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PHYLOGENETIC AND PHYTOGEOGRAPHICAL RELATIONSHIPS IN MALOIDEAE (ROSACEAE) BASED ON MORPHOLOGICAL AND ANATOMICAL CHARACTERS

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SUMMARY

Phylogenetic relationships among 24 genera of Rosaceae subfam. Maloideae and Spiraeoideae are explored by means of a cladistic analysis; 16 morphological and anatomical characters were included in the analysis. Published suprageneric classifications and characters used in these classifications are briefly reviewed. Additionally, some new features are here reported, such as seed shape, presence or absence of endosperm, and number of cell layers in the seed coat and in the endosperm. Parsimony analyses indicate that *Eriobotrya* and *Rhaphiolepis* form a well-supported clade that is the sister to the remainder of the subfamily. This result is in agreement with published ITS sequence data. Other clades are not supported, with the exception of the group *Amelanchier–Peraphyllum–Malacomeles*. Results of several studies point toward North America as centre of origin for Maloideae, considering the distribution of closely related Spiraeoideae such as *Vauquelinia* and *Lindleia*. A non-metric multidimensional scaling analysis of Takhtajan's biogeographic regions was carried out using presence/absence of genera as characters. Eastern Asia is a centre of diversity from which the number of shared taxa decreases in several directions. This can be associated with the retreat of many taxa belonging to the Early Tertiary tropical-subtropical flora towards the refuges of China, Indochina and Malaysia, after wet-temperate forests were progressively transformed during the Neogene, which seems to be the case of *Eriobotrya* and *Rhaphiolepis*. Finally, *Osteomeles* and *Chamaemeles* were postulated as long-distance dispersion events while *Hesperomeles* could have originated in North America and migrated into north-western South America.

Key words: Rosaceae, Maloideae, morphology, anatomy, phylogenetic and phytogeographical relationships.

INTRODUCTION

Maloideae is a very important and intensively studied subfamily of the Rosaceae. Most of the genera are from temperate regions of the Northern Hemisphere, but there is an extension into southern Asia, *Hesperomeles* grows in South America, and *Osteomeles* reaches several South Pacific islands. The most significant character state of the subfamily are the pome fruits and the basic chromosome number x = 17 (Sax, 1931).

In the classification of subfam. Maloideae used by Robertson et al. (1991), 28 genera were included (Table 1). However, those generic concepts were not followed by all authors. Gabrielian (1978) and Phipps et al. (1990) circumscribed *Sorbus* in a broad

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Table 1. Comparison of different treatments of Maloideae at the generic level.

	Possible genera	Koehne (1890)	Robertson et al. (1991)	Aldasoro et al. (this paper)
Tribe Sorbeae according to Koehne (1890)	*Amelanchier* Medik.	*Amelanchier*	*Amelanchier*	*Amelanchier*
	Aria (Pers.) Host	*Aria*	*Aria*	*Sorbus* subg. *Aria*
	Aronia Medik.	*Aronia*	in *Photinia*	in *Photinia*
	Chaenomeles Lindl.	*Chaenomeles*	*Chaenomeles*	*Chaenomeles*
	Chamaemespilus Medik.	in *Aria*	*Chamaemespilus*	in *Sorbus* subg. *Aria*
	Chloromeles (Decne.) Decne.	in *Malus*	in *Malus*	in *Malus*
	Cormus Spach	*Cormus*	*Cormus*	*Sorbus* subg. *Cormus*
	Cydonia Mill.	*Cydonia*	*Cydonia*	*Cydonia*
	Docynia Decne.	*Docynia*	*Docynia*	*Docynia*
	Docyniopsis (C.K. Schneid.) Koidz.		*Docyniopsis*	*Malus* sect. *Docyniopsis*
	Eriobotrya Lindl.	*Eriobotrya*	*Eriobotrya*	*Eriobotrya*
	Eriolobus (DC.) M. Roem.	*Eriolobus*	*Eriolobus*	in *Malus*
	Heteromeles M. Roem.	in *Photinia*	*Heteromeles*	*Heteromeles*
	Malacomeles (Decne.) Engl.	in *Amelanchier*	*Malacomeles*	*Malacomeles*
	Malus Mill.	*Malus*	*Malus*	*Malus*
	Micromeles Decne.	*Micromeles*	in *Aria*	in *Sorbus* subg. *Aria*
	Peraphyllum Nutt.	*Peraphyllum*	*Peraphyllum*	*Peraphyllum*
	Photinia Lindl.	*Photinia*	*Photinia*	*Photinia*
	Pourthiaea Decne.	in *Photinia*	in *Photinia*	in *Photinia*
	Pseudocydonia (C.K. Schneid.) C.K. Schneid.	in *Chaenomeles*	*Pseudocydonia*	*Pseudocydonia*
	Pyrus L.	*Pyrus*	*Pyrus*	*Pyrus*
	Rhaphiolepis Lindl.	*Rhaphiolepis*	*Rhaphiolepis*	*Rhaphiolepis*
	Sorbus L.	*Sorbus*	*Sorbus*	*Sorbus*
	Stranvaesia Lindl.	*Stranvaesia*	in *Photinia*	in *Photinia*
	Torminalis Medik.	*Torminaria*	*Torminalis*	*Sorbus* subg. *Torminalis*
Tribe Crataegeae according to Koehne (1890)	*Chamaemeles* Lindl.	*Chamaemeles*	*Chamaemeles*	*Chamaemeles*
	Cotoneaster Medik.	*Cotoneaster*	*Cotoneaster*	*Cotoneaster*
	Crataegus L.	*Crataegus*	*Crataegus*	*Crataegus*
	Dichotomanthes S. Kurtz		*Dichotomanthes*	*Dichotomanthes*
	Hesperomeles Lindl.	*Hesperomeles*	*Hesperomeles*	*Hesperomeles*
	Mespilus L.	*Mespilus*	*Mespilus*	*Mespilus*
	Osteomeles Lindl.	*Osteomeles*	*Osteomeles*	*Osteomeles*
	Pyracantha M. Roem.	*Pyracantha*	*Pyracantha*	*Pyracantha*

sense, to include *Aria*, *Chamaemespilus*, *Cormus*, and *Torminalis*. Phipps et al. (1990) also considered *Malus* in a broad sense, i.e. to include *Eriolobus* and *Docyniopsis*, and accepted *Aronia* and *Stranvaesia* at generic rank. We have followed the system of Robertson et al. (1991), except that we include *Chamaemespilus* in *Sorbus* subg. *Aria* according to Phipps et al. (1990) and *Eriolobus* in *Malus* according to Rehder (1920, 1940) (Table 1).

Maloideae was formerly treated as a separate family by Gray (1821) under the name Pomaceae, a position that has had little support. According to Weber (1964) this group should be considered as a subfamily of Rosaceae and the name Pomoideae replaced by Maloideae. Neither Lindley (1822) nor Decaisne (1874), after a thorough study of this group, proposed any subgroup classification. Two different classifications of subfam. Maloideae have been proposed: Koehne (1890) divided the subfamily in tribes *Crataegeae*, wherein the ovary wall hardens and each carpel develops into a separate pyrene and *Sorbeae*, with a membranous to cartilaginous carpellary wall and connate carpels. However, according to Kalkman (1988) this subfamily should be divided into two informal groups: *Maleae* which has only two (rarely one) ovules per carpel as opposed to several ovules in the *Cydonia* group. Recent studies based on morphology (Phipps et al., 1991; Rohrer et al., 1991, 1994), wood anatomy (Zhang, 1992), and DNA (Campbell et al., 1995) do not support either of these divisions.

Past morphological studies included general vegetative habit and branching, bark, dormant buds, foliage, inflorescences, flower and pome features (Sterling, 1965a, b, c; Phipps et al., 1991; Rohrer et al., 1991, 1994). This generated a large set of characters from which Phipps et al. (1991) used some for their cladistic analysis. We concentrated our efforts on those which showed a presumably lower level of homoplasy. To supplement this set of characters we surveyed some anatomical characteristics of pomes and seeds, which seemed to be informative.

The pome has several features which provided more information, such as: the shape and distribution of sclereids and their groupings and the structure of pyrenes and pome locules (Gabrielian, 1978; Iketani & Ohashi, 1991; Rohrer et al., 1991, 1994; Aldasoro et al., 1998a, b). Taxonomically important variation in the seed structure of Rosaceae was discussed by Péchoutre (1902) and Danilova (1996). The most significant characters were seed size and shape, seed coat width, and presence and size of endosperm. According to Péchoutre (1902) the presence of endosperm is widespread in all groups of Maloideae and several other Rosaceae.

Cladistic and molecular systematic essays carried out to clarify the phylogeny of Maloideae came across with great difficulties caused by hybridization between genera in old and strongly homoplasic groups (Phipps et al., 1991; Campbell et al., 1995). Phipps et al. (1991) obtained trees with a low consistency index. Kalkman (1988) proposed a Gondwanic origin for Rosaceae and Thorne (1983) suggested that *Kageneckia*, with $2n = 34$, might be part of an ancient Gondwana stock which could have some relation with the origin of the subfamily. This could shift the origin to the Early Palaeogene or even to the end of the Cretaceous. Other evidences point toward a North American origin, such as the distribution of several closely related Spiraeoideae (*Kageneckia, Vauquelinia* and *Lindleia*) or the presence of a fossil related to these taxa: *Paleorosa similkameensis* (Eocene of British Columbia; Basinger, 1976).

Maloideae were already well diversified during the Early Tertiary. Several fossil remains of *Amelanchier*, *Cotoneaster*, *Crataegus*, *Eriobotrya*, *Heteromeles*, *Lyonothamnus*, *Malus*, *Mespilus*, *Peraphyllum*, *Photinia*, *Pyracantha*, *Pyrus*, *Rhaphiolepis*, *Sorbus* and *Vauquelinia* were reported from lower Eocene to Pliocene in North America, Asia, and Europe (Zhilin, 1974, 1989; Taylor, 1990) (Table 2). Unfortunately, those data are not sufficient to explain the grounds of current geographical distribution of Maloideae: some of the genera are not reported as fossils (i.e., *Osteomeles*, *Chamaemeles*, *Dichotomanthes*, *Cydonia*, *Pseudocydonia* or *Chaenomeles*), others are only reported in the Neogene (i.e., *Eriobotrya* and *Rhaphiolepis*) and some significant regions have no meaningful fossil record (i.e., Malaysia, Indo-China, and North Africa). Most Maloideae reports are based only on fossil leaves and should be viewed with some caution

Table 2. Selected fossil records of Maloideae and related Spiroideae (*Lyonotamnus*, *Vauquelinia* and possibly *Paleorosa*).

Age	Geographic area	Taxon	Reference
Eocene	North America (Thunder Mountain, Idaho)	*Sorbus oblongifolia* Axelrod, *Malus collardii* Axelrod, *Amelanchier deweyensis* Axelrod	Axelrod, 1998
	North America (NE Washington)	*Photinia* spec.	Wolfe & Wehr, 1987
	North America (Allenby Formation, British Columbia, Canada)	*Paleorosa similkameensis* Basinger	Basinger, 1976; Cevallos-Ferriz et al., 1993
	North America (Green River Formation, Colorado)	*Vauquelinia liniara* MacGinitie, *V. coloradensis* (Knowlton) MacGinitie, *Malus pseudocredneria* (Cockerell) MacGinitie, *Peraphyllum septentrionale* (Lesq.) Axelrod, *Crataegus* spec.	MacGinitie, 1969
	North America (Gulf of Alaska)	*Heteromeles cuprovalis* (Axelrod) Wolfe	Wolfe, 1977
	China (Litang, Relu Formation)	*Sorbus litangensis* S. Guo	Guo, 1986
	China (Weinan, Shensi)	*Crataegus* spec.	Jun-rong, 1965
Oligocene	North America (Creede formation, Colorado)	*Peraphyllum septentrionalis* (Lesq.) Axelrod, *Sorbus potentilloides* (Knowlton) Axelrod, *Crataegus creedensis* Axelrod	Axelrod, 1987
	North America (Florissant Beds, Colorado)	*Sorbus diversifolia* (Lesq.) Cockerell, *Vauquelinia liniare* MacGinitie, *V. coloradensis* (Knowlton) MacGinitie, *Malus pseudocredneria* (Cockerell) MacGinitie	MacGinitie, 1953
	North America (Bridge Creek Flora, Oregon)	*Amelanchier covea* (Chaney) Chaney & Axelrod, *A. grayi* Chaney, *Crataegus merriamii* (Knowlton) H.W. Mey. & Manchester, cf. *Pyracantha* spec.	Meyer & Manchester, 1997
	North America (Rujada Flora, Oregon)	*Pyrus oregonensis* R.N. Lakh., *Crataegus newberryi* Cockerell	Lakhanpal, 1958
	North America (Upper Ruby River Basin, SW Nevada)	*Sorbus carcharodonta* Gray	Becker, 1961
	SW China (Jinggu, Yunnan)	*Sorbus* spec.	Hsu, 1983
	C Asia (Ashcheayrykian, N Aral region)	*Sorbus gabrieljanae* Budantzev	Budantzev, 1959; Zhilin, 1989
	C Asia (Kumsuat, N Aral region)	*Sorbus praetorminalis* Kryshtop. & Baik.	Takhtajan et al., 1963
	W Europe (Italy)	*Pyracantha* spec.	Eberle, 1965
	W Europe (Altenburg, Germany)	*Pyracantha kräuselii* H. Walther, *P. acuticarpa* (C. Reid & E. Reid) Szafer	Mai & Walther, 1978
Miocene	North America (Purple Mountain, W Nevada)	*Crataegus gracilens* MacGinitie, *Heteromeles stenophylla* Axelrod, *Amelanchier nevadensis* Axelrod	Axelrod, 1995
	North America (Buffalo Canyon Flora, W Nevada)	*Amelanchier desatoyana* Axelrod, *Heteromeles desatoyana* Axelrod, *Crataegus middlegatei* Axelrod, *Sorbus cassiana* Axelrod, *Lyonothamnus parvifolius* (Axelrod) Wolfe	Axelrod, 1991

Table 2 (continued)

Age	Geographic area	Taxon	Reference
Miocene (continued)	North America (Pyramid Flora, W Nevada)	*Sorbus mcjanetii* Axelrod	Axelrod, 1992
	NE China (Shanwang, Shandung)	*Crataegus miocuneata* J. Hsu & R.W. Chaney, *Eriobotrya miojaponica* J. Hsu & R.W. Chaney, *Malus parahupehensis* J. Hsu & R.W. Chaney	Hsu & Chaney, 1940
	SW China (Wulong Formation, Xizang)	*Crataegus* spec.	Li & Guo, 1976
	SW China (Bangmai Formation, Lincang, W Yunnan)	*Cotoneaster salicifolium* Franch., *Stranvaesia cosmophylla*, *Sorbus* spec.	Guo, 1993
	W China (Lawula formation, Tibet)	*Sorbus* cf. *wilsoniana* C.K. Schneid.	Jun-rong & Nai-qiu, 1987
	SE India (Cuddalore series, Tamil Nadu)	*Photinioxylon* spec.	Lakhanpal, 1970
	Japan (Itahana and Ogawa formations)	*Sorbus hokiensis* Ozaki, *S. lesquereuxi* Nath., *S. paleojaponica* Murai, *S. uzenensis* Huzioka	Ozaki, 1991
	C Asia (Ustyurt, N Aral region)	*Crataegus oxiana* Zhilin	Budantzev, 1959; Zhilin, 1974
	C Asia (Samartskaia)	*Cotoneaster* cf. *andromedae* Ung., *Photinia acuminata* Baik., *Pyrus sarmatica* (Kryshtop.) Baik., *Pyracantha* spec., *Mespilus* spec.	Kryshtopovich & Baikovskaja, 1965
	NE Asia (Sikhote-Alin, Vladivostok)	*Sorbus lanceolata* Tanai & Suzuki, *S. morosovae* Akhmetjev, *Crataegus botchiensis* Akhmetjev	Akhmetjev, 1973
	NE Asia (Primorski Kray)	*Rhaphiolepis* spec.	Baikovskaja, 1974
	E Europe (Stare Gliwice, Upper Silesia, Poland)	*Pyracantha acuticarpa* Reid., *Crataegus* cf. *oxiacantha* L., *C. nodulosa* Reid.	Szafer, 1961
Miocene-Pliocene	SW China (Teng-chong basin, Yunnan)	*Sorbus aronioides* Rehder in C.S. Sargent, *S. hemsleyii* (C.K. Schneid.) Rehder in C.S. Sargent	Jun-rong & Nai-qiu, 1982
Pliocene	North America (Mulholand Flora, California)	*Photinia sonomensis* Axelrod, *Lyonothamnus mohaviensis* Axelrod	Axelrod, 1944
	North America (Hoogendorn Mine, NW Alaska)	*Crataegus* spec.	Wolfe, 1972
	Japan (Kabutoiwa formations)	*Sorbus lesquereuxi* Nath., *S. paleojaponica* Murai, *S. uzenensis* Huzioka	Ozaki, 1991
	E Europe (Czorsztyna, W Carpathians, Poland)	*Pyrus* cf. *communis* L., *Malus* sp. pl., *Sorbus* cf. *aucuparia* L., *Sorbus* sect. *Aria* Pers., *Crataegus pentagyna* Waldst. & Kit.	Szafer, 1954
	W Europe (Célas, Vallée du Rhône, France)	*Pyrus canescens* Spach	Depape, 1922
	NW South America (Guasca Valley formation, Colombia)	*Hesperomeles*	Wijninga & Kuhry, 1993

because there are many instances of convergence between their leaves and those of other families (Manchester, 1999).

The aim of the present work is to integrate phytogeographical, morphological and anatomical data and DNA results in order to elucidate intergeneric relationships within the subfamily Maloideae and to explain its current geographical distribution.

MATERIAL AND METHODS

Pomes of all genera of subfam. Maloideae were collected in Sir Harold Hillier Gardens and Arboretum, Royal Botanic Gardens at Kew, Wakehurst Gardens, University of Liverpool Botanic Gardens at Ness, Jardim Botânico da Madeira, and Real Jardín Botánico de Madrid and preserved in Kew mixture (Forman & Bridson, 1989) (Appendix). Seeds were cut with a razor blade both longitudinally and transversely in order to examine their internal structure. Transverse sections were taken at one third of the length of the pome from the bottom and photographed by optical microscopy. Other sections were made with a SLEE-MAINZ-MTC microtome and stained with Fasga mixture (Tolivia & Tolivia, 1987), a dye consisting of Safranin plus Alcyan green 2GX (Gurr Chemical Co.). Hence, the various plant structures were stained in different colours: cellulose walls in blue, sclerenchyma in pink, suberin in red, and tannins usually in reddish. Because malachite green stains cellulose walls (Alexander, 1980) it was used in some cuts to contrast sclereids against other parenchymatic cells. For scanning microscopy, seeds were sectioned with a microtome, glued on aluminium stubs, coated with 40–50 nm gold, and examined in a JEOL-TSM T330A scanning electron microscope (SEM) at 20 kV.

Table 3. Characters and character states.

1. Leaf persistence: 0 = deciduous; 1 = evergreen or semi-evergreen.
2. Stamen number: 0 = lower than 30; 1 = higher than 40.
3. Number and arrangement of ovules in the carpel: 0 = 2 collateral ovules per carpel; 1 = 2 superposed ovules per carpel; 2 = 1 ovule per carpel; 3 = 3 or more ovules collateral and superposed forming columns in each carpel.
4. Style manner of emergence from ovary: 0 = without a pit surrounding the style group; 1 = with a pit surrounding the style group.
5. Fruit in pome: 0 = absent; 1 = present.
6. Sclereid features: 0 = isolated sclereids; 1 = small groups; 2 = large and irregular groups; 3 = large and rounded groups.
7. Pyrene presence and arrangement: 0 = without pyrene; 1 = *Cotoneaster*-type pyrene; 2 = *Crataegus*-type pyrene; 3 = solitary pyrene.
8. False locular septa: 0 = absent; 1 = present.
9. Seed section: 0 = flattened; 1 = widely elliptic.
10. Ratio seed width/fruit width: 0 = seeds occupying less than one half of fruit width; 1 = seeds occupying more than one half of fruit width.
11. Seed shape: 0 = oval or rounded seeds in a indehiscent pome; 1 = winged seeds, in a dehiscent fruit.
12. Presence of endosperm: 0 = present; 1 = absent.
13. Number of endosperm layers: 0 = 2–4 layers; 1 = more than 5 layers.
14. Seed coat width: 0 = 1 or 2 layers; 1 = more than 3 layers.
15. Presence of Phloridzin: 0 = absent; 1 = present.
16. Chromosome number: 0 = $x \neq 17$; 1 = $x = 17$.

Table 4. Character matrix used of Rosaceae subfam. Maloideae with *Kageneckia* and *Vauquelinia* as outgroups. Polymorphic data are coded as ‘0,1’. See Table 3 for a list of characters and character states.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Kageneckia	1	0	3	0	0	0	0	0	0	0	1	0	0	0	0	1
Vauquelinia	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Amelanchier	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1
Chaenomeles	0	1	3	0	1	1	0	0	0	1	0	0	0	1	0	1
Chamaemeles	1	0	0	0	1	1	3	0	0	1	0	0	0	1	0	1
Cotoneaster	(0,1)	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1
Crataegus	0	0	1	0	1	1	2	0	0	1	0	0	1	0	0	1
Cydonia	0	0	3	1	1	2	0	0	0	1	0	0	0	1	0	1
Dichotomanthes	1	0	0	0	1	1	3	0	0	1	0	0	0	1	0	1
Docynia	1	1	3	0	1	1	0	0	0	1	0	0	0	1	1	1
Eriobotrya	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1
Hesperomeles	1	0	(1,2)	0	1	1	2	0	0	1	0	0	1	0	0	1
Heteromeles	1	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1
Malacomeles	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1
Malus	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1
Malus sect. *Docyniopsis*	0	1	0	0	1	1	0	0	0	1	0	0	0	1	1	1
Mespilus	0	0	1	0	1	1	2	0	0	1	0	0	1	0	0	1
Osteomeles	1	0	2	0	1	1	2	0	0	1	0	0	1	0	0	1
Peraphyllum	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1
Photinia	(0,1)	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1
Pseudocydonia	0	0	3	0	1	2	0	0	0	1	0	0	0	1	0	1
Pyracantha	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1
Pyrus	0	0	0	1	1	2	0	0	0	1	0	0	0	1	0	1
Rhaphiolepis	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1
Sorbus subg. *Sorbus*	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1
Sorbus subg. *Aria*	0	0	(0,1)	0	1	3	0	0	0	1	0	0	0	1	0	1
Sorbus subg. *Cormus*	0	0	0	0	1	3	0	0	0	1	0	0	0	1	0	1
Sorbus subg. *Torminaria*	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1

Sixteen morphological, anatomical and chemical characters (Table 3 & 4) were used in the cladistic analysis. Characters were compiled from literature or based on author’s observations of herbarium and living material. A description of character and character states are presented in the Results section. Several other characters were tested but they were finally excluded due to high homoplasy indexes (HI higher than 0.625) or because they are continuous and do not present any clear gap.

Cladistic analyses were carried out using the software package PAUP 4.0 beta (Swofford, 1998). All characters were unweighted and unordered, data were analyzed and trees were constructed by using heuristic search. Polarization of characters into plesiomorphic and apomorphic states was assessed by using the outgroup comparison (Watrous & Wheeler, 1981). MacClade version 3.04 (Maddison & Maddison, 1992) was used to edit the data set analyzed by PAUP, as well as to map the distribution of particular character state changes. Furthermore, a bootstrap analysis was conducted (Felsenstein, 1985).

In the present work, *Vauquelinia* and *Kageneckia* were selected as outgroups. They were generally considered as related to Maloideae because similarities in the configuration of ovary, fusion of carpels and floral vascularization (Sterling, 1965a, b, c, 1966; Evans & Dickinson, 1999). This relation was also suggested by Campbell et al. (1995) and Evans & Campbell (2002) after studying the ITS and GBSSI sequences. According to Kalkman (1988) *Vauquelinia* belongs to a clade including Osmaronieae, Pruneae, Kerrieae, and Quillajeae (*Exochorda* Lindl., *Lindleya* Kunth and *Vauquelinia*) which is considered as sister group of Maloideae. Phipps et al. (1991) considered *Vauquelinia* as "typically spiraeoid except in number and winged seeds". Other authors preferred to include *Vauquelinia* and *Kageneckia* in Maloideae (Goldblatt, 1976; Morgan et al., 1994; Takhtajan, 1997).

To determine distribution areas which were most similar based on the occurrence of genera, we compared the regions pairwise, with respect to presence or absence of genera (Holloway & Jardine, 1968; Hengeveld, 1990). The biogeographic system by Takhtajan (1986) was used for this comparison. A matrix of biogeographical regions versus taxa (presence or absence) was made and the regions were compared by using the index by Kulczynski (1928). This index is appropriate for examination of general biotic similarity based on the number of shared taxa. The matrix was then used to carry out a non-metric multi-dimensional scaling analysis (NMS), assessing the goodness of fit for the resulting spatial configurations through stress values (Kruskal & Wish, 1978). In order to interpret the plot, a minimum spanning tree (MST) was superposed upon the vectors to detect any undue distortion imposed on multidimensional configuration of regions (Dunn & Everitt, 1982). Finally, this tree was superposed on the map of biogeographic regions (Takhtajan, 1986). NMS analysis was carried out by using the NTSYS-pc 1.7 package (Rohlf, 1992).

Previously the areas of endemism were defined. An area of endemism is a geographic region to which one or more taxa are confined (Axelius, 1991). Using current methods to identify areas of endemism, we have defined 8 areas: a) Central Asia, West Asia, Europe, North Africa; b) South East Asia; c) East Pacific islands; d) Caucasus, Anatolia; e) Macaronesia; f) West North America; g) Central and South America; h) East North America. Most of these areas have endemic genera, but in some cases genera are shared by two areas, i.e., *Osteomeles* in b and c, or *Cormus* in a and d.

RESULTS

Character selection, definition and coding

The characters used in the analysis are listed in Table 3 and 5 and discussed below. Many characters were evaluated but excluded as uninformative at this level of analysis for being either autapomorphic or too variable within genera.

Character 1: Leaf persistence. According to Phipps et al. (1991) this character could be codified in the following states: 0 = deciduous, 1 = wintergreen, 2 = evergreen. However, we preferred to simplify it using only two character states (deciduous and evergreen or semi-evergreen).

Character 2: Stamen number. Phipps et al. (1991) considered lower numbers as primitive and higher as derived and codified this character in four states. We have simplified this character into two states with a clear gap: lower than 30, which is considered as primitive and higher than 40 (in *Chaenomeles*, *Docynia* and *Malus* sect. *Docyniopsis*) which is considered as derived. The most frequent number in

Maloideae c. 20, is also the number reported in *Vauquelinia* (18–20 according to Hess & Henrickson, 1987). Fewer than 10 stamens is only reported in *Crataegus macrosperma* (Rohrer et al., 1994).

Character 3: Number and arrangement of ovules. In subfamily Maloideae each carpel includes generally two ovules except for *Osteomeles* and some *Hesperomeles*, which have only one per carpel, and *Chaenomeles*, *Cydonia*, *Docynia* and *Pseudocydonia* which have more than three. Phipps et al. (1991) considered lower numbers as more primitive, codifying them from 1 to 4. However, we think that both numbers: lower and higher than two should be considered as derived.

In *Vauquelinia* and most Maloideae the ovule arrangement is collateral which can be considered as the primitive condition. It is superposed in *Crataegus*, *Mespilus*, and some species of *Hesperomeles* and *Sorbus* subg. *Aria*. Most *Hesperomeles* species have a solitary ovule per carpel but *Hesperomeles oblonga* Lindl. has two superposed ovules per carpel (Sterling, 1964). We also have found many *Sorbus* species, mainly from East Asia, which have superposed ovules (see also the drawings of *S. corymbifera* (Miq.) Tiep & Yakovlev by Kalkman (1973) and of *S. caloneura* by Stapf (1910)). The genera with more than 3 ovules per carpel (*Chaenomeles*, *Cydonia*, *Docynia*, *Pseudocydonia*) show both types of arrangement: collateral and superposed, and they usually have several columns of ovules in each carpel. In *Docynia* they are superposed in 1 or 2 columns of ovules. Also *Kageneckia* shows multiple ovules disposed in both types of arrangement. We propose that the state of two collateral ovules could have evolved into the other three states mentioned: one solitary ovule, two superposed ovules and more than three ovules.

Character 4: Style manner of emergence from ovary. The presence of a pit in the floral cup surrounding the style group is shared by *Cydonia* and *Pyrus*, while all the other taxa and the outgroup do not have this structure; consequently the presence of this pit should be considered as a derived state of character (Aldasoro et al., 1998a). Other Maloideae have styles which emerge fused or independently from the top of the ovary. The grade of style fusion varies frequently even within each genus and it was not useful in this analysis. *Dichotomanthes* has a remarkable autapomorphy, namely the style emerging laterally from the base of the carpel (Gladkova, 1969).

Character 5: Fruit types. The fleshy fruit formed by fusion of parts of hypanthium and carpels is a shared feature of Maloideae and is usually called pome. *Dichotomanthes* has a rather distinctive fruit with a fleshy hypanthium which covers the only hard carpel (pyrene) but both hypanthium and pyrene are independent. This special fruit is generally considered as an early pome (Rohrer et al., 1994). Moreover, in *Dichotomanthes* sclereid shape and stiffness are very similar to those with hard *Crataegus*-type pyrenes (data not shown). *Dichotomanthes* wood anatomy (Zhang & Baas, 1992) and flavonoid chemistry (Challice & Kovanda, 1981) are also similar to other Maloideae. Consequently, we preferred to consider the fruit of *Dichotomanthes* as a pome. On the other hand, all the Spiraeoideae have dry fruits: capsules, achenes or follicules.

Character 6: Sclereid features. Four main sclereid arrangement types could be distinguished in the flesh of Maloideae pomes: most of sclereids isolated, with some sparse small groups, as in *Eriobotrya* and *Rhaphiolepis*; all sclereids forming small groups (less than 10 sclereids), as in *Malus*, *Photinia* and *Sorbus* subg. *Sorbus*; large but

Table 5. Features of flower, pome and seed in Maloideae genera; * indicates data which were taken from Robertson et al. (1991) and ** from Decaisne (1874); those data were all corroborated and the rest were obtained during the present study.

Genus	Leaf	Flower			Pome
	Persistence*	Stamen number*	Ovule number/locule*	Ovule arrangement	Pyrene type*
Kageneckia	evergreen	18–20	>10	collateral and superposed	absent (achene internally sclerified)
Vauquelinia	evergreen	18–20	2	collateral	absent (achene internally sclerified)
Amelanchier	deciduous	20	2	collateral	absent
Chaenomeles	deciduous	40–55	>10	collateral and superposed	absent
Chamaemeles	evergreen	10–15	2	collateral	single
Cotoneaster	deciduous or evergreen	10–20	2	collateral	contiguous
Crataegus	deciduous	5–20	2	superposed	separated by flesh
Cydonia	deciduous	25	>10	collateral and superposed	absent
Dichotomanthes	evergreen	20	2	collateral	single
Docynia	evergreen or semi-evergreen	40	3–10	both positions, collateral and superposed	absent
Eriobotrya	evergreen	15–25	2	collateral	absent
Hesperomeles	evergreen	20	1, 2	superposed	separated by flesh
Heteromeles	evergreen	10	2	collateral	absent
Malacomeles	evergreen	10–20	2	collateral	absent
Malus	deciduous, evergreen or semi-evergreen	15–30 (in sect. *Docyniopsis* up to 55)	2	collateral	absent
Mespilus	deciduous	20–30	2	superposed	separated by flesh
Osteomeles	evergreen	20–25	1	–	separated by flesh
Peraphyllum	deciduous	20	2	collateral	absent
Photinia	deciduous, evergreen or semi-evergreen	20	2	collateral	absent
Pseudocydonia	deciduous	20	>10	collateral and superposed	absent
Pyracantha	evergreen	15–20	2	collateral	contiguous
Pyrus	deciduous	15–30	2	collateral	absent
Rhaphiolepis	evergreen	15–20	2	collateral	absent
Sorbus					
subg. *Aria*	deciduous	20	2	some superposed, other collateral	absent
subg. *Cormus*	deciduous	20	2	collateral	absent
subg. *Sorbus*	deciduous	20	2	collateral	absent
subg. *Torminaria*	deciduous	20	2	collateral	absent

Table 5 (continued)

Pome (cont.)	Seed						
Sclereid groups in the outer layer of pomes (flesh)	ratio seed width/pome width	Coat width (μm)	number of cell layers of seed coat	epidermis width (μm)	endosperm number of layers	cotyledon shape**	seed: equatorial section**
solitary or small	0.5–0.7	14–18	2, 3	20–30	2–4	hemi-ellipsoidal	narrowly elliptic and winged
solitary or small	0.5–0.7	14–16	1, 2	20–30	2, 3	hemi-ellipsoidal	narrowly elliptic and winged
small	0.5–0.7	100	4, 5	0–20	3, 4	hemi-ellipsoidal	elliptic
small	0.1–0.2	140	8	20	3, 4	hemi-ellipsoidal	elliptic
small	0.2–0.4	50–58	3–5	10–12	3, 4	spirally folded	elliptic
small	0.4–0.5	10–15	1, 2	20–30	4, 5	hemi-ellipsoidal	elliptic
small	0.2–0.5	23–30	1–3	15–20	5–16	hemi-ellipsoidal	elliptic
great irregular	0.1–0.2	130	5	60–90	2–4	hemi-ellipsoidal	elliptic
small	0.4–0.5	28–32	3, 4	20–25	2, 3	hemi-ellipsoidal	elliptic
small	0.29	150	6	50–70	3	hemi-ellipsoidal	elliptic
solitary or small	0.7–0.9	200–400	15–18	0–25	0	hemisphaeric	rounded or widely elliptic
small	0.3–0.4	10–20	1, 2	10–15	7–15	hemi-ellipsoidal	elliptic
small	0.28–0.31	60–65	3, 4	35–40	3	hemi-ellipsoidal	elliptic
small	0.5–0.7	100	4, 5	80	3, 4	hemi-ellipsoidal	elliptic
small	0.3–0.5	60–110	3, 4	18–70	3, 4	hemi-ellipsoidal	elliptic
small	0.28	10	1, 2	10	9–13	hemi-ellipsoidal	elliptic
small	0.3–0.5	30–60	1, 2	40–50	6, 7	hemi-ellipsoidal	elliptic
small	0.5–0.7	240	10	–	3, 4	hemi-ellipsoidal	elliptic
small	0.19–0.46	35–110	3–5	8–50	3, 4	hemi-ellipsoidal	elliptic
great irregular	0.1–1.2	120	4, 5	20	3, 4	hemi-ellipsoidal	elliptic
small	0.3–0.5	8–16	1, 2	10–15	3, 4	hemi-ellipsoidal	elliptic
great irregular	0.2–0.4	120–170	7–10	50–60	2–4	hemi-ellipsoidal	elliptic
solitary or small	0.7–0.9	100–250	8–15	–	0	hemisphaeric	rounded or widely elliptic
large rounded	0.2–0.5	85–200	3–7	0–25	3, 4	hemi-ellipsoidal	elliptic or narrowly elliptic
large rounded	0.3	150	5, 6	10	3	hemi-ellipsoidal	narrowly elliptic
small	0.2–0.4	50–180	3–5	14–30	4, 5	hemi-ellipsoidal	elliptic
small	0.44	100–240	4–6	30	3	hemi-ellipsoidal	elliptic

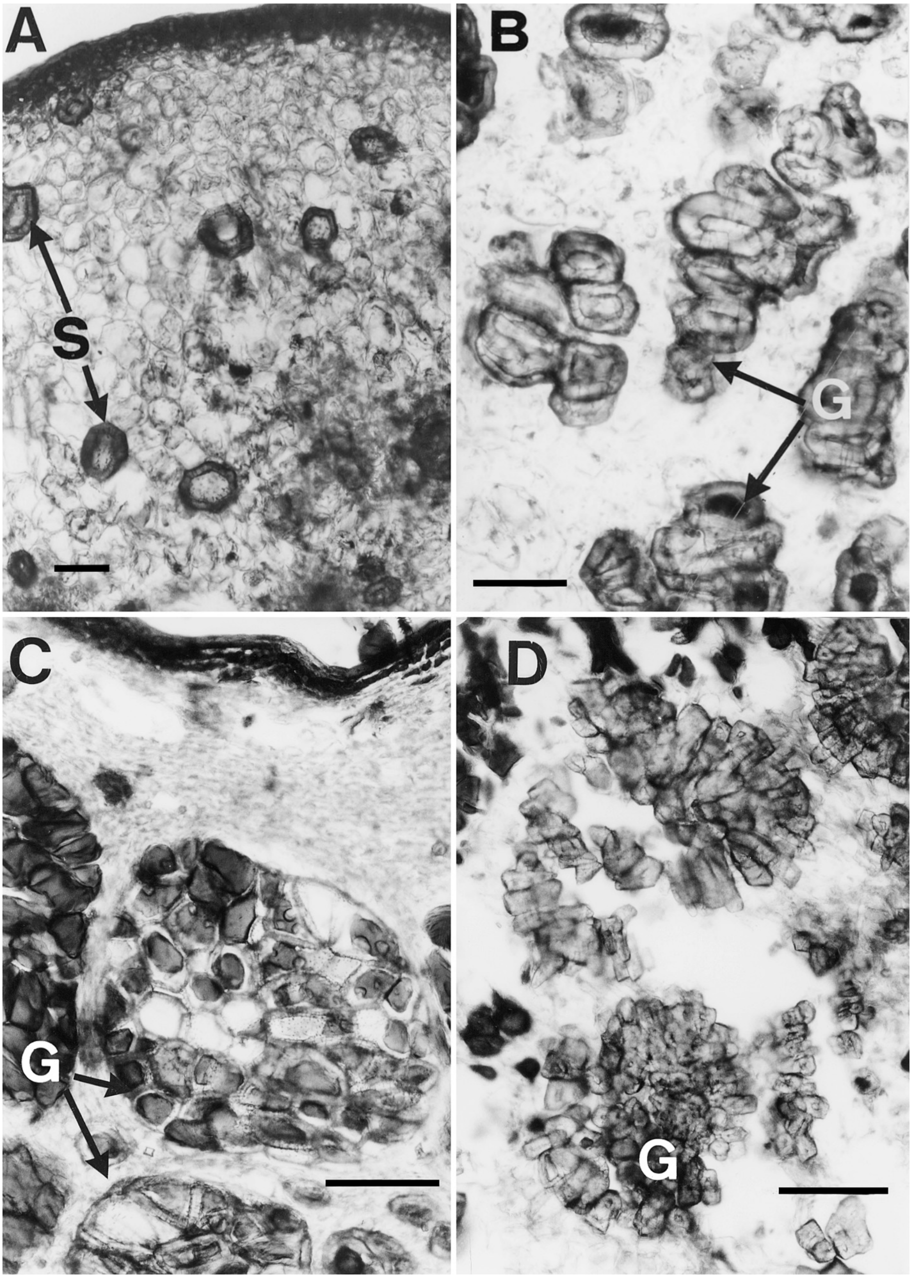

Fig. 1. Optical microphotographs of transverse cuts made of the pome flesh showing four types of sclereid arrangement. — A. *Eriobotrya benghalensis* (*Aldasoro 717*): isolated sclereids (S). — B. *Malus tschonoskii* (*Aldasoro 643*): small groups of sclereids (G). — C. *Sorbus lanata* (*Aldasoro 624*): rounded groups of sclereids (G). — D. *Pyrus syriaca* (*Aldasoro 668*): irregular groups of sclereids (G). Scale bars: A, B = 50 μm; C = 100 μm; D = 200 μm.

irregular groups, as in *Cydonia*, *Pyrus* and *Pseudocydonia*, and large and rounded groups, as in *Sorbus* subgenera *Aria* and *Cormus* (Fig. 1) (Aldasoro et al., 1998b). *Vauquelinia* and *Kageneckia* have small solitary sclereids more or less spread in the outer part of the pome and crowded sclereids in something similar to a pyrene in the inner part.

Isolated sclereids could evolve in several types of groups during the development of the subfamily: 1) small groups; 2) large and rounded groups showing a broad lumen; 3) large and irregular groups showing a small lumen with large walls; these states seem to be derived (Aldasoro et al., 1998a, b).

Character 7: Pyrene arrangement. Pulp structure in Maloideae may have been developed through the loss of sclerenchymatous cells (fleshy pomes) or through a specialized distributional pattern of sclerenchymatous cells (pyrene pomes), according to observations of Iketani & Ohashi (1991). The plesiomorphic condition seems to be a dry achene internally sclerified as in *Vauquelinia*. Three types of pyrenes could be distinguished in Maloideae (Phipps et al., 1991): 1) the *Cotoneaster*-type, with contiguous pyrenes, not separated by flesh (*Cotoneaster* and *Pyracantha*) (Fig. 2; Table 4); 2) the *Crataegus*-type with flesh separating the pyrenes (*Crataegus*, *Mespilus*, *Osteomeles* and *Hesperomeles*); 3) the solitary pyrene of *Dichotomanthes* and *Chamaemeles*. The remaining taxa of the subfamily have pomes without pyrenes. We found a layer of collapsed sclereids similar to an incipient pyrene surrounding the seeds of several *Malus* species. These layers were separated by flesh, as in the *Crataegus*-type pyrene. Phipps et al. (1991) suggested that the very hard pyrenes of the *Crataegus*-type have been derived from an hardening core like that of *Malus*, rather than a soft pyrene like *Pyracantha* and *Cotoneaster*.

Character 8: False locular septa. False septa partially divide locules in *Amelanchier*, *Malacomeles* and *Peraphyllum* (Rohrer et al., 1994). We have also simplified this character into two states (Phipps et al., 1991).

Character 9: Seed section. The outgroup and most of Maloideae have seeds with more or less flattened, elliptic equatorial sections, while *Eriobotrya* and *Rhaphiolepis* have a rounded or widely elliptic section. This characteristic seems to be meaning for

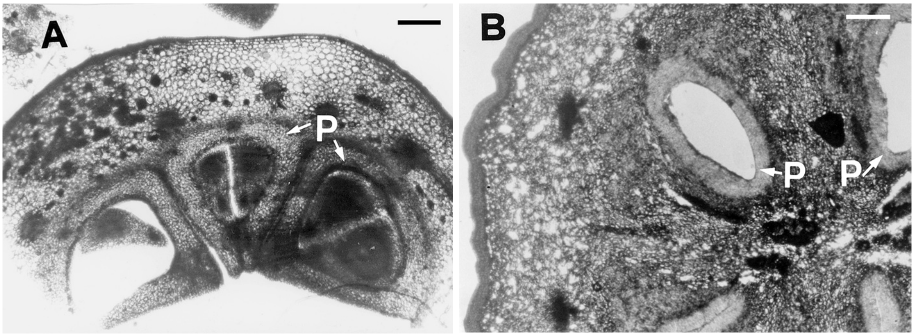

Fig. 2. Optical microphotographs of transverse cuts made of the pome showing pyrene types. — A. *Pyracantha crenatoserrata* (*Aldasoro 727*): connate pyrenes (P). — B. *Crataegus pentagyna* (*Aldasoro 682*): pyrenes separated by flesh (P). Scale bars = 0.5 mm.

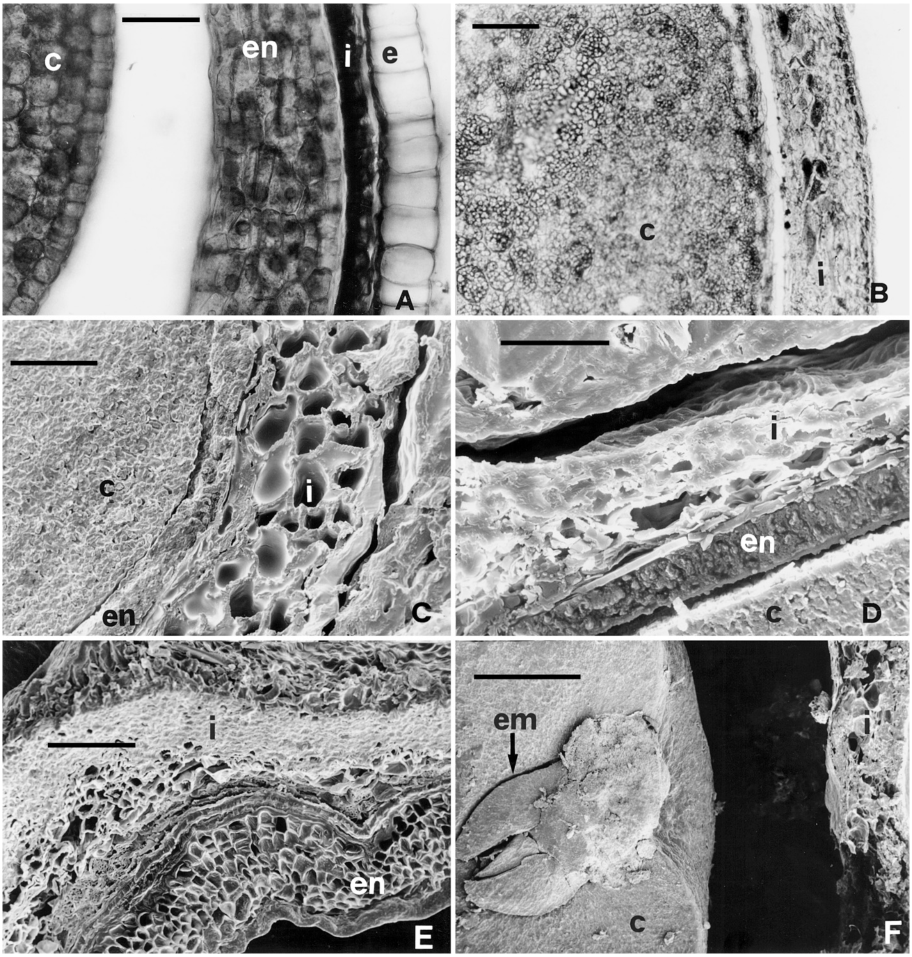

Fig. 3. Optical (A, B) and SEM (C–F) microphotographs of transverse cuts of seeds of subfam. Maloideae. — A. *Crataegus oresbia* (*Aldasoro 689*). — B. *Rhaphiolepis indica* (*Aldasoro 713*), endosperm absent. — C. *Photinia melanocarpa* (*Aldasoro 710*). — D. *Sorbus hemsleyi* (*Aldasoro 699*). — E. *Pyrus pashia* (*Aldasoro 641*). — F. *Rhaphiolepis indica* (*Aldasoro 713*), endosperm absent. — c = cotyledons, em = embryonic axis, en = endosperm, e = outer epidermis in palisade, i = integuments. Scale bars: A = 25 μm; B, C, E = 100 μm; D = 50 μm; F = 500 μm.

both genera, and we have considered the latter state as derived. It is interesting that both genera have proportionally larger seeds than other Maloideae and inhabit tropical or subtropical evergreen forests of South Eastern Asia (Vidal, 1965; Kalkman, 1973). Larger seeds survive longer in forest understorey under reduced light intensity (Foster, 1986). Moreover, *Eriobotrya* cotyledons are photosynthetic, greening during germination (Ernst, 1906).

Character 10: Ratio seed width/pome width. Some genera have seeds occupying more than one half of pome width, as is the case in *Amelanchier*, *Malacomeles*, *Peraphyllum*, *Eriobotrya* and *Rhaphiolepis*. The remaining genera have smaller seeds, occupying less than a 40% of pome width. Fleshiness of fruits is generally related to the type of dissemination by animals. Fruit dispersed by mammals generally have more flesh (Herrera, 1989) and should became more important after the Middle Tertiary (Tiffney, 1984; Primack, 1987).

Character 11: Seed shape. *Vauquelinia* and *Kageneckia,* which are closely related to Maloideae, show winged seeds, associated to anemochory and similar to those of some other Spiraeoideae. The rest of the genera have oval or rounded seeds included in the pome.

Character 12: Presence of endosperm. All *Eriobotrya* and *Rhaphiolepis* seeds studied in this work showed no endosperm development (Fig. 3B, F). Seeds of other genera of subfam. Maloideae retained variable amounts of endosperm. According to Péchoutre (1902) the presence of endosperm is widespread in many groups of Rosaceae, varying from a single layer in Roseae, Pruneae and Spiraeae, to 15 in some Maloideae (Table 4). Hess & Henrickson (1987) reported that seeds of *Vauquelinia* have no endosperm; however, we found in seeds of this genus 2 or 3 layers of endosperm cells.

Character 13: Number of endosperm layers. As it was previously mentioned, some genera of Maloideae have a more developed endosperm, as is the case in *Crataegus*, *Hesperomeles*, *Mespilus* and *Osteomeles*, which have the thickest endosperm consisting of more than 5 layers (Fig. 3A, Table 4). The endosperm of the remaining genera is generally 2–4 layers thick (Fig. 3C–E). Considering that the outgroups have 2 or 3 layers, some genera of Maloideae could have evolved towards an increase in the number of layers (*Crataegus, Hesperomeles, Mespilus* and *Osteomeles*), while others could loose it (*Eriobotrya* and *Rhaphiolepis*).

Character 14: Number of seed coat layers. The seed coat is most developed in *Erio botrya* and *Rhaphiolepis* seed, species showing 8–18 layers of cells (Table 4). *Pyrus*, *Sorbus* subg. *Aria* and subg. *Torminaria* seeds have testas with 3–10 cell layers. Some taxa with pyrenes such as *Chamaemeles* and *Dichotomanthes* have 3–5 layers, but in most of them (*Cotoneaster, Crataegus, Mespilus, Osteomeles* and *Pyracantha*) the testa has only 1 or 2 layers. *Vauquelinia* has a thin 1- or 2-layered testa with a conspicuous epidermis. A mucilaginous epidermis characterizes some species of *Cydonia*, *Malacomeles*, *Malus* sect. *Eriolobus* and *Photinia*, while in the other genera it was absent.

Character 15: Presence of Phloridzin (phloretin 2'-glucoside). Challice (1973) and Williams (1982) studied leaf phenolics in subfamily Maloideae reporting that the presence of this dihydrochalkone is a common feature in *Docynia*, *Malus* and *Malus* sect. *Docyniopsis*. Phloridzin is absent in the outgroups (Challice, 1974).

Character 16: Chromosome number. The basic chromosome number $x = 17$ is shared by some Spiraeoideae (*Kageneckia* and *Lindleia*) and all Maloideae, while *Vauquelinia* has $x = 15$.

Cladistic analysis

The cladistic analysis with equal weighting gave 702 minimal length cladograms, consisting of 35 steps, a consistency index (CI) of 0.771, a retention index (RI) of 0.851, a rescaled consistency index (RC) of 0.657, and a homoplasy index (HI) of 0.371. The strict consensus tree is showed in Fig. 4.

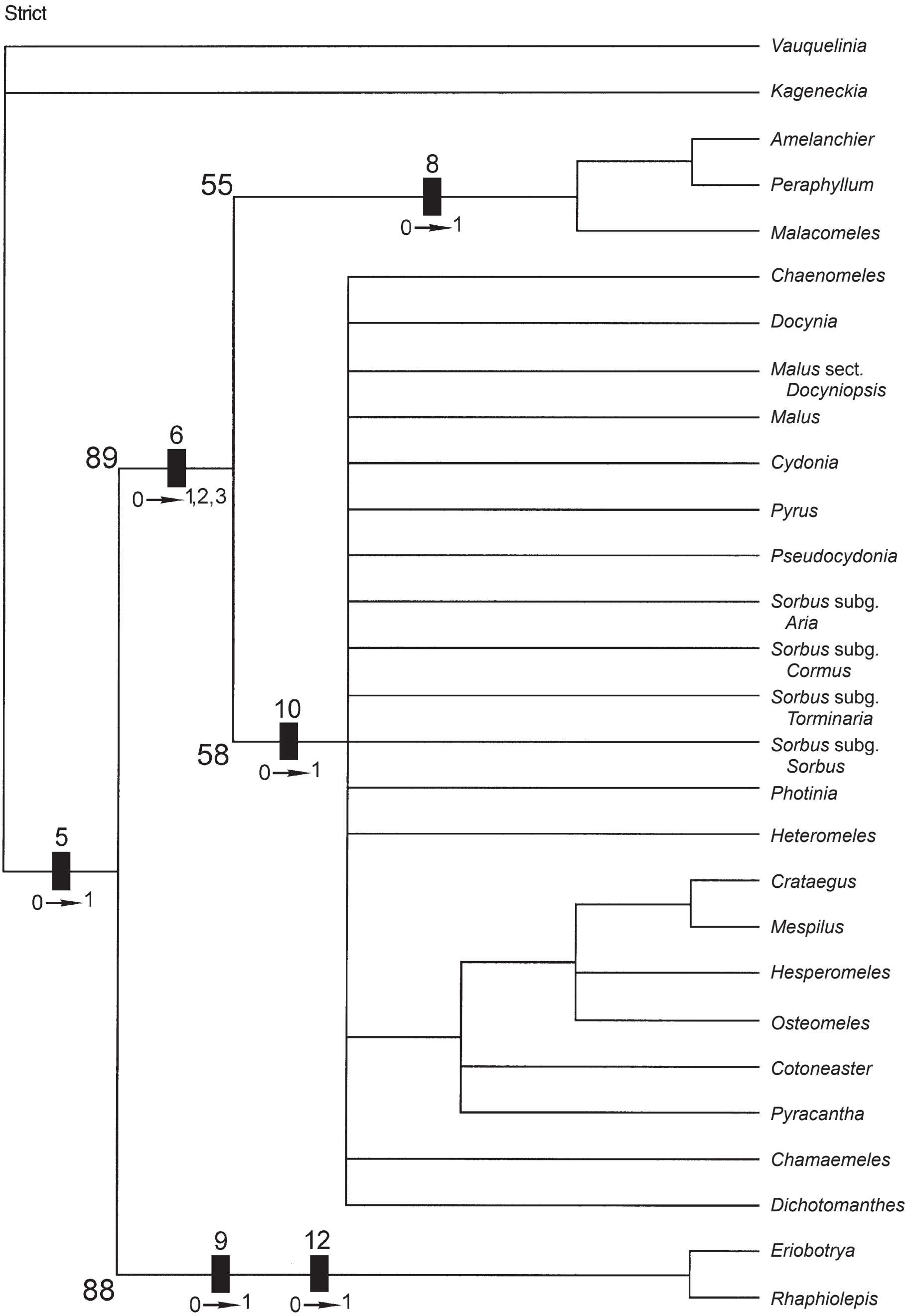

Fig. 4. Strict consensus of 702 most parsimonious trees based on the complete dataset. Number above branches indicates bootstrap values from 100 replicates. Solid bars are synapomorphies, above each bar the character number is shown and below are the changes suffered by its states; numbers beside the clades are bootstrap supports (only those higher than 50% are showed).

The consensus tree is not fully resolved and there is considerable homoplasy. The consensus tree shows several weak clades which were not firmly supported by the bootstrap values (Fig. 4). However, several groupings are constant. The ingroup is supported by one synapomorphy: the fruit in pome (character 5), while the outgroups share the winged seeds (character 11). The chromosome number x = 17 is also shared by two Spiraeoideae: *Lindleia* and *Kageneckia*, and consequently it is not a synapomorphy of Maloideae.

In the tree showed in Fig. 4 there are two major groups: one formed by *Eriobotrya* and *Rhaphiolepis* and another including the remaining genera. The first clade has a high bootstrap support and has two synapomorphic characters (9 and 12), while the second clade is supported by only one (6). Characters 9 and 12 are: the presence of rounded or widely elliptic seeds, and the absence of endosperm, respectively. The loss of endosperm seems an important feature, until now not found in any of the studied Maloideae (Péchoutre, 1902; Danilova, 1996; Takhtajan, 1997).

The second clade, including all the remaining genera of Maloideae, has low bootstrap values and is supported only by the presence of groups of sclereids in the flesh (character 6). There is a minor clade in this group formed by *Malacomeles*, *Peraphyllum* and *Amelanchier*, genera which shared a synapomorphy: the false septa dividing the locules in each carpel (character 8). They have small pseudoberry pomes with sparse groups of sclereids and without any layer of collapsed sclereids protecting the seeds. The rest of the taxa are in a group supported by character 10: they have more fleshy pomes (measured by a lower ratio seed length/pome length). The relations within this clade have not been fully solved as shown in the strict consensus tree (Fig. 4). The only recognisable group in this clade is formed by the genera with *Crataegus*-type pyrenes.

Analysis of regions

The sixteen regions used for this study varied in taxon richness from one genus (i.e., Fiji, Hawaiian, Polynesian and Andean Regions) to fifteen genera from the Eastern Asiatic Region: seventeen, if all the taxa used in cladistic analysis are considered (Fig. 5). The areas of highest endemism were the Eastern Asiatic Region with *Dichotomanthes* and *Pseudocydonia* (Tsun-shen et al., 1993) and the Madrean with *Heteromeles* and *Peraphyllum* (Axelrod, 1958; Raven & Axelrod, 1974). *Malacomeles* is almost endemic, living only in two regions: Madrean and Caribbean. Some other genera like *Docynia* have a very restricted distribution in the east of the Himalayas, extending in the limits of the Eastern Asiatic, Indochinese and Indian Regions (Browicz, 1969). Also *Eriobotrya* and *Rhaphiolepis* are restricted to the Eastern Asiatic, Indochinese, Malaysian and Indian Regions (Vidal, 1965). Another region with endemic genera is Macaronesia (with *Chamaemeles*). Two genera have disjunct distribution areas; they are: *Osteomeles*, which grows in East Asia and in many Pacific islands (Van Steenis & Van Balgooy, 1966), and *Photinia*, which is present in North and Central America and East Asia (Table 6). *Pyracantha* and *Pyrus* have two separate nuclei in the Palearctic Region: one in East Asia and the other in Europe (Browicz, 1992). 53% of Eastern Asiatic genera are evergreen while in the Indochinese and Malaysian Regions the percentages are 75% and 80%, respectively. The proportion of evergreens decreased towards the west: in the Indian Region 71.4% while in the Irano-Turanian Region it

Table 6. Distribution of genera of Maloideae in Takhtajan (1986) biogeographic regions. Acronyms to genera are: *Amelanchier* (AME), *Chaenomeles* (CHA), *Chamaemeles* (CHM), *Cotoneaster* (COT), *Crataegus* (CRA), *Cydonia* (CYD), *Dichotomanthes* (DIC), *Docynia* (DOC), *Eriobotrya* (ERI), *Hesperomeles* (HES), *Heteromeles* (HET), *Malacomeles* (MAC), *Malus* (MAL), *Mespilus* (MES), *Osteomeles* (OST), *Peraphyllum* (PER), *Photinia* (PHO), *Pseudocydonia* (PSE), *Pyracantha* (PRC), *Pyrus* (PYR), *Rhaphiolepis* (RHA), *Sorbus* (SOR).

Region	AME	CHA	CHM	COT	CRA	CYD	DIC	DOC	ERI	HES	HET	MAC	MAL	MES	OST	PER	PHO	PSE	PRC	PYR	RHA	SOR
Circumboreal	1	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1
Eastern Asiatic	1	1	0	1	1	0	1	1	1	0	0	0	1	0	1	0	1	1	1	1	1	1
N American Atlantic	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1
Rocky Mountain	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Macaronesian	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mediterranean	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1
Irano-Turanian	1	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1
Madrean	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	1
Sudano-Zambezian	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1
Indian	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	1
Indochinese	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1
Malaysian	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	1
Hawaiian	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Caribbean	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0
Andean	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Fijian	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Polynesian	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

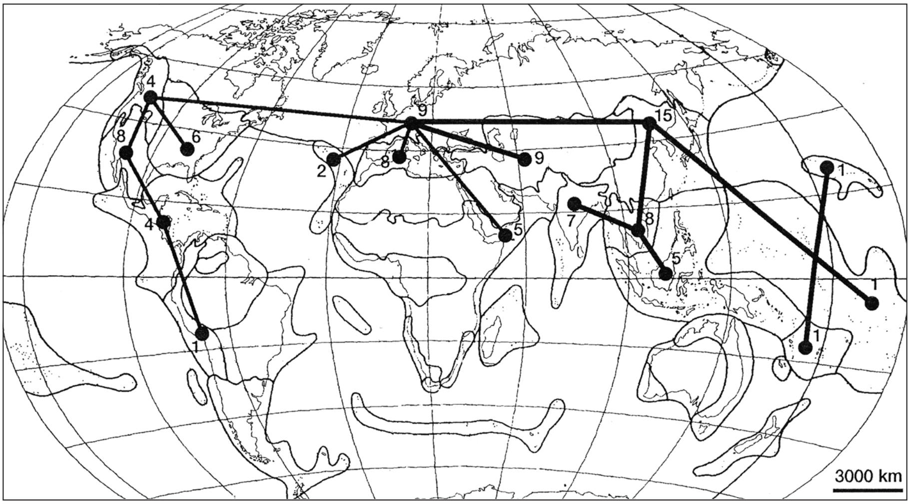

Fig. 5. Minimum Spanning Tree and Non-Metric Multidimensional Scaling (NMS) analysis superposed on a map showing Takhtajan biogeographic regions. Stress of NMS analysis was 0.169. The number of genera growing in each region is also showed on the map.

diminished to 22%. The highest rate of evergreens in North America is reached in the Madrean, Caribbean and Andean Regions.

While some genera have a very wide distribution (Holarctic) such as *Amelanchier*, *Crataegus*, *Malus*, *Mespilus* and *Sorbus* (only subg. *Sorbus*) (Browicz, 1971; Likhonos, 1974; Phipps, 1990; Phipps et al., 1990), *Cotoneaster*, *Pyracantha*, *Pyrus* and *Sorbus* (subg. *Aria*), are exclusively Palearctic (Phipps et al., 1990; Browicz, 1992; Aldasoro et al., 1996, 1998b).

The minimum spanning tree obtained from the analysis using multidimensional scaling showed a pattern of relationships among the biogeographical regions based on shared genera, and could indicate paths of migration of these genera (Fig. 5). The Eastern Asiatic Region showed three main links: 1) with Hawaiian, Polynesian and Fijian Regions (1 genus shared); 2) with Indian, Indochinese and Malaysian Regions (4 genera shared); and 3) with the Irano-Turanian (7 genera shared), Circumboreal (7 genera shared) and Mediterranean Regions (7 genera shared). The latter mentioned regions are related by the minimum spanning tree to the Rocky Mountains Region which is furthermore related to two areas, namely the North American Atlantic Region and the Madrean Region (related moreover to the Caribbean Region and finally to the Andean Region).

A high number of genera (15), many of them endemic, occur from southern to the south-east of China, and in the nearby boundaries of India and Burma included in Eastern Asiatic Region. This number is considerably higher than in all other regions, suggesting that the Eastern Asiatic Region could take an important role in diversification of Maloideae. The ensemble of Indochinese, Malaysian and Indian Regions have a set of genera which are also present in the Eastern Asiatic Region and show more mesophyllic requirements (*Dichotomanthes, Docynia, Eriobotrya, Osteomeles, Photinia, Pyracantha* and *Rhaphiolepis*). The Mediterranean, Irano-Turanian and Circumboreal

Regions have a quite similar composition, only lacking *Cydonia* in the Mediterranean Region (Browicz, 1982, 1996). The Madrean Region is one of highest endemicity (the other is the Eastern Asiatic) with *Heteromeles*, *Malacomeles* and *Peraphyllum*. The genera in common between the Caribbean and the Madrean Region are: *Crataegus*, *Hesperomeles*, *Malacomeles* and *Photinia*, the latter genus being the only representative of Maloideae in the Andean Region. Most of the Madrean, Caribbean and Andean taxa are mesophyllic, showing an evergreen foliage, such as *Hesperomeles*, *Heteromeles*, *Malacomeles* and some species of *Photinia*.

DISCUSSION

Phylogenetic relationships

The classification of Maloideae proposed by Koehne (1890) was based on the absence or presence of pyrenes. This structure, derived from the concentration of sclereids in the centre of the pome, is usually related to seed protection during their passage through the digestive tract of animals involved in zoochory (Herrera, 1989). Hutchinson (1964) and Kalkman (1988) did not recognize subgroups in Rosaceae. Hutchinson (1964) included all genera in the tribe Pomeae (= Maleae). Kalkman (1988) accepted Hutchinson's proposal but separated a group formed by *Chaenomeles*, *Cydonia*, *Docynia* and *Pseudocydonia* characterized by multiovulated carpels. These authors and also Robertson et al. (1991), Phipps et al. (1991) and Campbell et al. (1995), disavow the use of two tribes proposed by Koehne (1890).

The data obtained in our cladistic analysis also seem to disclaim Koehne's ordination, but they are in concordance with some of the clades obtained from ITS sequencing by Campbell et al. (1995). These data served to group *Eriobotrya* and *Rhaphiolepis* in a clade (beside *Vauquelinia*) separated from the other members of subfam. Maloideae. The affinity between both genera seems to be corroborated by shared pome and seed features, such as the rounded or oval seeds, and the absence of endosperm. No other member of subfam. Maloideae studied had such large seeds or lacked endosperm. Other shared character states were the small, generally isolated sclereids distributed unevenly in the flesh and the absence of a differentiated core. All these data support the separation of this branch from the rest of the subfamily.

Vauquelinia, with a dry fruit, is also very close to *Eriobotrya* and *Rhaphiolepis* (Campbell et al., 1995). The inclusion of *Vauquelinia, Kageneckia* and several other Spiraeoideae in subfam. Maloideae was previously recommended by Goldblatt (1976), Morgan et al. (1994) and Takhtajan (1997), and the discovery of a fossil closely related to both groups, *Paleorosa similkameensis*, served to avail this idea (Basinger, 1976; Evans & Campbell, 2002). Also the studies by Evans & Dickinson (1999) about floral anatomy of Spiraeoideae showed characters, such as the ovules with a papillate funicular obturator, and the development of the gynoecium from a ring primordium, which support the inclusion of these genera in an expanded subfam. Maloideae. However, other features of both genera do not favour this treatment. In our opinion, the most important are: dry capsular fruits, winged seeds which present endosperm, and different wood ray anatomy (Zhang, 1992), characters shared by several other Spiraeoideae. Consequently, we prefer to exclude *Vauquelinia* and *Kageneckia* from subfam. Maloideae, at least for the moment.

Another coincidence among our data, Campbell's analysis (Campbell et al. 1995) and the morphological studies by Robertson et al. (1991), was the clade of *Amelanchier*, *Peraphyllum* and *Malacomeles*. These plants share a pseudoberry pome and false septa in the locules. Additionally, in the group formed by the taxa with pyrenes, four genera with several *Crataegus*-type pyrenes are well supported. However, according to Campbell et al. (1995) a part of this clade (*Crataegus–Mespilus*) could be the sister group of the *Amelanchier–Malacomeles* clade.

The remaining genera of Maloideae form a polytomy that shows the scarcity of phylogenetically informative characters. However, three groups seem to merit a commentary: the group of species with pyrenes, the group *Pyrus–Cydonia–Pseudocydonia* and the subgenera of *Sorbus*. The eight genera with pyrenes (character 7, states 1, 2 and 3) do not appear as a clade in our consensus tree, suggesting that sclereids could group and originate pyrenes more than one time in the evolution.

The group *Pyrus–Cydonia–Pseudocydonia* also does not appear as monophyletic in the consensus tree, but is supported by a synapomorphic character: the large irregular groups of sclereids (character 6, state 2) and other: the pit surrounding the styles (character 4) which reverse in *Pseudocydonia*. Campbell et al. (1995) data, showed a *Cydonia–Pseudocydonia* clade. Several authors suggested that *Pyrus* may have branched from the ancestor of *Cydonia* and *Pseudocydonia* before the latter two taxa acquired the pluriovulate condition (Iketani & Ohashi, 1991; Aldasoro et al., 1998a). Robertson et al. (1991) related *Chaenomeles*, *Docynia*, and *Pseudocydonia* to *Malus* and Campbell et al. (1995) presented *Chaenomeles*, *Heteromeles*, *Malus*, *Photinia* and *Pyrus* in the same clade, which is separated from that of *Cydonia* and *Pseudocydonia*. Our morphological data do not support any of these hypothesis, because *Chaenomeles*, *Docynia* and *Malus* sect. *Docyniopsis* differ from *Pyrus* in having more than 40 stamens, and *Docynia*, *Malus* and *Malus* sect. *Docyniopsis* differ from *Pyrus* in having Phloridzin.

Delimitation of *Sorbus* is a controversial topic (Robertson et al., 1991). The four subgenera included in *Sorbus* were analyzed as independent terminal taxa in order to explore their phylogenetic relationships. In the consensus tree the four subgenera appeared in the basal polytomy. *Sorbus* monophyly is not reasonably supported here nor is there persuasive evidence in favour of its splitting.

Fossil record and present distribution

Kalkman (1988) reported that the Spiraeoideae *Vauquelinia* and other related genera belong to a clade that should be considered as sister group of the core of Maloideae. These relationships seem to be confirmed by several ways: 1) by phytochemical evidences (Challice, 1973), since *Lindleya* shares with Maloideae the presence of flavone C-gycosides; 2) by DNA evidence (Campbell et al., 1995; Evans & Campbell, 2002; Potter et al., 2002) such as ITS sequence data which showed differences between *Vauquelinia* and *Rhaphiolepis* only at 3.6% of the sites (Campbell et al., 1995); and 3) by analyses of flower development (Evans & Dickinson, 1999).

Maloideae could arise in some parts of Western Laurasia, since most of closely related Spiraeoideae grow in North America (*Lindleya*, *Lyonothamnus* A. Gray and *Vauquelinia*), only *Kageneckia* grows in South America. Relationships of the South American Spiraeoideae (mainly *Kageneckia*) to various northern genera are of interest, they can be related to North American *Lindleya*, *Lyonothamnus* and *Vauquelinia*, (Banwar, 1966; Raven & Axelrod, 1974). The last three genera belong to an ensemble of xerophilous taxa, mainly evergreen sclerophyllous shrubs or small trees, which inhabited for a long time the western coast of North America. Leaves of *Lyonothamnus* and *Vauquelinia* are very well recorded in western USA during most of the Palaeogene (Axelrod, 1944, 1958, 1991; MacGinitie, 1953, 1969).

Hybridization has been hypothesized in the genesis of Maloideae and is currently extensive among several genera (Gladkova, 1972; Robertson et al., 1991). This led some authors to consider that a basal reticulation due to intergeneric hybridization could be related with their phylogenetic origin. Sax (1931) proposed an alloploid event to explain their origin, with a Spiroideae ancestor ($x = 9$) and a Prunoideae ancestor ($x = 8$), which is supported by some anatomical and cytogenetic data (Stebbins, 1950; Challice & Kovanda, 1981). Nevertheless, neither DNA nor wood anatomy data did easily support this view and they may better suggest that Maloideae descend entirely from Spiroideae ancestors such as *Kageneckia* or *Vauquelinia* (Zhang, 1992; Morgan et al., 1994; Campbell et al., 1995; Evans & Dickinson, 1999; Evans & Campbell, 2002).

Unfortunately, anatomical and morphological data studied here are not sufficient to explain the current distribution of genera and the evolution of most character states in the subfamily. Several taxa during the Early Tertiary belong to genera with pyrenes (as *Crataegus* and *Pyracantha*). This is consistent with the hypothesis of Iketani & Ohashi (1991) who postulated that the pome of *Pyracantha* is the most primitive and the taxa included in Crataegeae are more primitive than those in Sorbeae. Other authors think that *Dichotomanthes* has a more primitive type of pome, in which the carpels are free from the hypanthium in spite of having other derivative traits, such as the solitary carpel with tomentose lateral stylodium (Gladkova, 1969, 1972; Takhtajan, 1997). However, our cladistic analysis favours *Eriobotrya–Rhaphiolepis* as sister group to the rest of Maloideae, including *Dichotomanthes*. This clade has some primitive states, including isolated sclereids, high seed/pome length ratio (also shared by the *Amelanchier* group), and evergreen leaves (also shared by several other genera), and they have also derivative features such as the lack of endosperm and seed shape.

If we see the present geographical distribution of Maloideae, a high number of genera (15) is outspread in an area including the South and South-East of China, and in the nearby boundaries of India and Burma, included in the Eastern Asiatic Region (Fig. 5). The core of subfamily Maloideae is essentially distributed in the Northern Hemisphere and better represented in subtropical areas of eastern Asia, where it could form a part of the Tertiary Laurasian Boreotropical flora (Tiffney, 1985). Most of early Tertiary floras of Asia have tropical-subtropical characteristics in common and included several Maloideae (Hsu, 1983; Ming-hong et al., 1983; Leopold et al., 1992; Guo, 1993). The presence in Indochina and Malaysia of *Eriobotrya* and *Rhaphiolepis* (included in the clade which is sister group of the rest of the subfamily) is congruent with an earlier separation of this clade and could be due to the retreat of a part of the oldest Palaeogene flora to the refuges of China, Indochina and Malaysia, while many wet-temperate forests were progressively transformed in many parts of Eurasia during a part of the Palaeogene and the Neogene (Tiffney, 1985). Both genera were found in north-eastern Siberia and northern China in Miocene sediments (see Table 2).

As commented, during the Neogene, forest xerophilization progressed in areas of Central and Northern China, Trans-Caucasia, Middle Asia, Turkey, Iran and South and East Europe, while the remnants of old Tertiary flora occupied separated refuges, such as south-eastern China, Indochina, Malaysia, Caucasus, southern Japan, western North America and northern Central America (Raven & Axelrod, 1974; Hsu, 1983; Tiffney, 1985), and the new xerophilic taxa spread to Caucasus, Siberia, Europe, and the drier parts of China and the Himalayas (Takhtajan, 1941, 1946; Gabrielian, 1961, 1978). Many of the genera of Maloideae would had to accommodate to these progressively xeric habitats.

A possible line of migration is the link between the Eastern Asia Region and the rest of the Holarctic Kingdom. Western North America and Eastern Asia probably shared a tropical-subtropical flora related to a Palaeogene linkage between the two areas, involving North Atlantic land bridges (Wolfe, 1975; Tiffney, 1985). The phylogenetic relationships do not always render a satisfactory explanation about the possible biogeographical episodes in the distribution of several taxa of the subfamily. However, some traits can be supposed: the well-supported clade of *Malacomeles–Peraphyllum–Amelanchier*, sharing the pomes with false septa, suggests an early pass to western North America. Also the disjunct distribution of *Photinia* could help this hypothesis. Several of these plants are adapted to sclerophyllous forests, and they were found fossil in Early or Middle Tertiary formations of western North America. This is the case with *Heteromeles*, *Peraphyllum* and *Photinia* (Table 2).

According to Raven & Axelrod (1974) *Hesperomeles* originated in North America and migrated into north-western South America. The only known report of this genus is a pollen record from the Late Pliocene of Colombia (Wijninga & Kuhry, 1993). As *Crataegus* is well represented in Eastern Asiatic flora and several features are shared by *Crataegus*, *Mespilus* and *Hesperomeles* (i.e. superposed ovules, pyrenes with flesh, and several layers of endosperm), the closest relative of *Hesperomeles* could be some primitive *Crataegus* (Phipps, 1983). In the case of *Chamaemeles* a long-distance dispersion can be postulated since it is strictly endemic of Madeira Island. However, the ancestor of this remarkable genus remains uncertain, because no current taxa of Maloideae has evergreen leaves, folded cotyledons and a solitary pyrene with one seed, but these character states could have been present in an ancestor of *Crataegus* from Middle Tertiary European coasts. The current distribution of *Osteomeles* can be explained only by long distance dispersal, which also seems the case for most Pacific Islands' taxa. The flora of Hawaii is also formed by taxa mainly coming in from East Asia (Fosberg, 1948).

The ultimate evaluation of the evolutionary hypotheses here developed, will be their congruence with other more elaborated datasets. Despite the seemingly high level of homoplasy (Phipps et al., 1991; Aldasoro et al., 1998a) a cladistic analysis of morphological and anatomical characters provides partial resolution among some genera of Maloideae that seems to be congruent with information from DNA sequence phylogenies and biogeography.

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APPENDIX. List of species whose seeds were examined: binomials, authorities, collectors, collection numbers, and location of voucher specimens as indicated by herbarium acronym.

Amelanchier canadensis (L.) Medik., *Aldasoro 721* (MA-580305)
Amelanchier ovalis Medik., *Aedo 3451* (MA-555587)
Chamaemeles coriacea Lindl., *Fernandes & Jardim 8677* (MA-593013)
Chaenomeles cathayensis (Hemsl.) C.K. Schneid., *Aldasoro 725* (MA-580296)
Chaenomeles japonica (Thunb.) Lindl., *Aldasoro 544* (MA-580297)
Cotoneaster buxifolius Wall. ex Lindl., *Aedo 3891* (MA-580425)
Cotoneaster integerrimus Medik., *Aldasoro 580* (MA-580292)
Cotoneaster salicifolius Franch., *Aedo 3890* (MA-580424)
Crataegus azarolus L., *Soler 779* (MA-580441)
Crataegus maineana Sarg., *Aldasoro 688* (MA-580301)
Crataegus mollis Scheele, *Aldasoro 723* (MA-580299)
Crataegus monogyna Jacq., *Soler 778* (MA-580446)
Crataegus oresbia W.W. Sm., *Aldasoro 689* (MA-580303)
Crataegus pentagyna Waldst. & Kit., *Aldasoro 682* (MA-580304)
Crataegus phaenopyrum (L.f.) Medik., *Aldasoro 722* (MA-580443)
Crataegus pruinosa (J.C. Wendl.) K. Koch, *Aldasoro 692* (MA-580302)
Crataegus pubescens (Humb., Bonpl. & Kunth) Steud., *Hinton 4047* (MA-305100)
Crataegus x *ruscinonensis* Gren. & Blanc, *Soler 777* (MA-580445)
Cydonia oblonga Mill., *Aldasoro 561* (MA-580295)
Dichotomanthes tristaniaecarpa Kurz, *Aldasoro 726* (MA-580294)
Docynia delavayi C.K. Schneid., *Aldasoro 729* (MA-580291)
Docynia indica (Wall.) Decne., *Aldasoro 730* (MA-581070)
Eriobotrya angustissima Hook.f., *Aldasoro 718* (MA-580309)
Eriobotrya benghalensis (Roxb.) Hook., *Aldasoro 717* (MA-580310)
Eriobotrya japonica (Thunb.) Lindl., *Aldasoro 715* (MA-580312)
Eriobotrya petiolata Hook., *Aldasoro 714* (MA-580313)
Eriobotrya tengyuehensis W.W. Sm., *Aldasoro 716* (MA-580311)
Hesperomeles ferruginea Lindl., *Cuatrecasas 28890* (MA-507790)
Hesperomeles lanuginosa Hook., *Cano 4179* (MA-515098)
Heteromeles salicifolia (C. Presl) Abrams, *Bartholomew 1479* (MA-382438)
Kageneckia oblonga Ruiz & Pav., *Basualto, Gebanero & Orellana 72* (MA-487971)
Lindleia mespilioides Kunth, *Calzada 19673* (MA-614228)
Malacomeles denticulata (Knuth) G.N. Jones, *Nicolás s.n.* (G)
Malus baccata (L.) Borkh., *Aldasoro 691* (MA-580307)
Malus florentina (Zucc.) C.K. Schneid., *Aldasoro 634* (MA-580439)
Malus floribunda Siebold, *Aldasoro 720* (MA-580306)
Malus fusca (Raf.) C.K. Schneid., *Aldasoro 539* (MA-580435)
Malus halliana Koehne, *Aldasoro 606* (MA-580442)
Malus ioensis (Wood) Britton, *Aldasoro 719* (MA-580432)
Malus kansuensis (Batalin) C.K. Schneid., *Aldasoro 681* (MA-580437)
Malus prunifolia (Willd.) Borkh., *Aldasoro 603* (MA-580440)
Malus sargentii Rehder, *Aldasoro 675* (MA-580433)
Malus sieboldii Rehder, *Aldasoro 648* (MA-580447)
Malus sikkimensis Koehne ex C.K. Schneid., *Aldasoro 689* (MA-580434)
Malus sylvestris (L.) Mill., *Aldasoro 132* (MA-580290)
Malus trilobata (Labill.) C.K. Schneid., *Aldasoro 665* (MA-580438)
Malus tschonoskii (Maxim.) C.K. Schneid., *Aldasoro 643* (MA-580308)
Malus yunnanensis C.K. Schneid., *Aldasoro 635* (MA-580436)
Mespilus germanica L., *C. Navarro 1166* (MA-580289)
Osteomeles schwerinae C.K. Schneid., *Aldasoro 724* (MA-580298)
Peraphyllum ramosissimum Nutt., *Aldasoro 731* (MA-581071)
Photinia beauverdiana C.K. Schneid., *Aldasoro 658* (MA-580213)
Photinia davidiana (Decne.) Cardot, *Aldasoro 709* (MA-580211)
Photinia melanocarpa (Michx.) K.R. Robertson & J.B. Phipps, *Aldasoro 710* (MA-580202)
Photinia pyrifolia (Lam.) K.R. Robertson & J.B. Phipps, *Aldasoro 594* (MA-580209)
Photinia salicifolia C. Presl, *Bartholomew 1479* (MA-382438)
Photinia serratifolia (Desf.) Kalkman, *Aldasoro 708* (MA-580210)
Photinia villosa (Thunb.) DC., *Aldasoro 678* (MA-580212)

Pseudocydonia sinensis C.K. Schneid., *Aldasoro 806* (MA-597421)
Pyracantha angustifolia C.K. Schneid., *Aldasoro 728* (MA-580444)
Pyracantha coccinea M. Roem., *Bolòs 546* (MA-341844)
Pyracantha crenatoserrata (Hance) Rehder, *Aldasoro 727* (MA-580293)
Pyrus betulifolia Bunge, *Aldasoro 670* (MA-579434)
Pyrus bourgaeana Decne., *Aldasoro 131* (MA-579428)
Pyrus calleryana Decne., *Aldasoro 707* (MA-579429)
Pyrus communis L., *Monasterio et al. 1168* (MA-529106)
Pyrus cordata Desv., *Aedo 2477* (MA-514838)
Pyrus elaeagnifolia Pall., *Aldasoro 690a* (MA-579437)
Pyrus georgica Kuth., *unknown collector* (MA-417326)
Pyrus nivalis Jacq., *Aldasoro 644* (MA-579431)
Pyrus pashia Buch.-Ham. ex D. Don, *Aldasoro 641* (MA-579430)
Pyrus phaeocarpa Rehder, *Aldasoro 669* (MA-579438)
Pyrus pyrifolia (Burm.f.) Nakai, *Aldasoro 667* (MA-579427)
Pyrus salicifolia Pall., *Aldasoro 690* (MA-579433)
Pyrus spinosa Forssk., *C. Navarro et al. 1405* (MA-579557)
Pyrus syriaca Boiss., *Aldasoro 668* (MA-579435)
Pyrus ussuriensis Maxim., *Aldasoro 676* (MA-579432)
Rhaphiolepis × delacourii André, *Aldasoro 666* (MA-580314)
Rhaphiolepis indica (L.) Lindl., *Aldasoro 713* (MA-580430)
Rhaphiolepis umbellata (Thunb.) Makino, *Aldasoro 545* (MA-580431)
Sorbus alnifolia (Siebold & Zucc.) K. Koch, *Aldasoro 672* (MA-580223)
Sorbus aria (L.) Crantz, *Aedo 3380* (MA-542774)
Sorbus aucuparia L., *Aedo 3383* (MA-544275)
Sorbus caloneura (Stapf) Rehder, *Aldasoro 687* (MA-580222)
Sorbus chamaemespilus (L.) Crantz, *Aedo 3140* (MA-544290)
Sorbus commixta Hedl., *Aldasoro 553* (MA-580221)
Sorbus domestica L., *Aldasoro 560* (MA-580217)
Sorbus esserteauiana Koehne, *Aldasoro 541* (MA-580220)
Sorbus folgneri (C.K. Schneid.) Rehder, *Aldasoro 711* (MA-580315)
Sorbus forrestii H.A. McAllister & C.M. Gillham, *Aldasoro 602* (MA-580214)
Sorbus hajastana Gabrieljan, *Aldasoro 679* (MA-580201)
Sorbus harrowiana (Balf.f. & W.W. Sm.) Rehder, *Aldasoro 637* (MA-580197)
Sorbus hedlundii C.K. Schneid., *Aldasoro 639* (MA-580201)
Sorbus hemsleyi (C.K. Schneid.) Rehder, *Aldasoro 699* (MA-582151)
Sorbus hupehensis C.K. Schneid., *Aldasoro 550* (MA-580218)
Sorbus hybrida L., *Aldasoro 453* (MA-543364)
Sorbus intermedia (Ehrh.) Pers., *Aldasoro 485* (MA-543306)
Sorbus japonica (Decne.) Hedl., *Aldasoro 704* (MA-580226)
Sorbus keissleri (C.K. Schneid.) Rehder, *Aldasoro 652* (MA-580225)
Sorbus koehneana C.K. Schneid., *Aldasoro 712* (MA-580429)
Sorbus lanata (D. Don) Schauer, *Aldasoro 624* (MA-580203)
Sorbus latifolia (Lam.) Pers., *Aldasoro 457* (MA-543362)
Sorbus megalocarpa Rehder, *Aldasoro 674* (MA-580200)
Sorbus meliosmifolia Rehder, *Aldasoro 660* (MA-580224)
Sorbus pallescens Rehder, *Aldasoro 700* (MA-580202)
Sorbus reducta Diels, *Aldasoro 638* (MA-580426)
Sorbus sargentiana Koehne, *Aldasoro 623* (MA-580216)
Sorbus scalaris Koehne, *Aldasoro 552* (MA-580219)
Sorbus subfusca (Ledeb.) Boiss., *Aldasoro 653* (MA-580204)
Sorbus takhtajanii Gabrieljan, *Aldasoro 680* (MA-580205)
Sorbus tamanschjanae Gabrieljan, *Aldasoro 589* (MA-580215)
Sorbus thibetica (Cardot) Hand.-Mazz., *Aldasoro 636* (MA-580428)
Sorbus tianshanica Rupr., *Kuklina 15167* (MA-531756)
Sorbus torminalis (L.) Crantz, *C. Navarro 1380* (MA-543440)
Sorbus vestita Lodd., *Aldasoro 621* (MA-580207)
Sorbus vilmorinii C.K. Schneid., *Aldasoro 629* (MA-580427)
Sorbus yuana Spongberg, *Aldasoro 703* (MA-580198)
Sorbus zahlbruckneri C.K. Schneid., *Aldasoro 702* (MA-580199)
Vauquelinia corymbosa Humb. & Bonpl., *Ventura & López 9249* (MA-527389)