

Advances in the study of the systematics of *Actinidia* Lindley

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Abstract *Actinidia* (Actinidiaceae) is of economic importance for its edible fruits. Traditional taxonomy divided the genus into four sections, *Leiocarpae* Dunn, *Maculatae* Dunn, *Strigosae* Li, and *Stellatae* Li. However, phylogenetic studies based on morphology and molecular markers have posed challenges to the four-section scheme. It appears that the natural classification of the genus points to the existence of two groups, one comprising *Leiocarpae*, and the other *Maculatae*, *Strigosae*, and *Stellatae*. Single- or low-copy genes would probably be useful in untangling the perplexity and the reticulate evolution of the genus. However, any phylogenetic studies must be firmly based on sound taxonomy and identification. Population sampling throughout the distribution range of the taxa should be carried out in order to study the variation pattern of the morphology and, ultimately, to clarify the confusion existing in some taxa. A combination of morphometrics and molecular data is highly desirable for resolving the uncertainty in *Actinidia* taxonomy.

Keywords *Actinidia*, Actinidiaceae, systematics, taxonomy confusion

flavors when mature. *Actinidia chinensis* Planchon and *A. deliciosa* (A. Chevalier) C. F. Liang & A. R. Ferguson—known as kiwifruits—are two species with the greatest economic importance, producing fruits of high commercial importance with more than 120000 ha of orchard planted, and with an annual production exceeding 1.35 million metric tons of fresh fruits (Ferguson and Huang, 2007). Studies have shown that the fruits of *A. chinensis* and *A. deliciosa* are exceptionally good sources of vitamin C and excellent sources of potassium and folate and, possibly, of vitamin E and vitamin K. They also contain a very effective laxative (Ferguson and Ferguson, 2003). Because of this economic value, there have been extensive studies on these two species and on the entire genus *Actinidia*, just as with other economic crops. Genetic diversity represents the most important raw material as basis for kiwifruit breeding and exploration. As a result, a nationwide survey of germplasm resources has been carried out in China (Cui et al., 2002), and much attention has been paid to the taxonomy and phylogeny of the genus. In the present paper, we will summarize the advances of the systematics of this genus and point out the perplexity of the studies.

1 Introduction

Lindley (1836) established the notable climbing genus *Actinidia* based on the specimens *Wallich 6634* collected from Nepal in 1821. Members of this genus have numerous stamens, radiating styles, and a berry, and comprise about 55 species distributed in East and South Asia (Li et al. 2007a). The plants are common in Chinese mountainous areas and are known as *Yangtao* or *Maotao* to the local populations. The fruits of members of most species of this genus are edible, with pleasantly sweet-sour

2 Systematic position

Early studies of the systematic position of *Actinidia* were reviewed by Dunn (1911), Soejarto (1980) and Zhang (1987), respectively. Here we recapitulate their views. When the genus was founded, it was assigned to Dilleniaceae (Lindley, 1836). Van Tieghem (1899) established the family Actinidiaceae to include *Actinidia* and *Saurauia* Willd.. Gilg, and Werdermann (1925) proposed Actinidiaceae in the broad sense to include *Actinidia*, *Saurauia*, *Clematoclethra* (Franch.) Maxim., and *Sladenia* Kurz. Contemporary taxonomists recognize Actinidiaceae as comprising three genera, *Actinidia*, *Saurauia*, and *Clematoclethra* (Soejarto, 1980, 2004; Cronquist 1981;

Woodland, 2000; Dressler and Bayer, 2004; Li et al., 2007a), distributed in tropical Asia and America (Dressler and Bayer, 2004; Soejarto, 2004). Actinidiaceae, of different circumscriptions, was put in the order Parietales, Theales, Ericales, or Actinidiales (e.g. Engler and Diels, 1936; Melchior, 1964; Thorne, 1983; Takhtajan, 1969, 1997). Molecular phylogenetic studies confirmed the placement of Actinidiaceae in Ericales (APG, 1998, 2003; Savolainen et al., 2000).

3 Cytology of *Actinidia*

Actinidia contains diploids, tetraploids, hexaploids, and octoploids with a base chromosome number of $x=29$; some taxa contain different ploidies (Ferguson and Huang, 2007; Huang et al., 2003).

The base chromosome numbers of *Saurauia*, *Clematoclethra*, and *Actinidia* have been established as 13, 12 and 29, respectively. Based on a basic chromosome number of $x=12$, He et al. (2005) proposed that *Clematoclethra* was derived through an aneuploid decrease from the $x=13$ of an extinct diploid *Saurauia*, while *Actinidia*, which has $x=29$, was derived from a palaeotetraploid of $x=14$, which, likewise, was also derived through an aneuploid increase from $x=13$ in an extinct diploid *Saurauia*, and whose doubling was to $n=2x=28$, resulting in 29 by centromere fission.

4 Infrageneric phylogeny of *Actinidia*

4.1 Classification based on morphology

Gilg (1893) separated eight species of *Actinidia* into two groups: *Monantheae* with a solitary flower, and *Pleiantheae* with cymes. This scheme neglected the fact that male individuals often have more flowers than female ones of the same species, and even on the same individuals the inflorescences could have different numbers of flowers. In 1911, Dunn (1911) published the first comprehensive taxonomic revision of *Actinidia* and established four Sections: *Ampulliferae* Dunn, *Leiocarpae* Dunn, *Maculatae* Dunn, and *Vestitae* Dunn. These Sections may be keyed as follows.

- 1a. Fruit without spots
 - 2a. Ovary bottle-shaped..... Sect. *Ampulliferae*
 - 2b. Ovary cylindrical.....Sect. *Leiocarpae*
- 1b. Fruit with spots
 - 3a. Leaves glabrous.....Sect. *Maculatae*
 - 3b. Leaves shaggy or woolly..... Sect. *Vestitae*

Later, Li (1952) combined *Ampulliferae* and *Leiocarpae* into one Section, Sect. *Leiocarpae*, because such species as *A. tetramera* Maxim. have the ovary intermediate in shape. He further divided *Vestitae* into two Sections: *Stellatae* Li for species

with simple hairs. The four Sections created by Li (1952), *Leiocarpae* Dunn, *Maculatae* Dunn, *Strigosae* Li, and *Stellatae* Li, may be keyed as follows.

- 1a. Fruit without spots.....Sect. *Leiocarpae*
- 1b. Fruit with spots
 - 2a. Leaves without stellate hairs
 - 3a. Branch and petiole glabrous.....Sect. *Maculatae*
 - 3b. Branch and petiole strigose.....Sect. *Strigosae*
 - 2b. Leaves with stellate hairs.....Sect. *Stellatae*

In 1977, Wu (1977) studied *Actinidia* of Yunnan, China, and adopted Li's (1952) infrageneric classification. In 1984, Liang (1984) also retained Li's (1952) scheme with a slight modification, subdividing Sect. *Leiocarpae* into Ser. *Lamellatae* C. F. Liang and Ser. *Solidae* C. F. Liang, and Sect. *Stellatae* into Ser. *Perfectae* C. F. Liang and Ser. *Imperfectae* C. F. Liang.

Morphologically, species of the genus *Actinidia* may be clearly separated into two major groups: one group, which includes *Leiocarpae*, has a glabrous ovary and the fruit has no spots; the other group, which includes *Maculatae*, *Strigosae*, and *Stellatae*, has a hairy ovary and the fruit has spots. Since the generic characters of the ovary and the fruit are stable, and they are closely correlated, the two groups based on these characters are natural.

Because we observed that the leaves of specimens of *A. callosa* Lindley, which is placed in Sect. *Maculatae*, occasionally have stellate hairs when young, and moreover, if we hold to the scheme of Li (1952), these specimens of *A. callosa* may be attributed to either Sect. *Maculatae* or Sect. *Stellatae*. In another case, the leaves of *A. venosa* Rehder have imperfect stellate hairs or occasionally are hairless, which makes the placement of this species uncertain. Generally, the leaves of *A. hemsleyana* Dunn, a member of *Strigosae*, are glabrous abaxially but, occasionally, they have imperfect stellate hairs, a characteristic of *Stellatae*. Beyond these examples, it may be noted that the character of hairs on the branches and petioles is not correlated with hairs on the leaves. Natural classification should be based firmly on the correlation of characters and on the discontinuity of variations (Davis and Heywood, 1963). In line with this principle, it may be argued that Sections *Maculatae*, *Strigosae*, and *Stellatae* are probably not natural groups, and should be merged into one, Sect. *Maculatae*, as suggested by Ferguson and Huang (2007) .

4.2 Classification based on modern methods

Recently, more objective, explicit and repeatable methods, such as numerical taxonomy, cladistics, and molecular phylogeny, have been used to study the phylogeny of *Actinidia*. The results of these studies have posed challenges to the system of Li (1952), but no satisfactory scheme has been proposed.

Numerical taxonomy based on digitized morphological descriptors revealed that the subdivision of the genus into

three sections, *Leiocarpae*, *Maculatae*, and *Vestitae*, would be more appropriate (Huang et al., 1999). Following a cladistic analysis of 22 morphological characters, Li et al. (2000) proposed that the genus should be divided into two subgenera, one containing Sect. *Leiocarpae*, and the other containing Sects. *Maculatae*, *Strigosae*, and *Stellatae*. Phenetics and cladistics of the genus based on micro-morphological characters of the leaf's hairs by He et al. (2000a, b) indicated that Sect. *Leiocarpae* appears to be monophyletic, while the other three are non-monophyletic. Finally, it should be pointed out that pollen morphologic studies also did not support a system consisting of four Sections (Jiang et al., 2004).

Testolin and Ferguson (1997), who used a molecular marker, namely isozyme, to evaluate Liang's system (Liang, 1984) for the first time, reported findings which did not correspond well with the scheme of Liang. Isozyme and restriction fragment length polymorphism (RFLP) of cpDNA revealed the existence of five species groups, but no phylogenetic reconstruction was attempted by the authors (Testolin et al., 1997). The results of randomly amplified polymorphic DNA (RAPD) analysis only revealed Sect. *Leiocarpae* to be monophyletic (Huang et al., 2002), the same as that observed with amplified fragment length polymorphism (AFLP) analysis (Li et al., 2005). However, Li et al. (2002) and Chat et al. (2004) showed that Sect. *Leiocarpae* was paraphyletic even when *A. rufa* (Sieb. & Zucc.) Planch. ex Miq. was omitted, while the other three Sections were polyphyletic. Furthermore, in an analysis using PCR-RFLPs of mt DNA (Li et al., 2003), it was found that all the four Sections were not monophyletic, but polyphyletic.

Subdivision of Sect. *Leiocarpae* into Series *Lamellatae* and Series *Solidae* (Liang, 1984) gained support from AFLP analysis (Li et al., 2005), while chemotaxonomy based on leaf flavonoids (Webby et al., 1994) only revealed the cohesion of *Solidae*.

Although the studies mentioned above have given us an insight into the phylogeny of *Actinidia*, to date, no ideal scheme in line with the morphological differentiation has been proposed. Previous studies (Testolin et al., 1997; Cipriani et al., 1998; Li et al., 2002; Chat et al., 2004) postulated the existence of hybridization and the resulting reticulate evolution in the genus. It is our view that, in the future, more informative and appropriate markers, for example, single- or low-copy nuclear genes, should be sought and used to reconstruct the phylogeny of *Actinidia*. As reviewed by Zhao et al. (2008), the phylogenetic utility of single- or low-copy nuclear genes has been investigated in various plant taxa, which show that these markers are useful in unravelling the reticulate evolution of plant groups (Ferguson and Sang, 2001; Lee et al., 2002). With DNA sequencing becoming more and more rapid, phylogenomics will be a new approach (Delsuc et al., 2005), which can be applied to help resolve the perplexity of *Actinidia*.

In previous studies concerning the phylogeny of *Actinidia*,

only one accession of a taxon was sampled, in most cases, from germplasm repositories. We believe that population sampling in the field of a greater number of taxa should be investigated to further advance our understanding of the phylogeny of *Actinidia* and, perhaps, shedding new light on interspecific relationships within the genus.

Further, in future investigations on the phylogeny of *Actinidia*, artificial crossing between parents of putative hybrid species should be carried out. Such a study will be able to confirm whether episodes of hybridization, indeed, have ever occurred, as previous studies have proposed (Testolin et al., 1997; Cipriani et al., 1998; Li et al., 2002; Chat et al., 2004), but have never been tested.

5 Taxonomy of *Actinidia*

Any attempt to elucidate the phylogeny of the genus *Actinidia* must be based on sound taxonomic identification of the taxa being studied. Misidentification or misinterpretation of a taxon may lead to a wrong conclusion on the phylogeny. Besides, any new classification scheme deduced from molecular phylogeny of the genus must also be interpretable in light of morphological differentiation of members of this plant group.

The classification of the genus *Actinidia* is difficult and the taxonomy of some taxa is still confusing. Dunn (1911) recognized 24 species, Li (1952) enumerated 36 species, but Li (1976) believed that there are only 25 species in the genus. Wu (1977) recognized the occurrence of 23 species of the genus in Yunnan Province of China, but believed that there are about 40 species in the genus. Liang (1984) described many new taxa and listed 51 species as occurring in China, but estimated that there are 54 species within the genus. However, in a more recent study, Wu et al. (2003) pointed out that the validity of every taxon that Liang (1984) established needed reconsideration. Meanwhile, Cui et al. (2002) accepted 61 species as occurring in China, and 65 within the genus; they also provided photographic illustrations for most of the species treated. Still, more recently, it was believed that the genus comprises 76 species (Ferguson and Huang, 2007). In the latest revision of the genus, Li et al. (2007a, b) recognized the existence of 52 species in China, and 55 worldwide, with numerous nomenclatures relegated to synonymy.

The classification of some taxa still needs further study. The species of *Actinidia* are highly variable in their vegetative structures (Li, 1952), as well as in their flowers and fruits, which is the main reason for the difficulty in the classification of the genus. It is also probable that the relatively high level of species interfertility accounts for the taxonomic confusion presently recognized within the genus (Chat et al., 2004). If any revision is to be sound and useful, it must be based on the study of as many herbarium collections as possible from throughout the entire distribution range of the taxa, and on the correlation and

discontinuity of character variations (Davis and Heywood, 1963). A combination of morphometrics and molecular data is advocated, in order to unravel the perplexity of *Actinidia* taxonomy. Molecular markers, which are effective in investigating the phylogeny of closely related taxa, such as AFLP (e.g. Koopman et al., 2001; Lihova et al., 2004; Sponner et al., 2007) and internal transcribed spacers (ITS), *trnL-trnF* (e.g. Lars and Pia, 2008; Shah et al., 2008), could be used in conjunction with morphological analysis based on population sampling. Clearly, a natural classification system of *Actinidia* still needs many more years of effort.

The followings are some notes on some of the problems concerning the classification of *Actinidia*.

(1) *A. chinensis*, *A. deliciosa*, and *A. chengkouensis* C. Y. Chang

In 1975, Liang (1975) described the new taxon *A. chinensis* Planch. var. *hispida* C. F. Liang. This name was later considered to be a synonym of *A. chinensis* Planch. var. *deliciosa* A. Chev. by Liang and Ferguson (1984). Earlier, Gui (1981) was the first to point out that the morphology of the winter bud, the fruit, and the pollen grain of the two entities were distinct from each other, but suggested the elevation of *A. chinensis* var. *hispida* (= *A. chinensis* var. *deliciosa*) to a specific status. Liang and Ferguson (1984) raised the varietal taxon to species status and made the combination *A. deliciosa* (A. Chev.) C. F. Liang & A. R. Ferguson. The main differences between the new species combination and *A. chinensis* lie in the fact that *A. chinensis* has soft tomentose hairs on branchlets, petioles and fruits, while *A. deliciosa* has rigid hairs on these parts (Liang, 1984; Li et al., 2007a). Furthermore, *A. deliciosa* is mainly distributed on the western side and *A. chinensis* in the eastern side in mainland China. Thus, the issue about whether the two entities belong to one or two species was highly controversial (Ferguson, 1990; Xiong, 1991; Webby et al., 1994; Hirsch et al., 2002; Huang et al., 2002; Jia et al., 2005; Chat et al., 2004; Li et al., 2007a, b).

To clarify this question, extensive population sampling across the distribution ranges of the two declared taxa is necessary. If the stability and correlation of characters found within one taxon are not different from such characters found in the other taxon, or if there is a clinal variation spanning the distribution ranges of the two taxa, then they should be treated as one species. Contrarily, they should be treated as two different species.

As to *A. chengkouensis*, morphologically this species is similar to *A. deliciosa*, and may represent a hybrid between *A. deliciosa* and some species within the Sect. *Strigosae* (Liang, 1984). Characteristically, the leaves of *A. chengkouensis* are sparsely stellate-tomentose, and hispid on midvein and lateral veins abaxially, but strigillose adaxially. On the other hand, the leaves of *A. deliciosa* are normally densely stellate-tomentose, and tomentose on midvein and lateral veins abaxially, but glabrous or

puberulent adaxially. Some individuals of intermediate form can also be found, whose leaves are sparsely stellate-tomentose and tomentose on midvein and lateral veins abaxially, but puberulent or strigillose adaxially. To answer the question of whether *A. chengkouensis* is a form of *A. deliciosa* with rigid hairs, further research is needed.

(2) *A. fortunatii* Fin. & Gagn., *A. glaucophylla* F. Chun, and *A. henryi* Dunn

In the treatment of *Actinidia* for the Flora of China (Li et al., 2007a), *A. glaucophylla* is considered as a synonym of *A. fortunatii*, following the opinion of Li (1952). The diagnostic characters of *A. fortunatii* lie in its glaucous and lanceolate leaves; however, *A. glaucophylla* may also have such leaves. Liang (1984) insisted that *A. fortunatii* is a distinct species from *A. glaucophylla*. However, after carefully re-examining the specimens previously studied for the Flora of China treatment, we found that some specimens which are attributable to *A. fortunatii* are distinct from those attributable to *A. glaucophylla*, in that the former constantly has long-tomentose hairs on its young branchlets and young petioles, while the latter has glabrous young branchlets and young petioles or occasionally is very sparsely setose on its petioles. Although the two taxa are very similar in the shape of their leaves, in their red flowers and cylindrical fruits, our re-examination pointed out that the two entities should not be lumped together. The characters of the trichomes on branchlets and petioles in individuals of *Actinidia* are relatively stable; therefore, they represent diagnostic features for taxon differentiation.

In the Flora of China (Li et al., 2007a), *A. henryi* is treated as a different species from *A. fortunatii*. Compared with *A. henryi*, *A. fortunatii* has rather narrow leaves and tomentose hairs on the branchlets and petioles. A careful re-examination of herbarium materials previously examined for the Flora of China treatment indicated the existence of an intergradation of leaf characters between the two species. If more materials become available, it will probably be proven that *A. fortunatii* should be merged with *A. henryi*, since their leaves are intergrading from being lanceolate into broadly ovate in the two taxa. Members of *A. henryi* sometimes also have tomentose hairs on branchlets and petioles, characteristic of *A. fortunatii*.

(3) *A. arguta* (Sieb. & Zucc.) Planch. ex Miq. and *A. melanandra* Franch.

A. arguta and *A. melanandra* are treated as two distinct species in the Flora of China (Li et al., 2007a). *A. melanandra* can be distinguished from *A. arguta* by its narrower glaucous leaves (Liang, 1984). However, sometimes, it is difficult to judge on dry specimens whether the leaves are glaucous. Furthermore, the leaf shape of the two taxa is rather similar, elliptic to broadly ovate. The question that still remains is whether the glaucous nature of the leaves is correlated with other traits in the two taxa, since this may affect their taxonomic status. Extensive field observations of this and other traits in the natural populations are needed.

(4) *A. vitifolia* C. Y. Wu and *A. rubus* Lévl. In the Flora of China treatment (Li et al., 2007a), these two taxa are treated as two distinct species. The diagnostic characters of *A. rubus* are obovate leaves with irregularly setose-serrulate leaf margins (Li, 1952; Wu, 1977). However, leaves of some individuals of *A. vitifolia* may also be broadly ovate or obovate to obovate-oblong, and the leaf margins and hairs on both surfaces also vary considerably. The main difference between the two taxa is that the flowers of *A. vitifolia* are white, while those of *A. rubus* are yellow. Extensive collections should be made in the type locality of *A. rubus*, which should determine whether the differences between *A. vitifolia* and *A. rubus* stand and justify their specific separation.

(5) *A. callosa* and *A. umbelloides* C. F. Liang In the Flora of China treatment (Li et al., 2007a), these two taxa are treated as two distinct species. *A. umbelloides* differs from its congeners in its solid pith and its umbellate inflorescences, which have 3–5 flowers (Liang, 1984). *A. callosa*, on the other hand, normally has a brown lamellate pith, though sometimes also a solid pith, and on the type specimens, *A. callosa* bears umbellate inflorescences. The distribution of *A. callosa* is very wide, encompassing that of *A. umbelloides*. Further studies on the variation pattern of both species may eventually prove that *A. umbelloides* is conspecific with *A. callosa*.

(6) *A. ulmifolia* C. F. Liang, *A. sorbifolia* C. F. Liang, *A. stellato-pilosa* C. Y. Chang, *A. obovata* Chun ex C. F. Liang, and *A. grandiflora* C. F. Liang Except for their type specimens, few additional herbarium collections attributable to any of these species exist. Therefore, the true identities of all these entities are still elusive.

(7) *A. rubricaulis* Dunn and *A. fasciculoides* C. F. Liang In the Flora of China treatment (Li et al., 2007a), these two taxa are treated as two distinct species. Liang (1984) pointed out *A. fasciculoides* axillary flower clusters have 2–6 flowers, whereas the flowers of *A. rubricaulis* always have a solitary flower in an axil. In contrast to Liang (1984), Li (1952) stated that the inflorescences of *A. rubricaulis* may also consist of 1–5 flowers in a fascicle. Therefore, in consideration of other characters, *A. fasciculoides* should probably be included within *A. rubricaulis* as a unique forma.

Acknowledgements This study was supported by grants from the Chinese Academy of Sciences (No. KSCX2-YW-Z-049), the National Natural Science Foundation of China (Grant Nos. 30570120 and 30370101) and Wuhan Botanical Garden, the Chinese Academy of Sciences (No. 0754521G04).

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