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Evolutionary History of the Genus *Pistacia* (Anacardiaceae)

M.G. Al-Saghir

Department of Environmental and Plant Biology, Ohio University Zanesville,
1425 Newark Road, Zanesville, Ohio 43701, USA

Abstract: Pistacia L. belongs to the family Anacardiaceae (cashew family), order Sapindales. Pistacia vera L. (cultivated pistachio) is by far the most economically important species in the genus. It has edible seeds and considerable commercial importance. The evolutionary history and the phylogenetic relationships between species within the genus are not well understood. A better understanding of these relationships is needed to make the species more useful for plant improvement or genetic studies. The objective of this perpestective is to provide additional insight into understanding the evolutionary history of Pistacia. In conclusion, Pistacia is a monophyletic genus and it contains two sections (Lentiscella and Pistacia) and it is originated in the Paleocene epoch. This is based on Anacardiaceae being pantropical in distribution with North and South America representing major diversification centers of the family including the geographical distribution of Pistacia. This perspective provides additional insight into understanding the evolutionary history of the genus Pistacia to make the species more useful for plant improvement or genetic studies.

Key words: Pistacia, evolutionary, history, vera, Anacardiaceae

INTRODUCTION

Pistacia L. belongs to the family Anacardiaceae (cashew family), order Sapindales (Stevens, 2008). It contains nine species and five subspecies according to the current study completed by AL-Saghir and Porter (2006) (not published). Species are xerophytic trees, deciduous or evergreen and dioecious, up to 8-10 m high. Leaves are pinnately-compound, with broad, elliptical to round-ovate leaflets. Buds are single, apical and usually vegetative. In both male and female trees, flowers are apetalous, subtended by 1-3 small bracts and 2-7 bracteoles and borne in racemes or panicles. Male flowers have 4-5 anthers inserted on a disc. Female flowers have a short, 3-fid style. The species are wind-pollinated and the fruit is a drupe (Zohary, 1952).

Pistacia vera L. (cultivated pistachio) is by far the most economically important species in the genus. It has edible seeds and considerable commercial importance. The other species grow in the wild and their seeds are used as a rootstock seed source and sometimes are used for fruit consumption, oil extraction, or soap production.

The pistachio is native to the arid zones of Central Asia; it has been cultivated for 3000-4000 years in Iran and was introduced into Mediterranean Europe by Romans at the beginning of the Christian era (Crane, 1978). Pistachio cultivation extended westward from its center of origin to Italy, Spain and other Mediterranean regions of Southern Europe, North Africa and the Middle East, as well as to China and more recently

States and Australia (Maggs, 1973; to the United Hormaza et al., 1994, 1998). Pistacia vera is the only species in this genus that is successfully grown in orchards; it produces edible seeds large enough to be commercially acceptable. Pistachios are adapted to a variety of soils and are probably more tolerant of alkaline and saline soil than most tree crops (Tous and Ferguson, 1996). Moreover, Pistachios thrive in hot, dry, desert-like conditions. Pistachios are utilized for the most part in the shell for fresh consumption; processed uses include candy, baked goods and ice cream. They also have folklore, medicinal and non food uses such as toothache relief. The resin is used for gum (dried resin) and as a blood-clotting agent in Europe and the Middle East. In India, the husks are used for dying cloth and tanning hides. Pistachios have been reported as a remedy for scirrhus and sclerosis of the liver, abscesses, poor circulation and other medical problems (Tous and Ferguson, 1996). Currently, Iran, the United States, Turkey and Syria are the main Pistachio producers in the world, contributing over 90% of the world production (FAO, 2002).

The current study supported the monophyly of *Pistacia*. The genus divided into two monophyletic groups: One group (Section *Pistacia*) contains *P. atlantica Desf.*, *P. chinensis Bunge*, *P. eurycarpa Yalt.*, *P. falcate* (Bess. ex Martinelli) Rech. f., *P. integerrima* (J.L. Stew. ex Brandis) Rech. f., *P. khinjuk* Stocks, *P. mutica* Fisch. and C.A. Mey., *P. palaestina* Boiss., *P. terebinthus* L. and *P. vera* L. while, the other group

(Section Lentiscella) contains P. aethiopica Kokwaro, P. lentiscus L., P. mexicana Humb., Bonpl. and Kunth, P. texana Swingle and P. weinmannifolia Poiss. ex Franch.

Zohary (1952) noted that evidence based on fossil, *P. lentiscus* originated 40 million years ago and the genus as a whole probably developed more than 80 million years ago. This conclusion is questionable since Anacardiaceae pollen and wood first appear in the Paleocene epoch, 65 to 55 million years ago (Hsu, 1983; Muller, 1984) and is found throughout the world. The origin for the order in which the Anacardiaceae occurs, Sapindales, dates back approximately 84 to 65 million years before present (Magallón and Sanderson, 2001; Wikström *et al.*, 2001).

Derived from this information and the fossil records of the genus, I hypothesize that Pistacia originated in the Paleocene epoch. Since, Anacardiaceae is pantropical in distribution and North and South America represent major diversification centers of the family and given the geographical distribution of Pistacia, I postulate that ancestral species of Pistacia came from North America. This hypothesis is supported by Pistacia fossil records from the Paleocene of Wyoming and Colorado (Edwards and Wonnacott, 1935). Migration may have taken place from western Laurasia (North America) to Eastern Laurasia (Europe and Asia) ending up in Central Asia via Europe where the genus radiated within Asia (West Asia and Mediterranean Basin) as hypothesized by Weeks et al. (2005) for the Burseraceae. This migration may have been facilitated by the boreotropical land bridge (Tiffney, 1985; Tiffney and Manchester, 2001), which spanned the North Atlantic during the early to middle eocene. Global temperatures during the Eocene were highest during this time period and tropical vegetation is known to have occurred in this land corridor (Wolfe, 1978; Zachos et al., 2001). Cooler temperatures during the Middle Eocene extirpated frost tolerant taxa in this region and the physical land connections disappeared sometime afterward (Weeks et al., 2005).

This vicariant scenario for *Pistacia* is indirectly supported by the localities of *Pistacia* fossils from the Early Eocene in England and Russia (Weeks *et al.*, 2005). Following the migration of ancestral *Pistacia* into the Old World, *Pistacia* appears to have dispersed and radiated within continental Africa during the Middle Eocene (44 Ma). The spread of *Pistacia* to India and Southeast Asia appears to have occurred in relatively recent geologic time (5.0 Ma), perhaps due to a Northeasterly range expansion of *Pistacia* coincident with the establishment of arid habitat in East Africa (Potts and Behrensmeyer, 1992; De Menocal, 1995).

The Oligocene origin of the American species, *Pistacia mexicana*, from a Southeastern Asian ancestor

(like *P. weinmannifolia*) may be due to long distance dispersal or migration through probable trans-Atlantic long distance dispersal (Renner, 2004).

I posit that the genus extended its distribution range away from Central Asia to West Asia and the Mediterranean basin, East Africa and the new world species by passive dispersal mediated by wind, water, birds or even by people. This is supported by evolution toward a smaller seed with a hard endocarp paralleling a change in reproductive strategy from distribution by ground squirrels (burying the seed, as with walnuts and oaks) to bird- or wind-mediated distribution, which would require a seed capable of passing through a bird's digestive system or being blown by the wind. (Jordano, 1989).

Species in both Section *Lentiscella* and *Pistacia*, which diverged relatively early, have evolved smaller leaves with more leaflets and a winged rachis and smaller hard seeds although these monophyletic groups probably evolved independently and gradually. Smaller elongated leaflets with pointed shoot apices also are more efficient for water removal from the leaf surface compared with simple rounded leaves and are more adequate for wind pollination. This would be a useful adaptation as the genus moved into higher rainfall regions (Parfitt and Badenes, 1997).

Li and Tanimura (1987) suggested that differences in mutation rates among organisms may be more a function of generation time than DNA repair rates. *Pistacia* species have a long generation cycle of at least 10 years to first flowering and a life-span estimated to be as much as 400 years in some cases. The average replacement cycle for pistachio is probably between 50 and 200 years in the wild, so it is not surprising that *Pistacia* has evolved much more slowly than the annual species used to derive standard mutation rate estimates (Parfitt and Badenes, 1997).

Zohary (1952) hypothesized that P. khinjuk to be directly descended from P. vera, a hypothesis that can not be supported or rejected so far. Zohary (1952) also considered P. khinjuk and P. vera to be the most primitive, each showing nine characters attributed to primitive species: simple leaves, odd-pinnate leaves, small number of leaflets per leaf, symmetrical leaflets, rounded leaflet apex, simple petiole (no wings), highly branched panicles, deciduous character and large fruit. This is consistent with a Central Asian center of diversity for the genus given that the natural range for P. vera spans this region. Pistacia species based on P. khinjuk and P. vera are the only Pistacia species with large edible drupes. Both species have a similar somewhat unique three-leaflet odd-pinnate leaf. Random Amplified Polymorphic DNA (RAPD) study completed by AL-Saghir and Porter (2006) indicated that *P. khinjuk* and *P. vera* form a very close pair, accordingly, I posit that *P. khinjuk* is indeed a direct descendant of *P. vera*.

This perspective provides additional insight into understanding the evolutionary history of the genus *Pistacia* to make the species more useful for plant improvement or genetic studies.

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