

# Phylogenetic Analysis of Chirality of Twining Plants

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**Abstract** Phylogenetic relations of twining chirality of *Dioscorea* sp. in China were analyzed based on the genes *matK*, *rbcl* and *tmL*; phylogenetic character of higher-level phylogeny of twining plants was analyzed at a high taxon level based on *matK* gene. A significant phylogenetic framework of chirality was found: (i) based on *matK* analysis, right-handed *Dioscorea* species in China congregate completely to form a monophyly; (ii) *rbcl* and *tmL* data sets also supported Chinese right-handed *Dioscorea* a monophyly, although with exceptions of the species *D. deprens* + and *D. esculenta*, respectively; (iii) the higher-level phylogeny of twining plants presented complex situations, forming a polyphyletic structure at a high taxon level. The results indicated chirality a credible character in the classification of *Dioscorea* species in China, and thus it was reasonable to sort right-handed species into sect. *Enantiophyllum* firstly in 'Flora of China'. At the world wide watch, however, chirality of *Dioscorea* sp., especially of higher-level phylogeny was actually polyphyletic and it should be cautious to use this character. Latest evidences were inclined to refuse the hypothesis that twining direction was determined by latitude or hemisphere, however, to our opinion further investigations were needed to approve this viewpoint. Studying on close relatives with both left-handed and right-handed such as *Dioscorea* sp. and building up mutations could be helpful to elucidate the mechanisms of the origin of plant chirality. Also, our study of phylogenetic relationships among twining plants will provide scientific information for further utility of chirality characters of plants.

**Key words** Twining plant; Chirality; Phylogenetic structure; Origin

The twining chiralities of stems of twining plant are divided into left lateral and right lateral, while the twining directions of most species are fixed<sup>[1]</sup>. Some scholars take chirality characteristic as the basic classification standard, which is suitable for the taxa with left-lateral material and right-lateral material such as plants in *Dioscorea* during studying taxonomic problems of twining plants. Burkill<sup>[2]</sup> divided plants in *Dioscorea* into two species according to chirality characteristic in Congo. In *Dioscorea* chapter of Flora Republicae Popularis Sinicae, right-lateral species are grouped into sect. *Enantiophyllum* from other species<sup>[3]</sup>. The physiology, ecology, origin and evolution of plant chirality always receive much concern, with the improvement of research means, many important achievements have been obtained. Thitamadee et al<sup>[4]</sup> think that the chiral phenomenon of plant is determined by the rotation direction of microtubule polymer and related to the genes which controlled microtubule protein. Kodama et al<sup>[5]</sup> believed that after compulsory reverse, all indexes of twining plant were increased significantly. There are many hypotheses such as coriolis factors, solar radiation angle and so on for origin of chiral characteristics of vines, while most hypotheses think that the chirality is related to the origin land in southern hemisphere or northern hemisphere. However, the latest researches are inclined to deny this point and phylogenetic analysis is helpful to resolve relevant problems.

The sequencings of some genes of many twining plants provide probability for phylogenetic analysis of plant chiral characteristics. Wilkin et al<sup>[7]</sup> used *matK* and *rbcl* genes to analyze phylogenetic relationships among 67 kinds of plants in *Dioscorea* sp., while left-lateral and right-lateral species have significant chiral separation characteristics. The chiral characteristics of plants in *Dioscorea* sp. in the New and Old Worlds

have several original evidences. The chapter of *Dioscorea* sp. in Flora Republicae Popularis Sinicae records chiral direction of every plant in *Dioscorea* sp., which provides convenience for studying development characteristics of chiral phylogenesis in a small unit. Wilkin's study only cover 14 species in China, which could not reflect the whole property of 52 *Dioscorea* sp. in China. Therefore, other sequenced data of *Dioscorea* sp. in China were analyzed, then combined with new gene markers, the phylogenetic relationships of chiral characteristics of plants in *Dioscorea* sp. were checked. In addition, through collecting chiral information and relevant gene sequences of twining plants in other genera and families, combining some *Dioscorea* sp. in China and the New World, the evolution characteristics of chiral character were checked in large taxa, which was combined with other experimental results to provide theoretical basis for further studying origins of twining chiral character.

## Materials and Methods

### Data sources

The chiral information of *Dioscorea* sp. was from the chapter of *Dioscorea* sp. in Flora Republicae Popularis Sinicae<sup>[3]</sup>. The chiral information of other species were from DELTA website<sup>[8]</sup>, Wilkin's identification results<sup>[7]</sup> and the appraising data of Herbarium of School of Life Sciences, Lanzhou University.

The sequence data were downloaded from GenBank (NCBI). For the *Dioscorea* sp. maturase K (*matK*) gene, ribulose 1, 5-bisphosphate carboxylase large subunit (*rbcl*) gene and tRNA-Leu (*tmL*) gene were used. Because the species components with different sequence data were not the same (Table 1) and different genes might have different evolution characteristics, the data related to three genes were created separately for phylogenetic analysis. For *matK* and *rbcl* gene, two species in relative species *Tacca* sp. were randomly selected as outgroups (*matK*, AY973841; *rbcl*, AF307480 and AY939890); while for *tmL* gene, there was no

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GenBank records of *Tacca* sp., so the *Lilium catesbaei*, AF303701 and *Medeola virginiana*, AY699226 in Liliaceae family with close relations were taken as outgroups (Table 1). The analysis of large taxa was conducted using matK

gene which with more sequence data and rich evolutionary information<sup>[9]</sup>, the *Amborella trichopoda* of angiosperm was taken as outgroup (Table 2).

Table 1 The species and outgroup information of *Discorea opposita* in China

Scientific name	Chinese name	Optical activity	matK	rbcl	tmL
<i>D. banzhuana</i>	Banzhuan Shuyu	left lateral	DQ974182	DQ408174	DQ841301
<i>D. bimanica</i>	Dubng Shuyu	left lateral	AY956481	AY667104	-
<i>D. bulbifera</i>	Huangdu	left lateral	AY956488	AY904791	-
<i>D. colletii</i>	Chanu Shuyu	left lateral	DQ974178	DQ408173	DQ841300
<i>D. delavayi</i>	Gaoshan Shuyu	left lateral	-	DQ974196	-
<i>D. deltoidea</i>	Sanjiaoye Shuyu	left lateral	-	-	DQ841305
<i>D. esculenta</i>	Ganshu	left lateral	AY956497	AY904794	DQ841298
<i>D. esquirolii</i>	Qiy Shuyu	left lateral	DQ974177	-	DQ841322
<i>D. futschauensis</i>	Fuzhou Shuyu	left lateral	DQ974175	-	DQ841316
<i>D. gracillima</i>	Xianxi Shuyu	left lateral	DQ974190	DQ408164	DQ841315
<i>D. hispida</i>	Baishugen	left lateral	AY957589	AF307463	DQ841323
<i>D. kamoonensis</i>	Maoyutou Shuyu	left lateral	EF028332	-	DQ841302
<i>D. melanophyma</i>	Hezhuya Shuyu	left lateral	-	DQ408176	DQ841303
<i>D. nipponica</i>	Chuanbng Shuyu	left lateral	-	AF307455	DQ841308
<i>D. pentaphylla</i>	Wuye Shuyu	left lateral	AY972483	AF307470	DQ841327
<i>D. sinukans</i>	Machang Shuyu	left lateral	-	-	DQ841320
<i>D. sinoparviflora</i>	Xiaohuadunye Shuyu	left lateral	DQ974179	-	DQ841326
<i>D. spongiosa</i>	Mianbi	left lateral	DQ974191	DQ974194	DQ841317
<i>D. tentaculigera</i>	Juanxuzhuang Shuyu	left lateral	AY973828	AY939886	-
<i>D. tenuipes</i>	Xibing Shuyu	left lateral	-	AB017340	-
<i>D. tokoro</i>	Shanbi	left lateral	DQ974186	DQ408180	DQ841312
<i>D. zingiberensis</i>	Dunye Shuyu	left lateral	AY973831	AY939889	DQ841318
<i>D. akata</i>	Shenshu	right lateral	AB040208	AY667098	-
<i>D. aspersa</i>	Liye Shuyu	right lateral	-	-	DQ841304
<i>D. cirrhosa</i>	Shugen	right lateral	DQ974189	DQ408184	DQ841324
<i>D. decipiens</i>	Duomao Shuyu	right lateral	AY956494	AF307454	DQ841329
<i>D. exalata</i>	Wuchi Shenshu	right lateral	EF028330	DQ408170	DQ841325
<i>D. fordii</i>	Shanshu	right lateral	EF028333	DQ974195	DQ841299
<i>D. glabra</i>	Guangye Shuyu	right lateral	AY956501	AF307456	-
<i>D. japonica</i>	Riben Shuyu	right lateral	DQ974183	AF307457	DQ841307
<i>D. persimilis</i>	Hebao Shuyu	right lateral	DQ974193	DQ408165	DQ841328
<i>D. polystachya</i>	Shuyu	right lateral	-	DQ408181	DQ841313
<i>D. wallichii</i>	Yingjiang Shuyu	right lateral	AY973830	AY939888	-
<i>T. palmatifida</i>	-	-	AY973841	AY939890	-
<i>T. leontopetaloides</i>	-	-	-	AF307480	-
<i>M. virginiana</i>	-	-	-	-	AY699226
<i>L. catesbaei</i>	-	-	-	-	AF303701

Table 2 The optical activity and sequence information of other twinning plants

Scientific name (optical activity)	matK	Scientific name (optical activity)	matK
<i>Discorea galottiana</i> (R)	AY956499	<i>Lonicera orientalis</i> (L)	AJ430196
<i>Discorea convolvulacea</i> (R)	AY956491	<i>Phaseolus vulgaris</i> (R)	DQ450863
<i>Discorea subhastata</i> (R)	AY972492	<i>Plumbago europaea</i> (L)	AY042634
<i>Discorea brachybotrya</i> (L)	AY956482	<i>Plumbago indica</i> (L)	AF204857
<i>Actinidia chinensis</i> (R)	ACU61324	<i>Polygonum aplanum</i> (L)	AF204858
<i>Actinidia eriantha</i> (R)	AF322616	<i>Polygonum bistorta</i> (L)	AF204859
<i>Actinidia polygama</i> (R)	AF322601	<i>Polygonum cuspidatum</i> (L)	EF153700
<i>Akebia quinata</i> (R)	AF542587	<i>Schisandra chinensis</i> (L)	DQ185526
<i>Asparagus cochinchinensis</i> (R)	AB029804	<i>Schisandra glaucescens</i> (L)	AY326501
<i>Asparagus filicinus</i> (R)	AB029805	<i>Schisandra henryi</i> (L)	AY326502
<i>Clerodendrum japonicum</i> (L)	AF315297	<i>Scyphanthus elegans</i> (L)	AF503334
<i>Clerodendrum thomsonae</i> (L)	AY840129	<i>Stemona japonica</i> (R)	AB040210
<i>Clerodendrum trichotomum</i> (L)	AF477760	<i>Stephania tetrandra</i> (L)	EF143877
<i>Humulus lupulus</i> (L)	AF345318	<i>Thryallis latifolia</i> (R)	AF344580
<i>Pomoea batatas</i> (R)	AJ429355	<i>Thunbergia akata</i> (R)	AF531811
<i>Pomoea mauritiana</i> (R)	AY491651	<i>Trichopus sempervirens</i> (R)	AY973844
<i>Jasminum nudiflorum</i> (R)	AF531779	<i>Vigna unguiculata</i> (R)	AY589510
<i>Kadsura bngpedunculata</i> (L)	AY326498	<i>Amborella trichopoda_1</i>	DQ185522
<i>Lapageria rosea</i> (L)	AY624480	<i>Amborella trichopoda_2</i>	AF543721
<i>Lonicera nervosa</i> (L)	AF446903		

Data analysis

The CLUSTALX software<sup>[10]</sup> was used to conduct aligning arrangement and to generate nexus files. The PAUP4b10<sup>[11]</sup> and MrModeltest 2 software package<sup>[12]</sup> were used to conduct model test for four gene datasets, then the most favorable Bayesian analysis model was chosen. Under different most favorable conditions, MrBayes 3.12<sup>[13]</sup> was used to create phylogenetic trees for four datasets to operate 1 000 000 generation (enough for convergence), while every 100 generations was sampled once. The sum tree was used to record phylogenetic trees. The first 25% was taken as burn-in, which was abandoned, and as a result the consistent trees with posterior probability was obtained.

Results

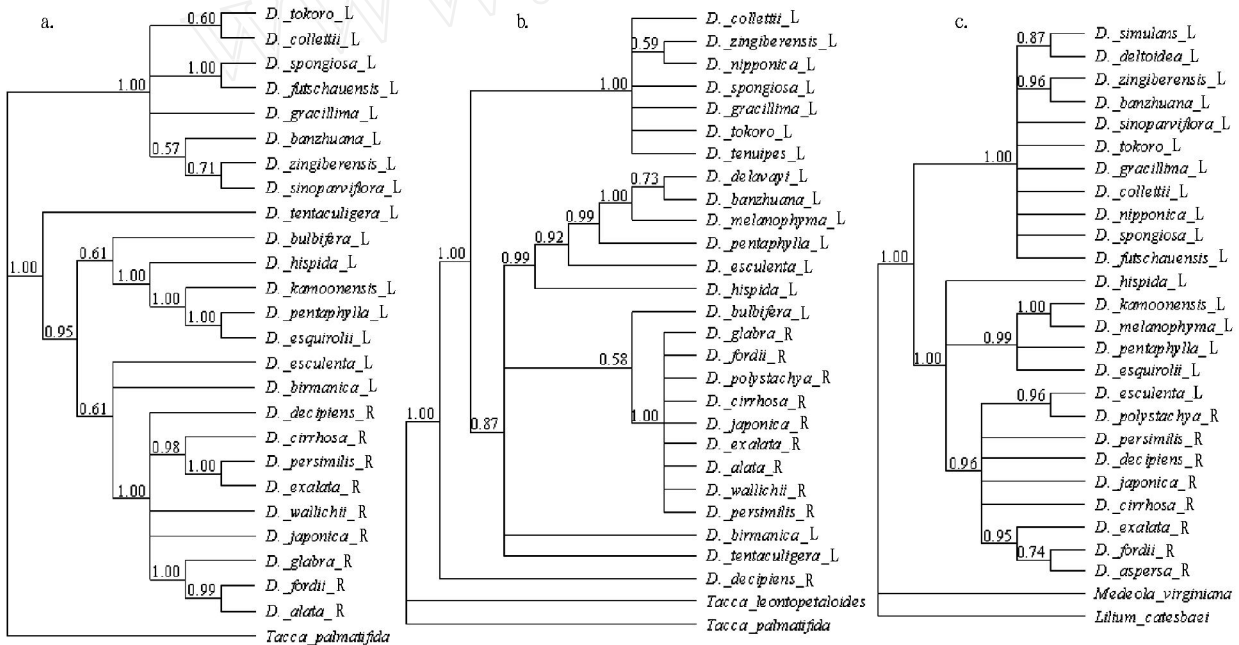
Chiral system structure of plants in Dioscorea sp. in China

The matK data contained 16 left-lateral species and 9 right-lateral species, with the optimum GTR + G model (nst=6, rates = gamma). There were 14 079 phylogenetic trees and the consistent trees with over 0.25 posterior probability were shown on

Fig. a. Based on consistent tree display of matK gene, all right-lateral species were separated from left-lateral species and to one class and the Bayes posterior probability was 0.61.

The rbcL data contained 16 left-lateral species and 10 right-lateral species, with the optimum model GTR + I + G model (nst=6 rates = invgamma). There were 14 874 phylogenetic trees and the consistent trees with over 0.5 posterior probability were shown on Fig. b. The consistent trees based on rbcL gene demonstrated that except D. decipiens, the right-lateral species were separated from left-lateral species and clustered into one class, while the Bayes posterior probability was 1.00.

The tmL data contained 17 left-lateral species and 8 right-lateral species, with the optimum model HKY + G model (nst = 2, rates = gamma). There were 14 981 phylogenetic trees and the consistent trees with over 0.5 posterior probability were shown on Fig. c. It was concluded from Fig. c that 8 kinds of right-lateral species were clustered into one class, while the right and left lateral were separated (except for D. esculenta) and the Bayes posterior probability was 1.00.



A stands for the consensus trees generated from matK; b stands for the consensus trees generated from rbcL sequence; c stands for the consensus trees generated from tmL; L: left-handed; R: right-handed; Above branches represent posterior probability values (only ones > 0.5 are shown).

Fig. 1 Consensus trees generated from matK, rbcL and tmL

System characteristics of chiral characteristics in large taxa

matK data in large taxa (not including Dioscorea sp.) contained Actinidiaceae, Lardizabaceae, Liliaceae, Verbenaceae, Cannabaceae, Convolvaceae, Oleaceae, Magnoliaceae, Phlegmaceae, Caprifoliaceae, Fabaceae, Plumbaginaceae, Polygonaceae, Menispermaceae, Stemonaceae, Loasaceae, Maphignaceae and Acanthaceae. Among them, there were 18 left-lateral species and 15 right-lateral species. The optimum model for matK data was GTR + I + G model (nst=6, rates = invgamma) and the phylogenetic tree display based on matK gene demonstrated that there were many independent events for left-lateral and right-lateral specifications. Among Dioscorea sp. (branch E), some left-lateral species in China (branch A) were separated from other plants in Dioscorea sp. at basal part. In sub-branch D, one left-lateral

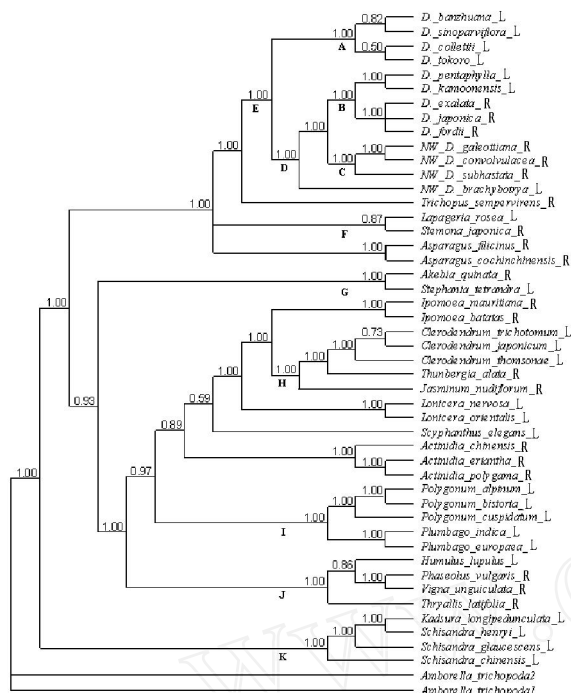
species in new world took relatively basal position, while three right-lateral species of new world species were separated from some left-lateral and all right-lateral species in China. While in sub-branch B, the left-lateral and right-lateral species were divided into two branches (Fig. 2).

There were complex relations among other species. Some branches were aggregated by two kinds of chirality, such as branch F, G, H and J et al, while some species with same chirality were aggregated into one class, such as branch I and branch K et al. Generally, the right-lateral species and left-lateral species on every node had obvious separation (posterior probability was nearly 1.00).

Discussion

Relative stability of chiral characteristics

Generally, from our study, the chiral characteristics of



L: left-handed; R: right-handed; NW: new world species. Above branches represent posterior probability values (only ones > 0.5 are shown).

Fig. 2 Maximum parsimony tree generated from matK sequences analysis

twining plants were relatively stable characteristics. During the analysis of *Dioscorea* sp. in China, the results of three groups of gene marker have demonstrated that left-lateral and right-lateral species have obvious systematic isolation phenomenon. In matK data, the right-lateral species are clustered into independent clade, while in rbcL and tmL datasets, except for *D. decipiens* and *D. esculenta*, the species display good monophyletic characteristics of right-lateral species. However, the two deviations are not existed in matK data; we suggested that the lack of informative sites had make *D. esculenta* be mistakenly grouped in right-lateral group. The experimental data and Wilkin's result support monophyletic characteristics of right-lateral species in *Dioscorea* sp. in China. In addition, the right-lateral species and left-lateral species are not divided into two branches and the analysis results of three kinds of genes demonstrate that the sect *Enantiophyllum* is a later evolution unit. The conclusions have demonstrated that taking the characteristics as classification standard in *Fibra Republicae Popularis Sinicae* is reasonable. It is notable that not all right-lateral species in *Dioscorea* sp. are monophyletic group. Wilkin et al<sup>[71]</sup> and this experimental results all have demonstrated that the left-lateral species and right-lateral species in new world species are separately clustered into one group, which have far relations with sect *Enantiophyllum*. In addition, the phylogenetic analysis of large taxa also demonstrates that chirality is not an old characteristic but shows obvious multiphylogenetic characteristics. Therefore, exploring classification problems in *Dioscorea* sp. or even higher taxa, chirality should be used carefully.

Chiral origin

The chirality is commonly existed in organisms, such as twining chirality of vine, petal rotary chirality<sup>[14]</sup>, chirality of *Gabapervias* shell<sup>[15]</sup> and DNA chirality and protein chirality<sup>[16]</sup> etc. Since Darwin era<sup>[11]</sup> or even earlier, people have paid

much attention to the happen and origin of twining chirality of vine as well as proposed many hypothesis. Many hypothesis pay much attention to physical differences in southern hemisphere and northern hemisphere, for example, solar radiation angle hypothesis believes that the daily variations of solar radiation angle in southern hemisphere and northern hemisphere are opposite, while Coriolis force hypothesis believes that Coriolis force makes opposite deflection of growth and movement<sup>[6]</sup>. Edwards et al think that these two hypotheses are wrong, namely, geography properties in southern hemisphere and northern hemisphere are not related. The natural vines seldom show inverse mutations at species level, besides, molecular phylogenetic evidences demonstrated that chirality at least has stability at species level. During speciation, species make the big change of distribution range through diffusive migration, besides, Edwards et al<sup>[71]</sup> have investigated 11 sampling points and the location is less than 25° in northern hemisphere. However, the species identification is not conducted, i.e. all individuals are treated equally in their study, we suggest that their conclusions need to be further discussed.

Other experiments have demonstrated that chirality is a single multiple-occurred characteristics<sup>[17]</sup>. Our results support multi-line characteristics, i.e. the species with the same chirality are not clustered in one group in large taxa level. However, this can not deny the potential relations between chirality and physical differences in southern hemisphere and northern hemisphere. Although the chiralities of twining plants have relative stability, there are also some site mutations, namely, the fact of change chiral direction. The molecular biological studies have demonstrated microtubule protein participates in determining chiral characteristics of plant<sup>[18]</sup>. In *Arabidopsis thaliana*, the artificial mutants could have left-lateral and right-lateral characteristics<sup>[4,19]</sup>, so physical differences in southern hemisphere and northern hemisphere could cause the fixation and separation of chirality in long time and large spatial scale, because during the long evolution process, plants can change their distribution areas in southern hemisphere and northern hemisphere through geological events (plate movement) and species dispersal. Therefore, combining geological events to study small evolution unit such as *Dioscorea* L., *Wisteria* Nutt<sup>[20]</sup> and creating a method of mutant are helpful to resolve chiral problem.

The twining plants have many species and are distributed in many genera and families. Some of them are used as foods, drugs and ornamental resources. From the evolutionism angle, the generation and evolution of one property must have adaptability problems of physiological ecology. While revealing mechanism and laws of this adaptability can make human know life phenomena profoundly, besides, it is helpful for human to control, screen and improve objective characteristics. The experiment has conducted phylogenetic analysis of chirality of twining plants to provide reliable basic data of revealing evolution problem of chiral origin, meanwhile, it also provides scientific basis for chirality utilization in agriculture and horticulture field et al.

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## 缠绕植物手性的系统发育分析

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**摘要** 利用 *matK*、*rbcL* 与 *tml* 基因, 分析了中国薯蓣属植物缠绕手性的系统发生关系; 利用 *matK* 基因, 从大分类单元角度进一步分析了缠绕植物的系统特征。结果显示左、右旋缠绕植物物种存在显著的系统发育特征: *matK* 数据中的右旋薯蓣聚成独立的进化枝与 *rbcL* 基因的分析共同支持右旋物种的单系性; *rbcL* 和 *tml* 的数据均较好地显示了右旋薯蓣的单系特征 (除多毛叶薯蓣 (*D. decipiens*) 和甘薯 (*D. esculenta*) 外); 在大分类单元上, 缠绕植物手性性状则呈现出明显的多系特征。结果表明在中国区薯蓣属的分类中, 手性特征是较可靠的性状特征, 《中国植物志》薯蓣属章节直接将右旋物种归入周生翅组 (*sect. Enantiophyllum*) 较合理。但在世界范围上看, 在小分类单元的薯蓣属内和薯蓣科及其他大分类单元内, 手性特征都具有单独多次起源的性质, 因此在执行分类时应当慎用这个性状。对于手性特征的起源问题, 最新的观点倾向于否定南北半球物理差异相关的假说, 但其结论的正确性有待商榷。结合地质事件研究薯蓣属等具有两种手性方向的小分类单元, 以及构建突变体的方法, 有助于最终解决植物手性的起源问题。

**关键词** 缠绕植物; 手性; 系统发育结构; 起源

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