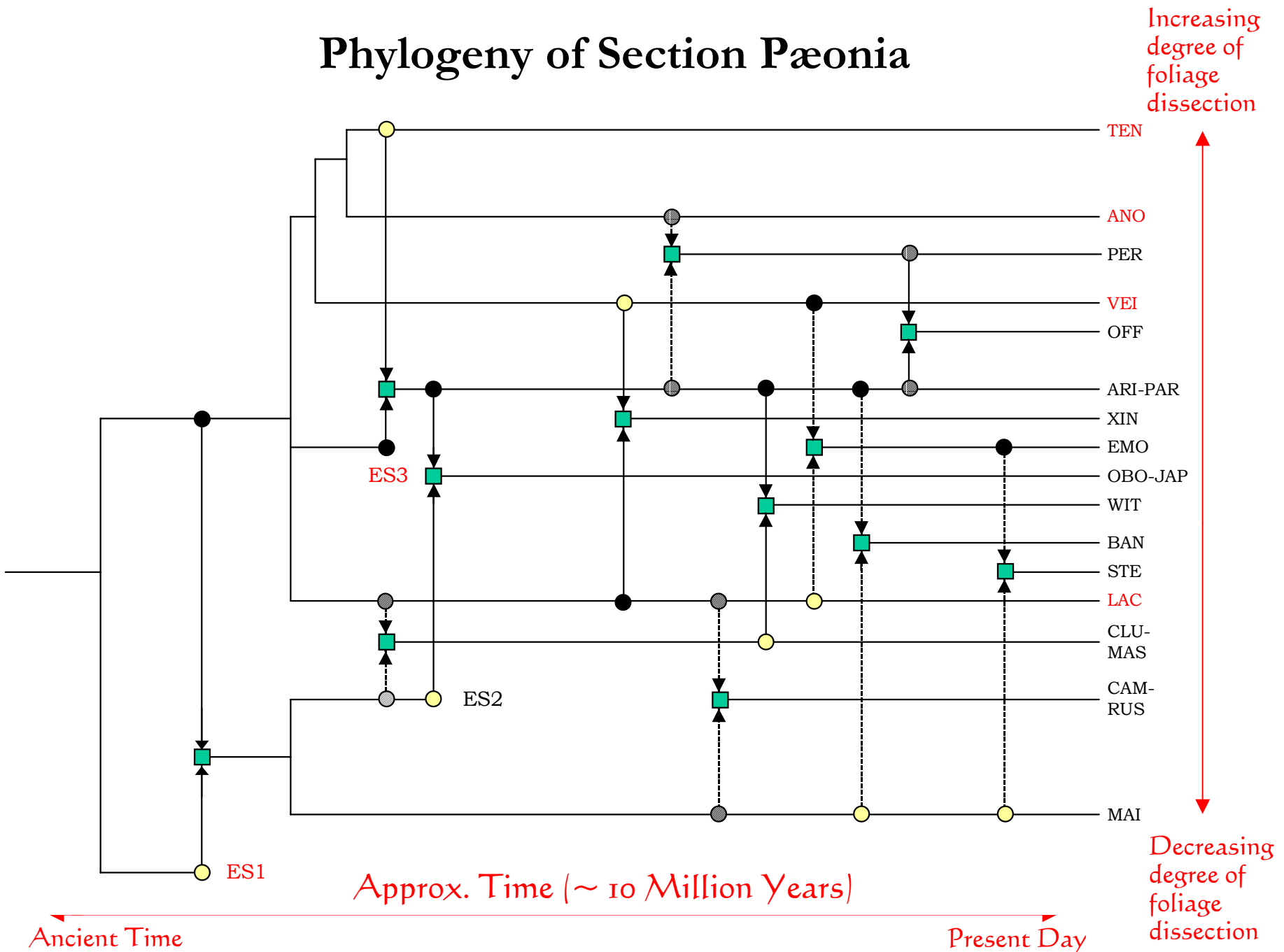


- The results and conclusions presented in this talk are based on numerous recent studies by Sang et al. The most important of these landmark studies is listed below:
 - Sang T., Crawford J. D., Stuessy T. F., Chloroplast DNA phylogeny, reticulate evolution and biogeography of Pæonia (Pæoniaceae), *American Journal of Botany*, 84 (8), 1120-1136, 1997.
- ◊ The phylogeny charts which follow are based primarily on Figure 7 (page 1131) from the above paper, but have been modified to include the results of more recent studies.

Phylogeny of Section Pæonia

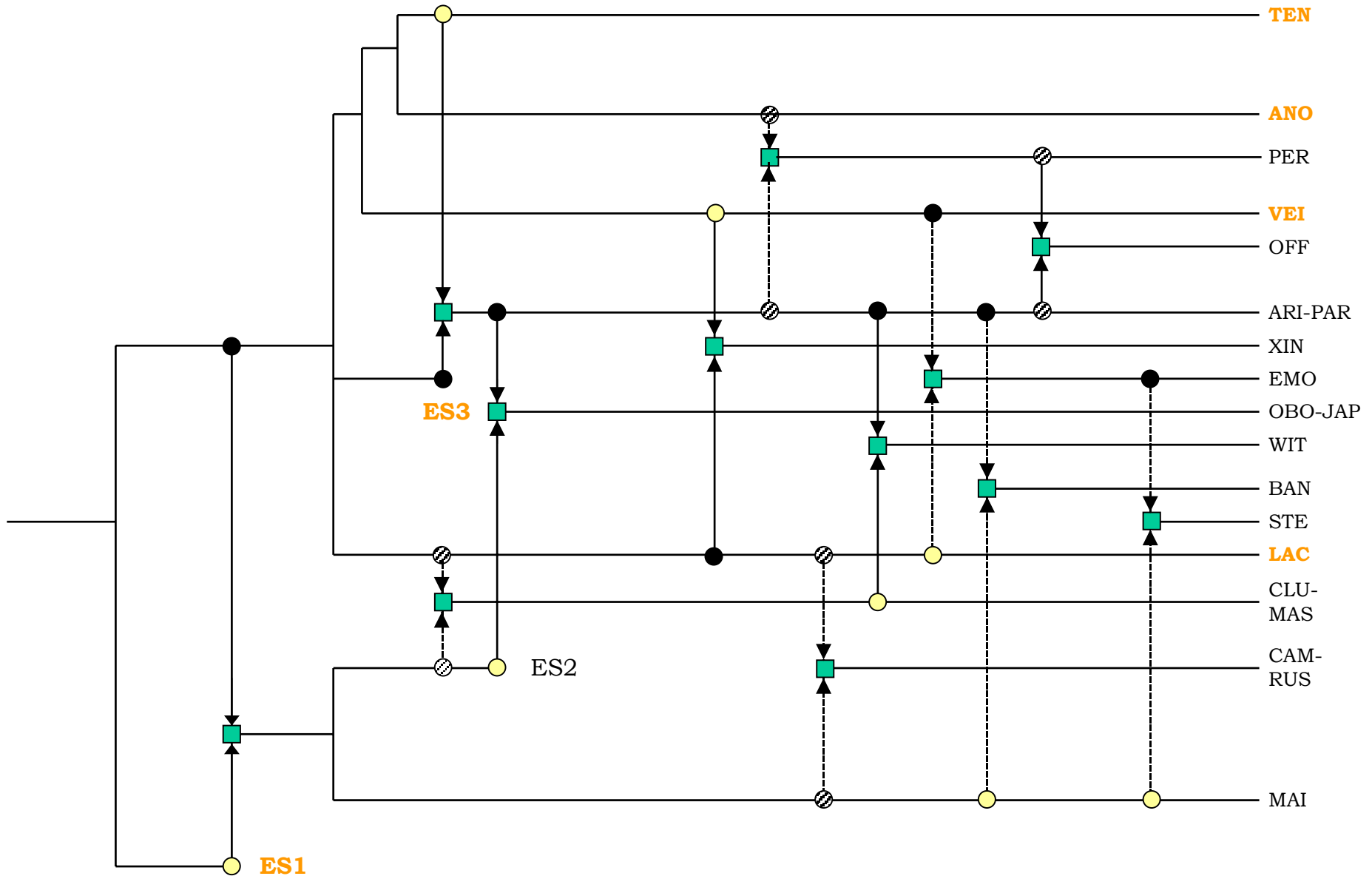


Phylogeny of Section Pæonia



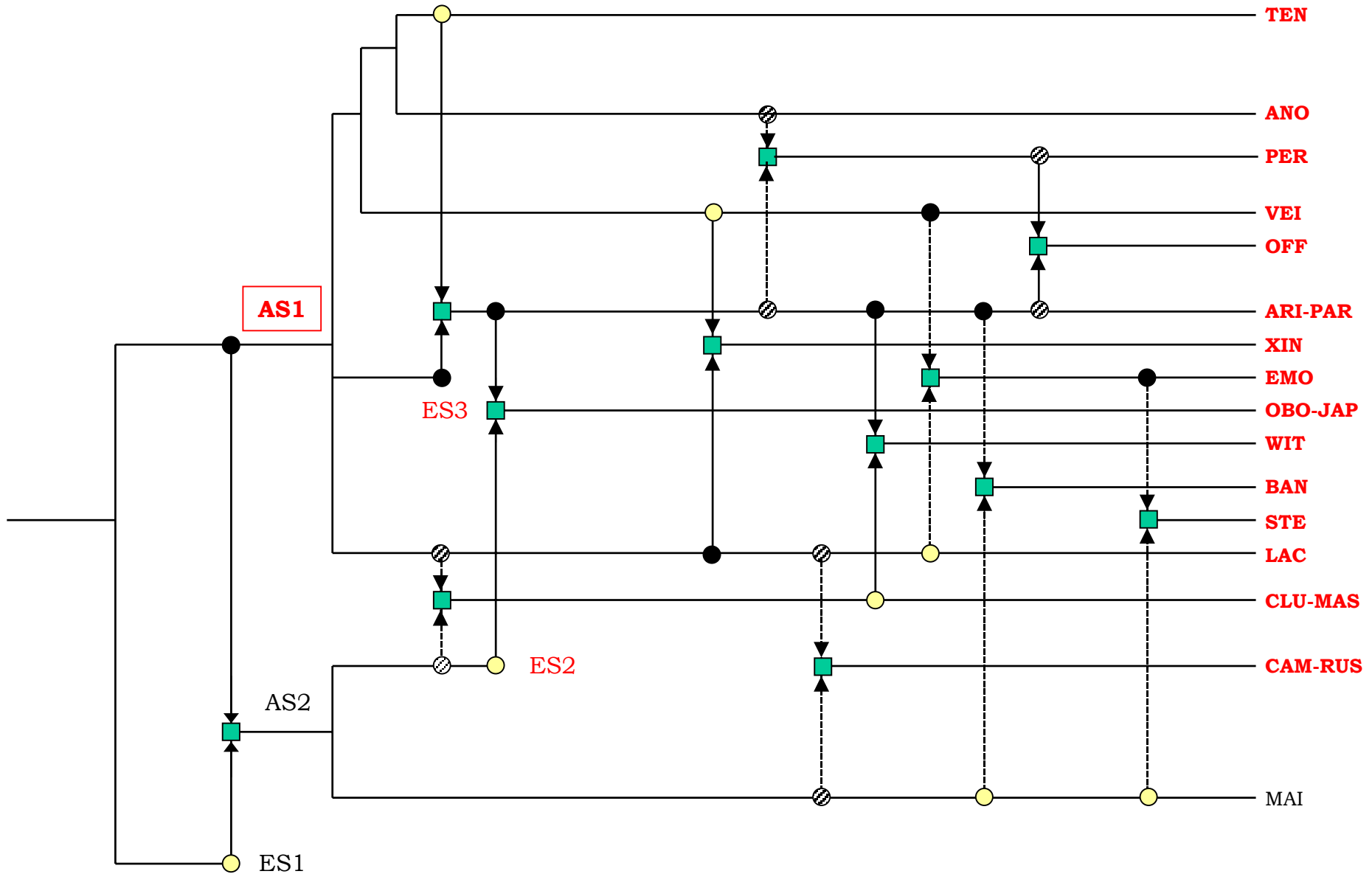
Phylogeny of Section Pæonia

Non-hybrid species in gold



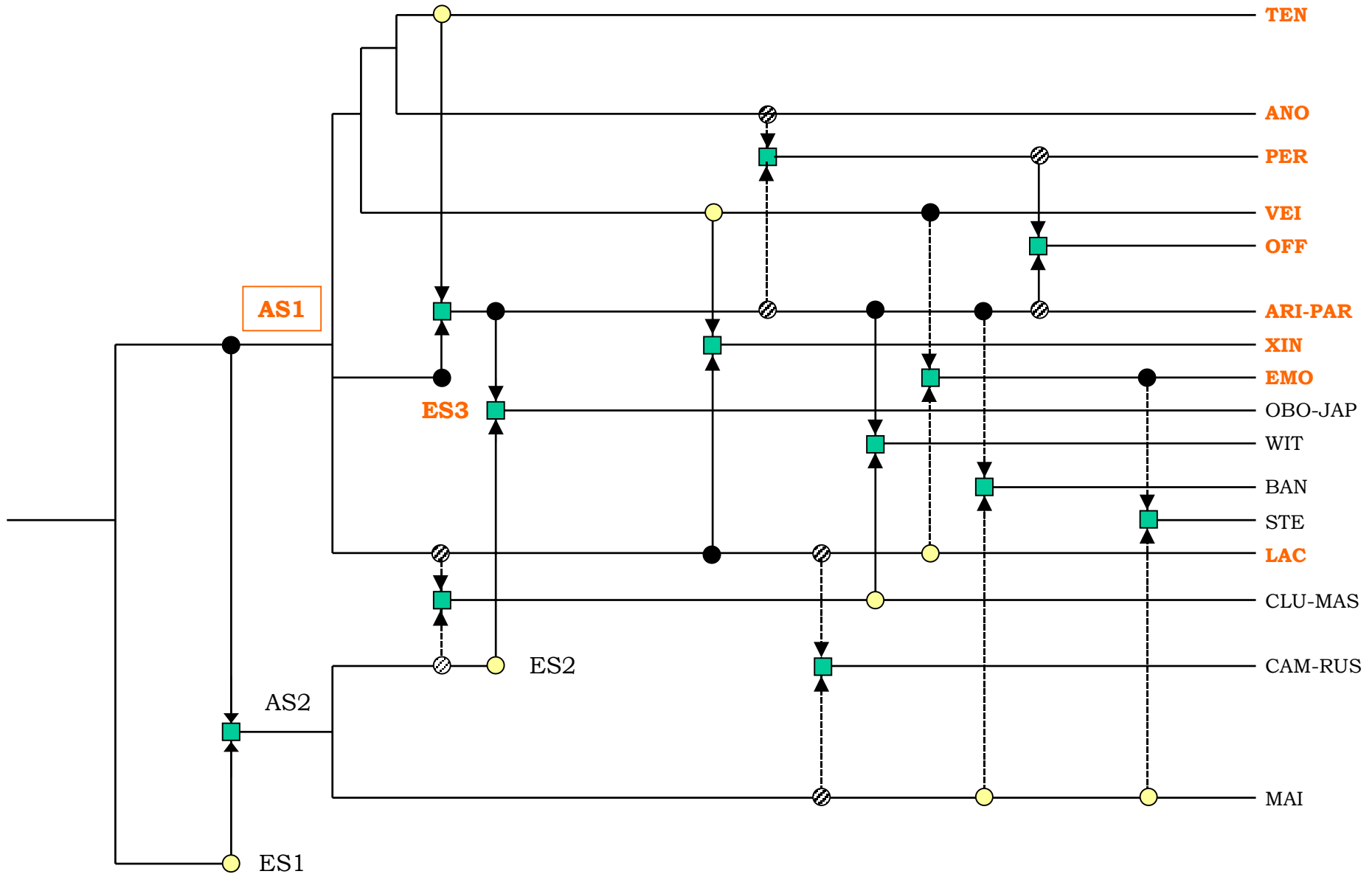
Phylogeny of Section Pæonia

Descendants of Ancient Species 1 (AS1) in Red



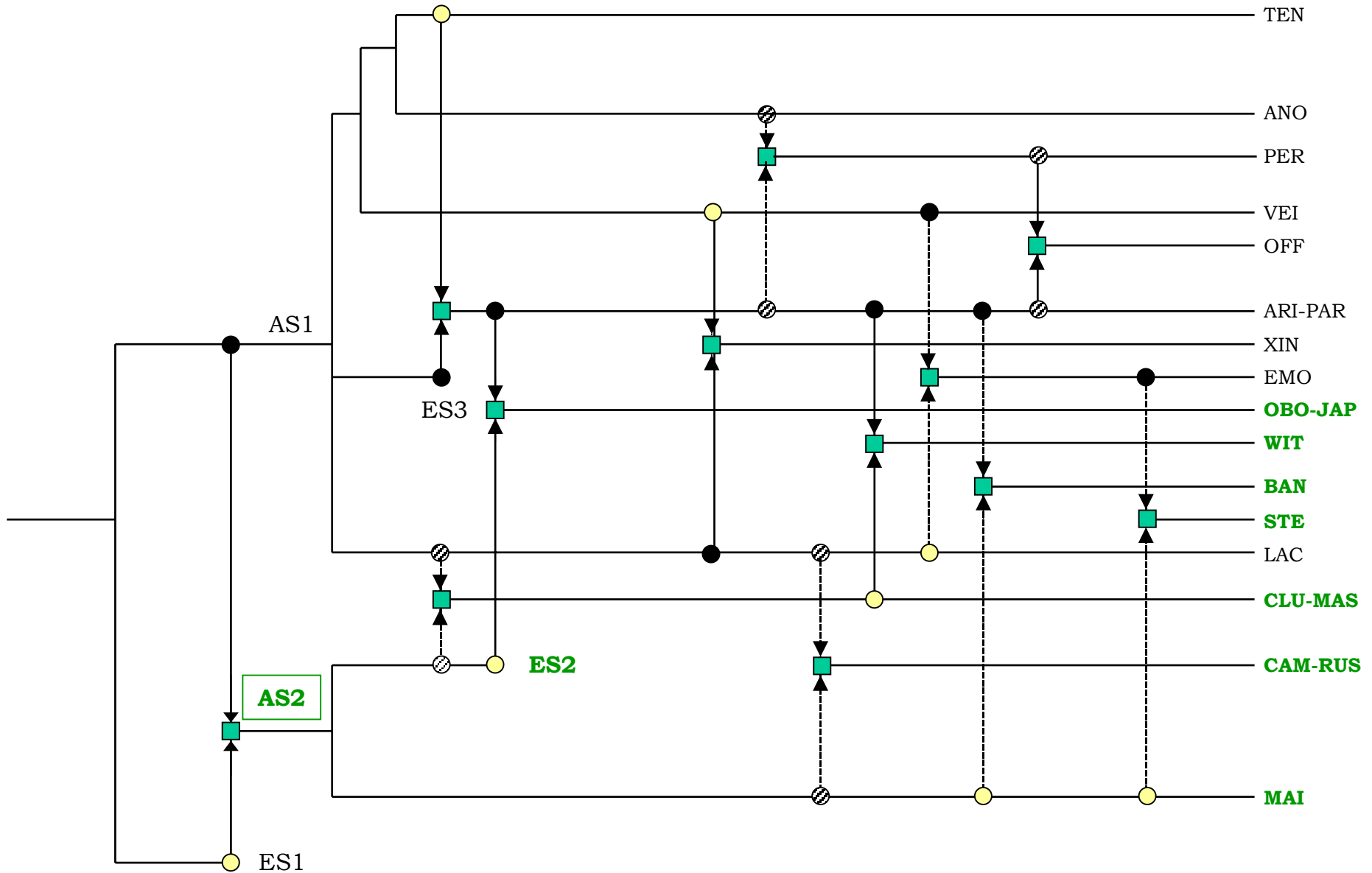
Phylogeny of Section Pæonia

Pure Descendants of Ancient Species 1 (AS1) in Orange



Phylogeny of Section Pæonia

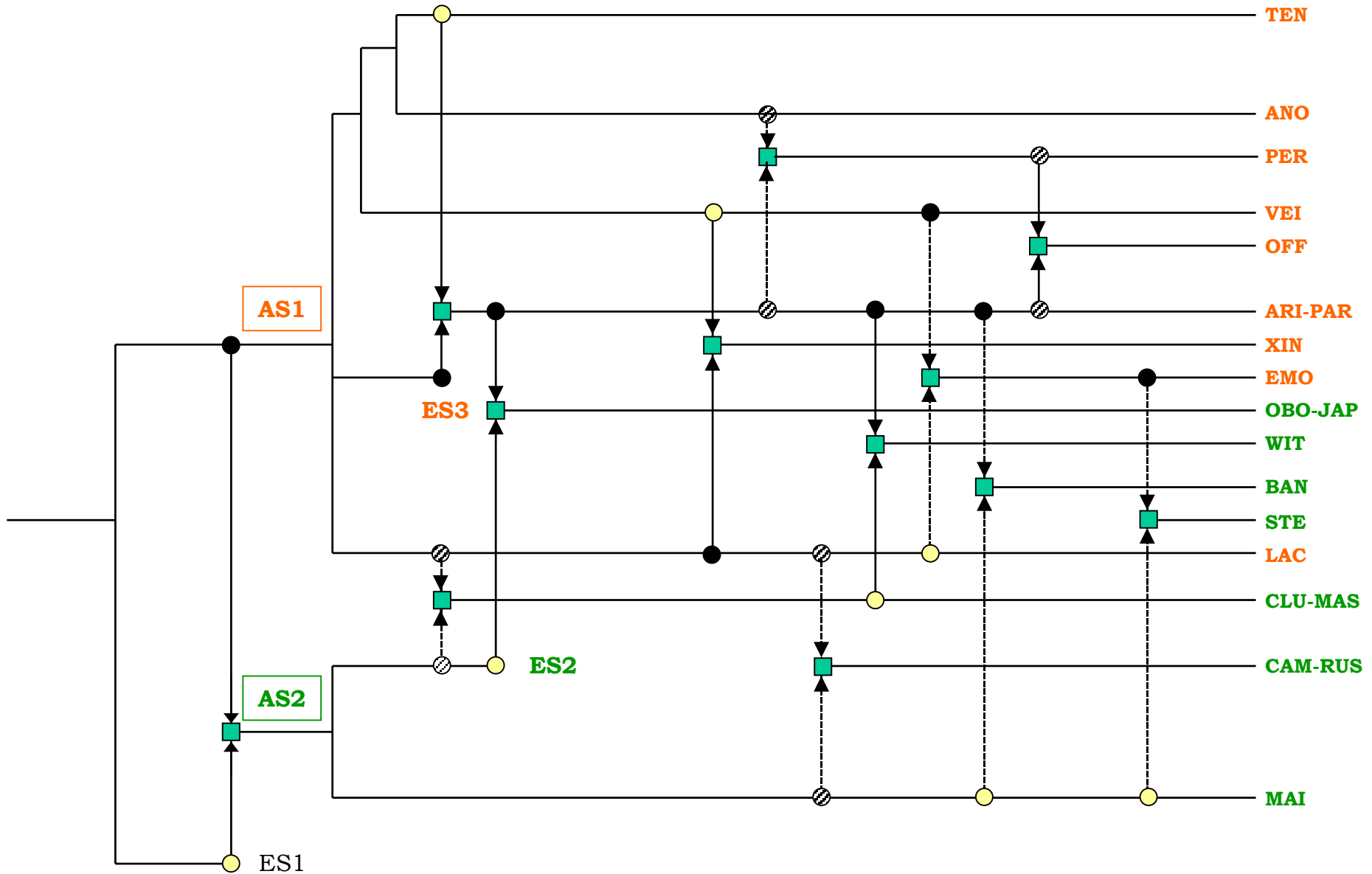
Descendants of Ancient Species 2 (AS2) in Green



Phylogeny of Section Pæonia

Pure Descendants of Ancient Species 1 (AS1) in Orange

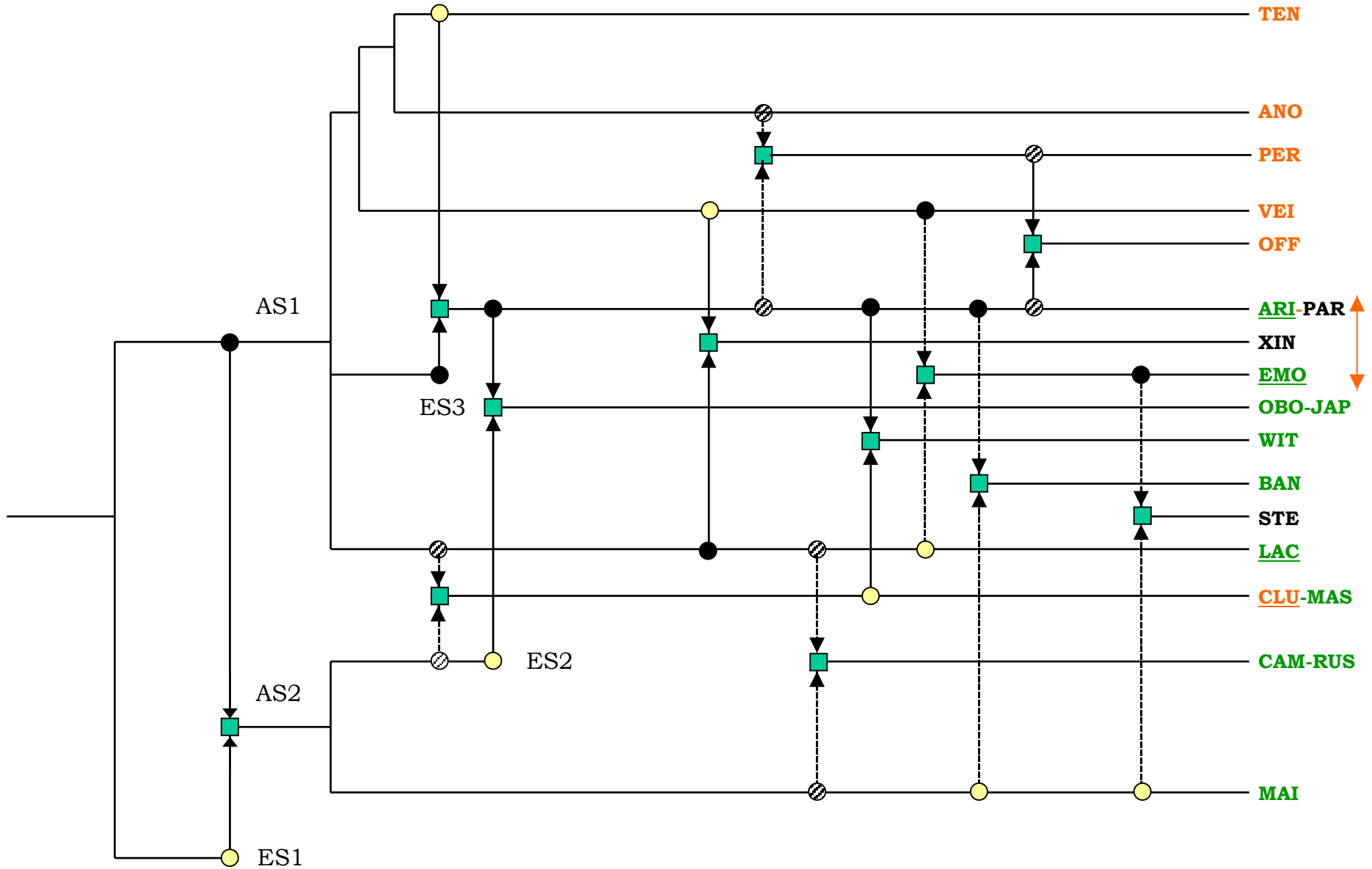
Descendants of Ancient Species 2 (AS2) in green



Phylogeny of Section Pæonia

Stern's Section Dissectifoliae

Stern's Section Foliolatae





DNA Sequence Analysis



Analyzing both nuclear and chloroplast (maternally inherited) DNA sequences allows identification of:

- ▶ Hybrid species
- ▶ Parental species (often including identification of maternal & paternal parents)
- ▶ Groups of closely related species sharing the same parentage (“Sister Groups”)
- ▶ Number and order of hybridization events (identification of double, triple, quad hybrids)
- ▶ Approx. time of origin (i.e., when the new hybrid species was created)



Surprising Conclusions



Two of the more surprising conclusions of these DNA sequence studies are:

- ▶ The high proportion of diploids among the hybrid species (9 of 21)
 - Hybrid species in nature are most often polyploids
- ▶ Most of the hybrid species are found in the Mediterranean region whereas their parental species are presently restricted to Asia



Summary of the Extinct Species in Section Paeonia



- DNA sequence studies have established that three (3) ancient species in section Paeonia are extinct:
 - ▶ Fortunately, many descendents of these extinct species still exist
 - ▶ This is known because the “fingerprints” (DNA sequences) of these ancient species can still be seen in the genes of their descendents.

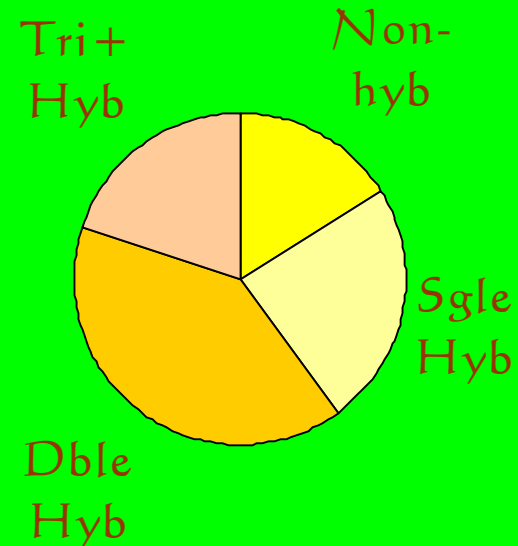


Hybrid Distribution of Section Paeonia Species



Hybrid Distribution of Species in Section Paeonia

Non-hybrids (4)	= 16%
Single Hybrids (6)	= 24%
Double Hybrids (10)	= 40%
Triple/Quad Hybrids (5)	= 20%
Total Hybrids (21)	= 84%
Total Species = 25	



Non-hybrid species make-up only about 1/6 of the total



Hybrid Status of Species in Section Pæonia



Summary of the 25 Species in Section Pæonia

Non-Hybrid Species	Single Hybrid Species	Double Hybrid Species	Triple or Quad Hybrid Species
Anomala	Mairei	Peregrina	Wittmanniana (4)
Veitchii	Emodi	Sterniana	Banatica
Tenuifolia	Xinjiangensis	Clusii	Obovata
Lactiflora	Arietina	Rhodia	Japonica
	Humilis	Broteri	Officinalis (4)
	Parnassica	Coriacea	
		Mlokozewitschi	
		Mascula	
		Cambessedesii	
		Russi	
4	6	10	5

Hybrid Species Produced by Other Species in Section Pæonia



Number of times each species in Section Pæonia was a parent of another hybrid species

Species	No. of Hybrids	Species	No. of Hybrids
<i>Anomala</i>	1	<i>Xinjiangensis</i>	0
<i>Veitchii</i>	2	<i>Sterniana</i>	0
<i>Tenuifolia</i>	1	<i>Cambessedesii</i>	0
<i>Lactiflora</i>	4	<i>Russi</i>	0
<i>Mairei</i>	3	<i>Wittmanniana</i>	0
<i>Emodi</i>	1	<i>Banatica</i>	0
<i>Arietina</i> - <i>Parnassica</i>	5	<i>Obovata</i>	0
<i>Clusii</i> - <i>Mascula</i>	1	<i>Japonica</i>	0
<i>Peregrina</i>	1	<i>Officinalis</i>	0
Extinct Species 1	1		
Extinct Species 2	2		
Extinct Species 3	1		



Distribution of Hybrid Species in Section *Pæonia*



Species grouped by relative age

<i>Ancient Species</i>	<i>Intermediate Species</i>	<i>Modern Species</i>
Tenuifolia	Emodi, Xinjiangensis	Sterniana
Anomala	Cambessedesii, Russi	Banatica
Veitchi	Peregrina	Officinalis
Lactiflora	Wittmanniana	
Mairei		
Clusii – Mascula Group		
Obovata, Japonica		
Arietina – Parnassica Group		



"Sister" Groups in Section Pæonia



Species which share the same parents are grouped into "sister" groups

Ari – Par Group	Clusii – Mascula Group	Obovata – Japonica Group
Arietina	Clusii	Obovata
Humilis	Rhodi	Japonica
Parnassica	Broteria	
	Coriacea	
	Mlokosewitschi	
	Mascula	



“Sister” Groups in Section Paeonia (Cont’d)



Species which share the same parents are grouped into “sister” groups

Cam – Rus Group		Emo – Xin Group
Cambessedesii		Emodi
Russi		Xinjiangensis



Closely Related Species That Share a Single Parent



Species which share one parent can be grouped into “step-sister” groups

Per – Off Group		Ban – Ste Group
Peregrina		Banatica
Officinalis		Sterniana



Distribution of Descendants in Section Paeonia



Descendants of AS _I	Descendants of AS ₂	Descendants of Both
Tenuifolia	Mairei	Cambessedesii, Russi
Anomala	Extinct Species 2	Clusii – Mascula Group
Veitchi		Sterniana
Lactiflora		Banatica
Emodi, Xinjiangensis		Obovata, Japonica
Peregrina, Officinalis		Wittmanniana
Ari – Par Group		

Impacts on the Classification of the Genus



Extensive natural hybridization within section *pæonia* has made the classification of this section extremely difficult

► Attempts to classify the herbaceous peonies solely from morphological characteristics without the knowledge of which species were derived from hybridization, will undoubtedly lead to inaccurate and erroneous results

• Therefore, all previous peony classifications based solely on morphological characteristics must be viewed as inadequate and thus should be rejected

– This includes the recent classification presented in the new Halda book, *The Genus Pæonia*

• Since the majority of species in section *Pæonia* are of hybrid origin, identification of these hybrid species is essential to an accurate classification of this section



Section Pæonia

Classification Restrictions



- For the purposes of classification, species in “sister” groups and “step-sister” groups must remain together :

- ▶ This limits the classification problem to the grouping of only 13 distinctly separate groups

- 4 non-hybrid species + 9 hybrid species groups



Classification Options for Section *Pæonia*



Option 1

Sub-section 1	Sub-section 2	Sub-section 3
<i>Tenuifolia</i>	<i>Mairei</i>	(<i>Cambessedesii</i> , <i>Russi</i>)
<i>Anomala</i>		<i>Clusii</i> – <i>Mascula</i> Group
<i>Veitchi</i>		<i>Sterniana</i>
<i>Lactiflora</i>		<i>Banatica</i>
(<i>Emodi</i> , <i>Xinjiangensis</i>)		(<i>Obovata</i> , <i>Japonica</i>)
(<i>Peregrina</i> , <i>Officinalis</i>)		<i>Wittmanniana</i>
<i>Ari</i> – <i>Par</i> Group		



Classification Options for Section *Pæonia*



Option 2

Sub-section 1		Sub-section 2
<i>Tenuifolia</i>		<i>Mairei</i>
<i>Anomala</i>		(<i>Cambessedesii</i> , <i>Russi</i>)
<i>Veitchi</i>		<i>Clusii</i> – <i>Mascula</i> Group
<i>Lactiflora</i>		<i>Sterniana</i>
(<i>Emodi</i> , <i>Xinjiangensis</i>)		<i>Banatica</i>
(<i>Peregrina</i> , <i>Officinalis</i>)		(<i>Obovata</i> , <i>Japonica</i>)
<i>Ari</i> – <i>Par</i> Group		<i>Wittmanniana</i>

Comparison of Classifications for Section *Pæonia*



Comparison with Classification of Stern(1946)

Sub-section 1		Sub-section 2
Tenuifolia	Only 4 of the 25 species were placed differently by Stern	Mairei
Anomala		Cambessedesii, Russi
Veitchi		Clusii – Mascula Group
Lactiflora		Sterniana
Emodi, Xinjiangensis		Banatica
Peregrina, Officinalis		Obovata, Japonica
Ari – Par Group		Wittmanniana



Classification Options for Section Pæonia



Option 3

Sub-section 1 (Dissectifolae)	Sub-section 2 (Foliolatae)	Sub-section 3 (Intermediatae)
Tenuifolia	Lactiflora	(Obovata, Japonica)
Anomala	Mairei	Sterniana
Veitchi	(Cambessedesii, Russi)	Banatica
Ari – Par Group	Clusii – Mascula Group	Wittmanniana
(Peregrina, Officinalis)	Extinct Species 1	(Emodi, Xinjiangensis)
Extinct Species 3	Extinct Species 2	



Proposed Re-classification for Section Pæonia



Proposed classification of Section Pæonia based on the work of Sang et al.

<i>Dissectifoliae</i>		<i>Foliolatae</i>
<i>Tenuifolia</i>		<i>Mairei</i>
<i>Anomala</i>		<i>Cambessedesii</i> , <i>Russi</i>
<i>Veitchi</i>		<i>Clusii</i> – <i>Mascula</i> Group
<i>Lactiflora</i>		<i>Sterniana</i>
<i>Emodi</i> , <i>Xinjiangensis</i>		<i>Banatica</i>
<i>Peregrina</i> , <i>Officinalis</i>		<i>Obovata</i> , <i>Japonica</i>
<i>Ari</i> – <i>Par</i> Group		<i>Wittmanniana</i>



Halda's Proposed New Classification of Genus *Paeonia*



Classification of Genus *Paeonia* proposed by Halda

<i>Albiflora</i>	<i>Emodi</i>	<i>Paeonia</i>	<i>Tenuifoliae</i>	<i>Flavonia</i>
<i>Lactiflora</i>	<i>Emodi</i>	<i>Peregrina</i> , <i>Officinalis</i> , <i>Banatica</i>	<i>Tenuifolia</i>	<i>Mlokozewitschii</i>
	<i>Sterniana</i>	<i>Ari – Par Group</i>		<i>Wittmanniana</i>
		<i>Clusii – Mascula Group</i>		
		<i>Cambessedesii</i> , <i>Russi</i>		
		<i>Anomala</i> , <i>Veitchi</i> , <i>Xinjiangensis</i>		
		<i>Obovata</i> , <i>Japonica</i> , <i>Mairei</i>		



Comments on Halda's New Classification



Halda's new classification of the genus does not hold up in the light of these recent DNA sequence studies :

- ▶ There is no DNA evidence to support the placing of *p. lactiflora* as a separate Sub-genus or even a separate Section. At best, *p. lactiflora* could only be treated as a separate sub-section under Section *Paeonia*
- ▶ Likewise, there is no evidence to support a separate section (or even a sub-section) for *Tenuifolia* or *Emodi*
- ▶ In addition, there is nothing to support placing the two yellow species, *p. mloko* and *p. wittmanniana*, into a separate section (or sub-section)



Parentage of Hybrid Species in Section *Pæonia*



Maternal Parent		Paternal Parent		Hybrid Species (11)
Lactiflora	x	Veitchii	=	Xinjiangensis
Veitchii	x	Lactiflora	=	Emodi
Emodi	x	Mairei	=	Sterniana
Ancient Species 1	x	Unknown <u>extinct</u> species 1	=	Mairei
Arietina-Parnassica Group	x	Clusii-Mascula Group	=	Wittmanniana
Arietina-Parnassica Group	x	Mairei	=	Banatica
Arietina-Parnassica Group	x	Unknown <u>extinct</u> species 2	=	Obovata
Arietina-Parnassica Group	x	Unknown <u>extinct</u> species 2	=	Japonica
Unknown <u>extinct</u> species 3	x	Tenuifolia	=	Arietina
Unknown <u>extinct</u> species 3	x	Tenuifolia	=	Humilis
Unknown <u>extinct</u> species 3	x	Tenuifolia	=	Parnassica



Parentage of Hybrid Species in Section Paeonia



Parent 1		Parent 2		Hybrid Species (10)
Anomala	x	Arietina- Parnassica Group	=	Peregrina
Lactiflora	x	Unknown <u>extinct</u> species 2	=	Clusii, Rhodia, Broteri
Lactiflora	x	Unknown <u>extinct</u> species 2	=	Coriacea, Mloko, Mascula
Lactiflora	x	Mairei	=	Cambessedesii, Russi
Arietina-Parnassica Group	x	Peregrina	=	Officinalis

Arietina- Parnassica Group = Arietina, Humilis, and Parnassica

Clusii-Mascula Group = Clusii, Rhodia, Broteri, Coriacea, Mlokosewitschi, Mascula



Conclusions of Recent DNA Studies on Pæonia



Analysis of recent DNA data supports the classification of the genus into three (3) sections :

Moutan

Onæpia

Pæonia

► Classification of the largest section (Pæonia) is complicated by the fact that significant natural hybridization has occurred within the section.

- However, it appears that only 2 or at most 3 sub-sections are needed to adequately group the approximately 25 species which make up this section



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