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基于叶绿体全基因组核苷酸变异位点的大豆属(*Glycine* Willd.)植物的分子鉴定新方法

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摘　要

高通量测序技术大幅降低了获得基因组序列的成本，为大豆属植物资源多样性的精准鉴定提供了新的数据来源。我们利用来自大豆属7个近缘种的叶绿体全基因组的2363个核苷酸变异位点作为分子性状编制分子鉴定检索表，成功鉴定7个近缘种。这些特有变异位点的数量及核苷酸构成存在种间差异。大豆(*Glycine max* (L.) Merr.)、白毛烟豆(*G. stenophita* B.E.Pfeil & Tindale)、镰荚烟豆(*G. falcata* Benth.)、绢毛烟豆(*G. canescens* F. J. Herm.)以及扁豆荚大豆(*G. dolichocarpa* Tateishi & H. Ohashi)的特有变异位点中，A或T的比例(26.74%~42.62%)均高于C或G(9.84%~21.31%)；短绒野大豆(*G. tomentella* Hayata)中，A、T或C的比例(26.36%~27.91%)均高于G的比例(19.38%)；玫红野大豆(*G. syndetika* B. E. Pfeil & Craven)中，T或G的比例(30.00%)均高于A或C的比例(18.33%~21.67%)。结果显示叶绿体基因组的单核苷酸变异位点信息，可用于大豆属植物的分子鉴定。本研究对于大豆属植物种质资源的分类鉴定、保护和利用具有重要价值。

关键词

大豆属，叶绿体全基因组，核苷酸变异位点，植物鉴定

A Novel Method for Molecular Identification at Species Level in *Glycine* Willd. Using Variable Nucleotide Characters from Complete Chloroplast Genomes

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Abstract

High-throughput sequencing technology has greatly decreased the experimental cost for yielding genome sequences and provided a new source of data for accurate identification of plant resource diversity in genus *Glycine*. 2363 species-specific variable nucleotide characters in the complete chloroplast genome of 7 *Glycine* species were used as molecular traits to identify *Glycine* plants and compile a molecular classification key for the first time. There are differences in aspects of amount and base composition of variable nucleotide characters between the species. The proportion of A or T (26.74%~42.62%) is higher than that of C or G (9.84%~21.31%) in *Glycine max* (L.) Merr., *G. stenophita* B.E.Pfeil & Tindale, *G. falcata* Benth., *G. canescens* F.J.Herm. and *G. dolichocarpa* Tateishi & H. Ohashi. The proportion of A or T or C (26.36%~27.91%) is higher with that of G (19.38%) in *G .tomentella* Hayata. The proportion of T or G (30.00%) is higher than that of A or C (18.33%~21.67%) in *G. syndetika* B. E. Pfeil & Craven. Our results indicated that species-specific variable nucleotide characters from the chloroplast genomes could be used for discrimination of different genotypes in *Glycine*. This study is valuable for identification, conservation and utilization of plant germplasm resources of *Glycine*.

Keywords

***Glycine* Willd., Complete Chloroplast Genome, Variable Nucleotide Character, Plant Identification**

1. 引言

大豆(*Glycine max*)是粮、油和饲料蛋白兼用的重要经济作物之一，常用来加工各种豆制品、榨取豆油、酿造酱油和提取蛋白质，大豆食品提供了人类必需的营养。大豆食品产业是食品经济中的大健康支柱产业。联合国粮食与农业组织(Food and Agriculture Organization of the United Nations, FAO)的数据显示，大豆产量超过其它所有油料作物之和[1] [2] [3] [4]。

2023 年底的数据显示，全球大豆产量为 3.9888 亿吨。巴西的大豆产量(~1.61 亿吨/年)世界第一。中国的大豆总产量(~2,084 万吨/年)世界第四。中国的大豆消费总量(~1.17 亿吨/年)世界第一，占全球大豆消

费市场的约 30%。在中国，80%以上的大豆用于豆油压榨和饲料加工，近 20%的大豆用于食品加工和农用种子等其他消费。大豆油占中国植物油消费总量的约 50% [3] [4] [5]。豆粕(大豆提取豆油后的副产品)、豆渣(生产豆奶或豆腐过程中的副产品)或大豆磨成的粗粉常用作畜禽饲料。中国是一个畜牧业大国，大豆是畜禽养殖用蛋白粕的主要原料，这也是中国大豆消费量居世界第一的主要原因。中国每年的大豆进口量约 1 亿吨。中国 97%以上的进口大豆来自大豆产量全球排名前三的巴西、美国和阿根廷，从加拿大、乌拉圭、俄罗斯等国有少量进口[3] [4]。中国的大豆产量和需求量差距巨大，对进口的依赖度高，大豆进口量在全球贸易中的所占比例较高，实现大豆完全自给需要做大量工作。

中国是大豆食品加工和消费大国，已有 4000 多年的大豆种植和食用历史。每年 85%以上的国产大豆用于食品加工。大豆食品种类多，例如，豆腐、豆花(豆腐脑)、腐竹、豆腐干、豆酱、豆腐乳、豆浆、豆奶、大豆蛋白配料、大豆肽等[3] [4] [6] [7]。利用大豆、豌豆、面筋等植物蛋白作为原料开发的仿肉制品，市场销售额有持续增长的趋势[8]。

大豆食品加工业对原料大豆品质的要求精细化程度较高。例如，亚麻酸、油酸和亚油酸含量较低的大豆品种适用于加工豆浆和豆奶类，是由于大豆籽粒中可溶性固形物、亚麻酸、油酸和亚油酸影响豆浆的整体风味。豆芽生产需要选用小粒、发芽率高、脂肪含量低的大豆品种。中小粒径、种皮黑色或褐色、蛋白质含量低、糖分含量高的大豆品种适用于生产豆豉。酱油酿造则选用蛋白质含量和糖分含量高的大豆品种。吸水能力强、粒形整齐一致、小粒径的大豆适于加工纳豆[3] [4] [6]。

大豆的营养化学品质具有产地差异。营养化学品质包括蛋白质、脂肪、碳水化合物、无机盐等物质的含量。根据大豆育种、生产以及消费等多方面的需求和技术指标，培育出了一些品质特色较为明显的新品种。植酸(phytic acid，植物种子中的一种有机磷类化合物)可以与蛋白质螯合，减缓蛋白质凝固速率，影响豆腐的得率和质地[3] [9]，由此培育出了适宜加工豆腐的‘齐黄 34’和‘中黄 13’等品种。此外，还培育出了适宜加工豆浆的品种‘东农 252’和‘东农 253’，适宜加工豆腐干的大豆品种‘东农 42’、‘吉育 204’以及‘东农 48’，适宜加工豆腐乳的品种‘辽豆 66’等[3] [4]。蛋白产品中存在豆腥味时，难以进入国际高端产品市场，附加值不高。为了适应需求，也培育出了无腥味的大豆品种[3] [4]。然而，在生产和原料供给方面，混种、混收、混用仍然是大豆食品加工领域的难题[3]。

栽培大豆产量与品质的提升受到遗传瓶颈的制约[10] [11]。栽培大豆经历了几次遗传瓶颈，包括在当地的驯化、地方品种被引种到世界其它地区以及后来的选择育种，这些过程导致遗传多样性降低，是阻碍大豆改良的主要原因[12]。野生大豆的遗传背景多样，可适应不同的生态环境，具有抵抗生物和非生物胁迫的特性。遗传多样性是作物改良的基础。大豆的野生近缘种具有相对较高水平的遗传多样性，尤其是多年生大豆，可以作为改良大豆的潜在基因资源[12]。

大豆属植物资源多样性的研究一直是关注的热点，与其它植物一样，也经历了多个阶段，包括形态学、细胞学、同工酶和多种 DNA 分子标记阶段[10]。目前，已经发展到全基因组研究时代[13]-[23]。基因组和转录组测序能够发现野生大豆中存在的、驯化过程中丢失的、与理想性状相关的等位基因。大豆野生近缘种的收集、保存以及基因组特征的剖析有助于促进大豆的育种和粮食生产的可持续发展[12]

多数文献主要侧重野生大豆和栽培品种两类资源的研究。例如，对 31 份大豆(包括野生大豆和栽培大豆品种)的全基因组重测序发现，野生大豆中等位基因多态性水平明显高于栽培大豆[24]。对大豆品种‘齐黄 34’的全基因组重测序，检测到 1,519,494 个单核苷酸多态位点，为分子标记辅助育种提供了丰富的标记资源[25]。对中国 6 大生态区 1024 份大豆属 *Soja* 亚属的代表性材料(203 份野生大豆、栽培大豆 375 份地方品种和 446 份现代育成品种)的简化基因组测序结果显示，存在“遗传瓶颈”和“单倍型新生”现象[11]。在另一项研究中，利用不同生态区的 182 份一年生野生大豆、396 份地方品种和 446 份育成品种组成的中国大豆种质资源群体，通过全基因组重测序，分析了大豆群体的基因组演化特征[26]。利用

228 份普通大豆材料的重测序数据开发出 100 个二态 DNA 标记，用于大豆的基因型鉴定[27]。组装了大豆属有代表性的多年生物种的基因组，包括 5 个二倍体和 1 个异源多倍体，为深度理解多倍体基因组进化和大豆的改良提供了遗传基础信息[28] [29]。利用高通量测序技术分析了野生大豆 *G. soja* 和大豆属的另外 9 个种的叶绿体全基因组的结构、基因组成、遗传变异和系统发育关系[30]。

Table 1. Samples and Genbank accession numbers of chloroplast genome sequences used in this study
表 1. 供试样品名称及叶绿体基因组序列号

	拉丁学名 Latin name	中文名称 Chinese name	序列号 Genbank accession no.
1	*Glycine dolichocarpa*	扁豆荚大豆	KC893636.1
2	*Glycine syndetika*	玫红野大豆	KC893638.1
3	*Glycine canescens*	绢毛烟豆	KC893635.1
4	*Glycine tomentella*	短绒野大豆	KC893633.1
5	*Glycine falcata*	镰荚烟豆	KC893637.1
6	*Glycine stenophita*	白毛烟豆	KC893634.1
7	*Glycine max*	大豆	ON470219.1
8	*Pueraria edulis*	食用葛	OM048895.1

注：食用葛(豆科 Fabaceae 葛属 *Pueraria* DC.)为外类群对照

根据形态特征，全球的大豆属植物约有 28 种和亚种[1] [2]，隶属于被子植物的蔷薇目(Rosales)的豆科(Fabaceae)。基因编辑技术的进步使大豆属全部物种的基因资源进入了可利用范围。但是，尚未见到大豆属野生种资源多样性的分子分类检索表的报道。植物的叶绿体基因组的基因结构、组成以及基因数量高度保守，已广泛用于植物遗传多样性评价、物种的分子鉴定和系统发育关系研究[13]-[23]。本研究利用叶绿体全基因组序列的核苷酸变异位点，首次建立大豆属植物的分子鉴定检索表方法，对于大豆属植物种质资源的保护和可持续利用具有重要意义。

2. 材料与方法

Table 2. Base composition of variable nucleotide sites for classification of the seven species of *Glycine*
表 2. 大豆属 7 个种的具有分类价值的核苷酸变异位点数目及碱基构成

*	A (%)**	T (%)**	C (%)**	G (%)**	Total*** 合计(%)
1-1a	324 (29.37)	324 (29.37)	235 (21.31)	220 (19.95)	1103 (46.68/33.82)
1-1b	268 (24.30)	277 (25.11)	272 (24.66)	286 (25.93)	1103 (46.68/33.82)
1-2a	204 (30.86)	200 (30.26)	125 (18.91)	132 (19.97)	661 (27.97/20.27)
1-2b	168 (25.42)	144 (21.79)	186 (28.14)	163 (24.66)	661 (27.97/20.27)
1-3a	74 (28.14)	95 (36.12)	44 (16.73)	50 (19.01)	263 (11.13/8.07)
1-3b	78 (29.66)	74 (28.14)	58 (22.05)	53 (20.15)	263 (11.13/8.07)
1-4a	34 (26.36)	36 (27.91)	34 (26.36)	25 (19.38)	129 (5.46/3.96)
1-4b	33 (25.58)	28 (21.71)	31 (24.03)	37 (28.68)	129 (5.46/3.96)
1-5a	30 (34.88)	23 (26.74)	17 (19.77)	16 (18.60)	86 (3.64/2.64)
1-5b	20 (23.26)	17 (19.77)	24 (27.91)	25 (29.07)	86 (3.64/2.64)
1-6a	19 (31.15)	26 (42.62)	6 (9.84)	10 (16.39)	61 (2.58/1.87)
1-6b	15 (24.59)	9 (14.75)	23 (37.70)	14 (22.95)	61 (2.58/1.87)
1-7a	11 (18.33)	18 (30.00)	13 (21.67)	18 (30.00)	60 (2.54/1.84)

续表

1-7b	18 (30.00)	20 (33.33)	13 (21.67)	9 (15.00)	60 (2.54/1.84)
合计					2363/3261

注：*该列的序号与检索表内的序号对应；**核苷酸变异位点数(在 4 种碱基中的占比)；***此列括号中，前一个数字是在物种特有变异位点总数(2363)中所占的比例；后一个数字是在全部核苷酸变异位点总数(3261)中所占的比例

1-1a. Type T50T117C144C176T193T277A294T847T1586G1587C1616T1628G1801C1836G1842C1870G2038A2093
G2144C2485T2519T2862A2932T2991A3022G3070G3091T3226C3230A3232T3342G3466G3473A3561A3575
A3941T4031C4109A4137A4269G4373G4382C4419A4420A4421T4450G4452A4454A4495A4496T4499C4500
T4501A4612T4637C4697T4796C4826C4875T4948G4967A4973A5070T5088C5118T5122C5223C5226C5442
T5719A6457C6604A6962C7152G7231T7322G7523T7621A7625T7751T7817A7857T8465G8651A8985G9383
G9581G9646T9674C10128T10271C10413G10443G10462C10698G10713T10823T10833T10834T11063A11543
A11651A11663T11765A11820T11994T12002A12015T12050C12371T12416G12554T12656A12785G12813T12847
G12900G12906G12992C12999A13011G13026A13100T13232G13236A13357A13358C13624G13682G13866A14207
C14426G14472T14505A14506T14512G14592A14602A14609A14672C14685G14806A14818A14823G14946A14996
A15098T15106A15238G15256A15290T15299C15330C15335T15547C15724A15829G15877A16084G16270G16271
C16517G16558C16723A16943C17131C17311G17322T17337A17371C18128C18239G18262C18331G18469T18584
T18646T18652A18661C18840T18881A19186C19210A19501C20029T20338T20380A20435T20436T20800A20971
G20977A20992T21025A21241A21454A22064T22127C22220A22328T22383T22658C22718A22916C23093G24023
C24048A24100G24215A24285C24498C24517G24757A24797T24970C25080G25120G25124C25216T25234A25282
T25293C25324A26050T26057C26109C26126A26143T26213C26333A26364C26366C26409T26530A27522G28178
C28310A28688T28841A29113A29282G29419C29427G29639G29738A29739G29777C29840G29938A30053G30074
T30087G30119C30156G30167G30191A30206T30333A30353C30408G30495C30554C30589A30745G30746A30747
A30748G30825C30919G31049A31118T31393A31402T31482C31504T31525A31609A31676A31706C31816T31977
A32044T32050A32181T32362G32457T32530C32572C32640A32824A33137G33145A33242T33335A33416A33534
T33618C33701T33745C33812T33882A33907A33911G33913A33915A33916T33924T33927G34023C34143G34206
T34297C34402C34585T34610G34613C34680G34841G34930A34961C35186T35278A35595T35857T36156G36489
T36684A36912G37009C37158T37434A37478A37562G37719T37746C38322A38659T39177G39479A39639C39658
C39780T39966T40496T40781C41258G41307A41738A41754A41785T41988T42138C42148G42318T42417A42426
A42569A42615C42927T43050T43188G44119A44134T44337A44448A44487A44662A44703C44764G44881C44968
G45099C45178C45838A45901G45954C46005G46041T46099G46296A46533G46576C46713A47055G47106A47232
G47289C47449A47562C47676T47721C48070T48174G48176C48467T48542G48552A48587G48615G48667A48713
T48826G48923T48988A49080T49335T49575G49610G49755G50065T50102G50117G50373T50638T50888T51158
A51725A51979C51990T51992T52079G52343T52553C52631T52696G52906T53199T53200G53227A53276G53280
C53539G53833A54057C54187A55004T55025A55245T55284A55287C55318C55415T55632A55667G55812T55882
T55906G55961A56013C56029T56061T56078T56108T56256A56285A56299G56559A56580A56581A56667C56826
T56827C56831C56856T56878A57170A57196C57322T57347G57401C57420C57504A57512T57620T57919C58048
A58121A58125C58272G58281C58414G58460A58488C58705G58717T58724G58812A58813G58829G58830
G58833A58859C58944C58946G58949G58950G58955A59142G59148G59163C59166T59224T59225C59251
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1-1b. Type C50G117T144T176G193C277C294A847A1586A1587A1616C1628T1801A1836T1842A1870T2038C2093
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The six species other than *G. max*

1-2a. Type G137A186A197G204T216T217T218A300A303A1029A1702C1877T1948T2200A2209A2401T2509T2840
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1-2b. Type C137C186G197T204A216A217A218C300T303G1029C1702A1877G1948C2200G2209G2401C2509C2840
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C140468C142093C142208G142452T143435C144646C144825A145214T146150A146983C147813A150546G151964
G153007C153273G154074G154084A154875 …… 白毛烟豆以外的 6 种
The six species other than *G. stenophita*

1-3a. Type A157C231G1645T1983T2783A3590A3592A3943G4404G5181T6087A7040A7663C8327A8795A8969A9557
G10809G11831A12001A12345A12592G13132T13491T14292T14467G15407G15473A17989C18658G18889A18904
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T42867G43863C44804G46996T47823A47907G48095T49582G49769C50119C50128T50470C50921C51593C52786
C52879C52927T53117C53640C53835T54073A54162A54673G54920T55006T55509A55613T55912T55947A56220
C56443T56468T56469A56699C57275A57300A57683T57870T58349G58647G60032T60446T60451T60986G61604
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G72636C72714A73306T75480T76083C78020C78202T79294T80326A80579A80580A80581T80812T80901T80977
A81024C81165A81227C81362T81631A82177A82597G83039G83155G83528G83786T84191G84210G84924G85307
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G114521A115136T115487T115556G116399A116972A117814T117866T118007C118270T118431A119287A119368
A119621A122032C122626G122730T122970A123152T123153C123156T123165A123528T123855T124431A124497
A125090A125225T125420A125782G126216T126426C127674T127900A127901A127927G128629C128773T128969
C129077T129190G129575A134137T139597C139615A140283A142036T142390C143436C144311G144836T148032
A154878T154886 …… 镰荚烟豆 *G. falcata*

1-3b. Type G157A231T1645G1983G2783C3590G3592C3943A4404A5181C6087G7040G7663A8327G8795G8969C9557
T10809T11831T12001G12345T12592T13132G13491C14292A14467T15407T15473G17989T18658A18889C18904
G19460G21995C23633C24964C24987A25076T25849T25938C27361G28061G29392T29414G29516T29619A30460
G30463A30465C30466A30467A30533A30597A32064G32106A32111T32112T32113T32668T32822A33526A33542
C33562T33930A33963T34099G34147A34159T34623G34648G35554C36934C37506G38741C39438C39711C42510
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T65984T66997T67351G68000C68022G69111A69365C69397A70776C71130A71459A71510T71511A71597T72042
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C81024A81165G81227T81362C81631G82177C82597T83039A83155T83528T83786C84191A84210T84924T85307
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T111710A111908A112192A112257G112306A112312T112360G112410A112465A112973G113052T113213C114345
T114521C115136A115487A115556T116399T116972T117814A117866C118007A118270A118431T119287T119368
G119621T122032A122626A122730C122970G123152A123153T123156A123165G123528C123855C124431T124497
T125090T125225A125420C125782T126216G126426A127674C127900G127901G127927T128629A128773G128969
A129077C129190T129575G134137A139597A139615C140283G142036C142390A143436A144311C144836G148032
T154878A154886 …… 镰荚烟豆以外的 6 种

The six species other than *G. falcata*

1-4a. Type G285A1054A1852T2257A3139C3433C3514C3847A4619G4827C4966G5034T5182A5217G8028C9908
C10904C10958G11892T12681T12726A13118T13345A13912C14066A17977A18337T18859G19198C19273
G19951C23726C24077C24249T24624G24739G25738A26169C26911C28004T28490A29314T30729T31086
G31102T31712T31745T32855C33304G33934G34826T36153A38553T41084C43767T44718C47427A48049
C48448A49609C53350T55044A55096G55534A56215T56770G57356C58442T59183A61564C62649C63786
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C73074C74326A77446G77958A78870T79029A81068T81294A83179T83780T84035C84358G85050A85471
C93538A100826C111849A112064G112362C112759G113179A113604T114312A114881A115024C115324
C115649G115796T116222G121215C122430G123078A123858A125147A125336A126277A127441G127567
A128281G128662T129269T139743G147031 …… 短绒野大豆 *G. tomentella*

1-4b. Type T285G1054G1852C2257C3139T3433A3514A3847G4619T4827A4966T5034G5182G5217C8028G9908
G10904A10958C11892A12681G12726C13118A13345T13912T14066G17977C18337C18859T19198A19273
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A31102G31712A31745G32855T33304T33934T34826C36153G38553C41084A43767G44718T47427C48049
A48448T49609A53350G55044T55096T55534G56215A56770C57356G58442G59183C61564A62649A63786
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A73074G74326G77446T77958T78870G79029C81068C81294T83179G83780G84035G84358A85050G85471
G93538C100826T111849G112064A112362G112759C113179T113604C114312C114881G115024A115324
A115649T115796A116222T121215A122430C123078G123858T125147C125336C126277T127441T127567
G128281T128662A129269G139743C147031 …… 短绒野大豆以外的 6 种

The six species other than *G. tomentella*

1-5a. Type T1811T2088A2358A3622A4524T4633G7693T9779A10672C12887A13713T14788C18683C24832G25033A26028
T29137G32774C34839A35341A35519G36243T37275T38966T39455A41636T43731A46292C46978C48911T49770
G49772T49774C49779A49781T50780A51185A51623C52800T54155A56548C56680A56767A59175T61758T63997
T64010C64149A66115A67215G68912T70682A71742C73156G74683T76564C78309C78468G83161A83632A85056
T85217T89671G91833C97150A101530C111632A115880A116159A116195A116313G117083A119322A120228A120324
T121522G122163G122182G124709G124755G124965C129024T139039G143419C148736A150898

…… 绢毛烟豆 *G. canescens*

1-5b. Type $C_{1811}G_{2088}C_{2358}G_{3622}C_{4524}C_{4633}A_{7693}A_{9779}G_{10672}A_{12887}G_{13713}A_{14788}A_{18683}A_{24832}T_{25033}G_{26028}$
$C_{29137}C_{32774}A_{34839}C_{35341}T_{35519}T_{36243}C_{37275}G_{38966}A_{39455}C_{41636}C_{43731}T_{46292}A_{46978}A_{48911}G_{49770}$
$T_{49772}G_{49774}A_{49779}C_{49781}G_{50780}G_{51185}C_{51623}A_{52800}A_{54155}G_{56548}T_{56680}G_{56767}G_{59175}G_{61758}C_{63997}$
$G_{64010}A_{64149}G_{66115}G_{67215}T_{68912}C_{70682}T_{71742}A_{73156}T_{74683}G_{76564}A_{78309}A_{78468}T_{83161}C_{83632}G_{85056}$
$C_{85217}G_{89671}C_{91833}A_{97150}C_{101530}A_{111632}C_{115880}G_{116159}C_{116195}G_{116313}T_{117083}T_{119322}G_{120228}C_{120324}$
$C_{121522}T_{122163}C_{122182}T_{124709}T_{124755}T_{124965}A_{129024}G_{139039}T_{143419}G_{148736}C_{150898}$

…… 绢毛烟豆以外的 6 种

The six species other than *G. canescens*

1-6a. Type $G_{3546}A_{5348}T_{5458}A_{10723}T_{10724}C_{12383}A_{18857}A_{19449}T_{19648}T_{24098}G_{25079}G_{27220}C_{29857}T_{31069}G_{31081}$
$A_{31517}T_{32791}A_{34618}A_{41042}T_{47067}T_{47274}T_{47958}T_{48186}A_{48576}C_{51403}A_{55981}C_{58282}T_{59335}T_{64647}T_{65811}$
$G_{67089}G_{69298}A_{69305}A_{71389}C_{75798}A_{76343}T_{83930}T_{84218}A_{96606}T_{101513}A_{107986}G_{108004}C_{112094}T_{113884}$
$G_{115355}G_{115832}T_{115991}A_{116112}G_{121253}A_{121362}T_{122539}A_{122640}A_{124757}T_{125443}T_{126245}T_{126246}T_{126247}$
$T_{126248}T_{126328}A_{139056}T_{143963}$ …… 扁豆荚大豆 ***G. dolichocarpa***

1-6b. Type $C_{3546}G_{5348}C_{5458}G_{10723}A_{10724}T_{12383}C_{18857}G_{19449}A_{19648}G_{24098}T_{25079}C_{27220}T_{29857}A_{31069}C_{31081}$
$C_{31517}C_{32791}G_{34618}G_{41042}A_{47067}A_{47274}C_{47958}C_{48186}G_{48576}A_{51403}T_{55981}A_{58282}A_{59335}C_{64647}G_{65811}$
$C_{67089}T_{69298}G_{69305}C_{71389}T_{75798}T_{76343}C_{83930}C_{84218}G_{96606}C_{101513}C_{107986}A_{108004}A_{112094}C_{113884}$
$T_{115355}A_{115832}A_{115991}C_{116112}T_{121253}G_{121362}C_{122539}G_{122640}C_{124757}C_{125443}A_{126245}G_{126246}A_{126247}$
$A_{126248}C_{126328}G_{139056}C_{143963}$ …… 扁豆荚大豆以外的 6 种

The six species other than *G. dolichocarpa*

1-7a. Type $G_{5512}T_{7305}T_{8102}G_{26155}T_{29041}G_{29261}A_{30752}G_{32097}T_{32098}C_{33008}C_{37380}T_{37933}T_{39779}C_{43892}C_{49619}$
$T_{51607}A_{52432}G_{53210}G_{56181}A_{58367}C_{60333}G_{65765}G_{67140}T_{69922}G_{74251}C_{74624}T_{76022}T_{76480}C_{80641}T_{82107}$
$G_{82965}G_{85180}A_{85398}G_{92128}A_{92129}A_{92130}G_{92131}A_{92132}C_{104355}T_{107991}G_{107996}A_{112053}C_{113533}G_{113966}$
$C_{115946}T_{118149}T_{119303}C_{119790}A_{121491}A_{125334}G_{126660}A_{127123}G_{128788}T_{128854}G_{136214}T_{148437}C_{148438}$
$T_{148439}T_{148440}C_{148441}$ …… 玫红野大豆 ***G. syndetika***

1-7b. Type $A_{5512}G_{7305}A_{8102}T_{26155}G_{29041}T_{29261}C_{30752}T_{32097}G_{32098}A_{33008}T_{37380}A_{37933}G_{39779}A_{43892}T_{49619}$
$C_{51607}C_{52432}T_{53210}A_{56181}T_{58367}A_{60333}T_{65765}T_{67140}A_{69922}T_{74251}A_{74624}C_{76022}C_{76480}A_{80641}C_{82107}$
$A_{82965}T_{85180}T_{85398}T_{92128}C_{92129}T_{92130}T_{92131}C_{92132}T_{104355}C_{107991}A_{107996}G_{112053}A_{113533}T_{113966}$
$T_{115946}C_{118149}G_{119303}A_{119790}C_{121491}G_{125334}T_{126660}C_{127123}T_{128788}C_{128854}A_{136214}G_{148437}A_{148438}$
$A_{148439}G_{148440}A_{148441}$ …… 玫红野大豆以外的 6 种

The six species other than *G. syndetika*

Figure 1. Molecular taxonomic key to seven taxa in genus *Glycine* based on the species- specific variable nucleotide characters from the complete chloroplast genome

图 1. 基于叶绿体基因组的物种特有核苷酸变异位点的大豆属 7 个种的分子分类检索表

供试样品的名称及其叶绿体基因组的序列号如表 1 (https://www.ncbi.nlm.nih.gov)。7 个样品代表大豆

属的 7 个种。根据本团队发表的方法[14] [15] [16] [17] [31] [32] [33]编制分子分类检索表。具体而言，首先，利用 MAFFTv7.055b 软件[34] (http://mafft.cbrc.jp/alignment/software)获得比对序列矩阵。比对后的序列矩阵的长度为 154,886 个核苷酸，由左向右，左端(5’-端)起的第 1 个核苷酸字母的位置编号为 1，最右端的核苷酸字母的位置编号为 154,886。用 MEGA 7.0 [35]和 DnaSP v6 软件[36] (http://www.ub.edu/dnasp/)检测核苷酸变异位点(图 1，表 2)。每个物种的特有核苷酸变异位点作为分子分类性状，用于编写大豆属植物的分子分类检索表(见图 1)。以食用葛(*Pueraria edulis* Pamp.)作为外群对照，用 MEGA 7.0 软件的 Tamura 3-parameter model 参数模型推断遗传关系(图 2)和计算遗传距离(表 3)。

3. 结果

大豆属这 7 个种的叶绿体基因组的长度为 152,518~153,023 个核苷酸，比对序列的长度为 154,886 个核苷酸。在比对序列中，共检测到 3261 个核苷酸变异位点，占叶绿体基因组序列全长的~2.14%。其中，各物种的特有核苷酸变异位点数目的合计为 2363 个，占变异位点总数的 72.46%。利用种级水平的特有核苷酸变异位点成功编制分子分类检索表，7 个近缘种得到精准鉴定(图 1 和图 2)。大豆的特有变异位点数量(1103 个)最多，占物种特有变异位点总数的 46.68%，依次为白毛烟豆(661 个，27.97%)、镰荚烟豆(263 个，11.13%)、短绒野大豆(129 个，5.46%)、绢毛烟豆(86 个，3.64%)、扁豆荚大豆(61 个，2.58%)以及玫红野大豆(60 个，2.54%) (表 2)。在核苷酸构成方面，大豆、白毛烟豆、镰荚烟豆、绢毛烟豆以及扁豆荚大豆中，特有变异位点中的 **A** 或 **T** 的比例高于 **C** 和 **G**；短绒野大豆中，**A**、**T** 或 **C** 的比例均高于 **G**；玫红野大豆中，**T** 或 **G** 的比例高于 **A** 和 **C**。特有变异位点的数量及其核苷酸构成存在种间差异(表 2)。大豆位于大豆属的系统发育关系树状图的相对基部位置，与其余 6 个近缘种的遗传距离(0.01350~0.01391)都相对较远，扁豆荚大豆与玫红野大豆之间的遗传距离(0.00115)最近(表 3)。

Table 3. Pairwise genetic distances between the seven species of *Glycine* based on complete chloroplast genome sequences
表 3. 基于叶绿体全基因组序列的大豆属 7 种之间的遗传距离

	植物名称 Plant name	1	2	3	4	5	6
1	扁豆荚大豆 *G. dolichocarpa*						
2	玫红野大豆 *G. syndetika*	0.00115					
3	绢毛烟豆 *G. canescens*	0.00144	0.00143				
4	短绒野大豆 *G. tomentella*	0.00200	0.00200	0.00216			
5	镰荚烟豆 *G. falcata*	0.00411	0.00413	0.00436	0.00446		
6	白毛烟豆 *G. stenophita*	0.01063	0.01070	0.01088	0.01088	0.01077	
7	大豆 *G. max*	0.01350	0.01352	0.01368	0.01391	0.01369	0.01333

4. 讨论

大豆的相关科学研究历史悠久。1929 年，魏岩寿发表了中国的第一篇 Science 论文，也是中国首次用现代科学方法详细记述豆腐乳制造过程的论文[37] [38]。在北京的国家植物标本馆(PE)中，大豆属植物

的目前馆藏标本共有 3399 份(https://www.cvh.ac.cn/spms/list.php?taxonName = Glycine)，约有 10 个种和亚种，最早的标本记录为 1901 年，其中，野大豆(*Glycine soja* Siebold & Zucc.)及其原亚种(*Glycine soja* subsp. *soja*，异名 *Glycine ussuriensis* Regel & Maack)有 2282 份(占大豆属植物标本总数的 67.14%)，大豆(也称黄豆，*G. max*) (异名 *Glycine hispida* (Moench) Maxim.)有 980 份(28.83%)，宽叶蔓豆(*G. gracei* B. E. Pfeil & Craven)有 54 份(1.59%)，短绒野大豆 *G. tomentella* (异名 *G. tomentosa* Benth.)有 40 份(1.18%)，烟豆(*G. tabacina* (Labill.) Benth.) (异名 *G. clandestina* J.C. Wendl.)有 30 份(0.88%)，绢毛烟豆(*G. canescens*)有 5 份(0.15%)，扁豆荚大豆(*G. dolichocarpa*)有 3 份(0.09%)，宽叶大豆(*G. latifolia* (Benth.) Newell & T. Hymowitz)有 2 份(0.06%)，车轴大豆(*G. latrobeana* (Meisn.) Benth.)有 2 份(0.06%)，小叶烟豆(*G. microphylla* (Benth.) Tindale)有 1 份(0.03%)。利用“*Glycine*”关键词查询到的标本中，有一些标本名称存在字母输入错误，也有一些标本名称实际上不是大豆属植物，而是其它属的植物的异名，例如，*Glycine javanica* L.、*Glycine pinnata* Merr.、*Glycine hainanensis* Merr. & F. P. Metcalf 以及 *Glycine wightii* (Wight & Arn.) Verdc.等，有待通过国家植物标本资源库和植物物种信息与大数据平台的反馈机制或专家立项进行整理。

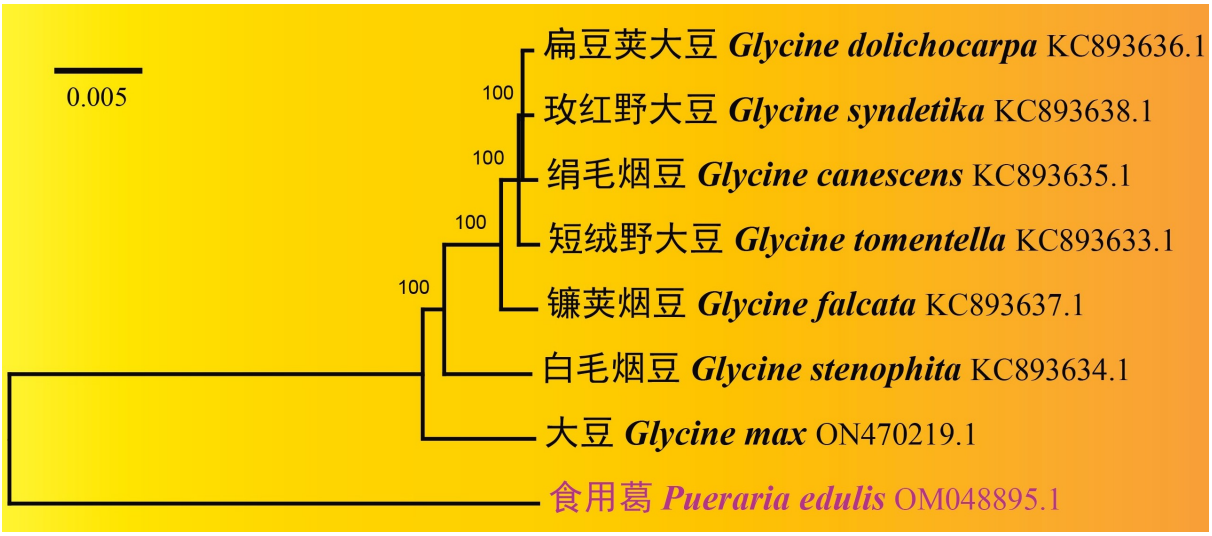

Figure 2. Phylogenetic tree of the seven *Glycine* species based on complete chloroplast genome sequences using the neighbour-joining method with the Tamura3-parameter model. The numbers near the branches are bootstrap support values (%) of 1000 replications

图 2. 基于叶绿体全基因组序列的大豆属 7 个种的系统发生关系。分支图中的数字为 1000 次重复抽样的自展支持率

没有馆藏标本的大豆属植物约 18 种，占该属植物全部种类的近 64.3%，名称如下：1) 白花大豆(*G. albicans* Tindale & Craven)、2) 异色大豆(*G. aphyonotos* B. E. Pfeil)、3) 沙烟豆(*G. arenaria* Tindale)、4) 银毛烟豆(*G. argyrea* Tindale)、5) 弯果烟豆(*G. curvata* Tindale)、6) 紫斑果烟豆(*G. cyrtoloba* Tindale)、7) 镰荚烟豆(*G. falcata*)、8) 硬毛烟豆(*G. hirticaulis* Tindale & Craven)、9) 硬毛烟豆(原亚种) (*G. hirticaulis* subsp. *hirticaulis*)、10) 狭叶硬毛烟豆(亚种) (*G. hirticaulis* subsp. *leptosa* B. E. Pfeil)、11) 绿花大豆(*G. lactovirens* Tindale & Craven)、12) 白毛大豆(*G. montis-douglas* B. E. Pfeil & Craven)、13) 澎湖烟豆(*G. pescadrensis* Hayata)、14) 西澳烟豆(*G. peratosa* B. E. Pfeil & Tindale)、15) 单叶大豆(*G. remota* M. D. Barrett & R. L. Barrett)、16) 锈萼烟豆(*G. rubiginosa* Tindale & B. E. Pfeil)、17) 白毛烟豆(*G. stenophita*)以及 18) 玫红野大豆(*G. syndetika*)。大豆属植物的自然分布范围较广(https://powo.science.kew.org/)，原产地包括俄罗斯、中国、朝鲜半岛、澳大利亚、日本、越南、菲律宾、老挝、马里亚纳群岛(Marianas)、斐济(Fiji)、新喀里多尼亚岛(New Caledonia)、新几内亚岛(New Guinea)、汤加(Tonga)、瓦努阿图(Vanuatu)等。经过 100 多

年的标本采集，仅馆藏到大豆属全部 28 种中的约 10 种，还不足以支持在 DNA 分子水平上全面研究大豆属植物的分类鉴定和系统发育关系。对 21 国 40 个植物标本馆的 4500 份标本的调查显示，50%以上的热带植物标本的名称鉴定存在错误[39]，植物鉴定仍然是具有挑战性的世界性课题。本研究显示，针对重要经济作物的野生近缘类群，标本馆的收集工作应该拓展至全球尺度上开展，而不局限于区域采集[39] [40] [41]。通过全球生物多样性信息数据库(GBIF: Global Biodiversity Information Facility) (https://www.gbif.org/)和英国邱园的世界植物在线(Plants of the World Online) (https://powo.science.kew.org/)网络平台，可以获取大豆属植物分类和标本方面的大量信息。中国农业科学院作物科学研究所保存有野生大豆和栽培大豆资源 8000 份以上[42]。因此，国际各植物标本馆之间复份标本的馆际交换能有效补全大豆属的其它物种的标本，分类学家和农作物专家配合标本馆联合开展，是推进相关研究的有效途径之一。本研究中的这 7 个种代表了大豆属植物的不同演化线，在大豆的长期驯化和育种过程中，其余 6 个种的基因资源尚未参与大豆的演化[12] [26] [42]，表明利用基因编辑技术等先进手段[4] [13]改良大豆的潜力巨大。

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