植物研究　2025,45(6):851~860
Bulletin of Botanical Research

研究论文Original Paper

东南亚苦苣苔科两新属

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摘　要　广义的斜蒴苣苔属(*Loxocarpus* R. Br. sensu lato)为马来西亚植物区系和巽他古陆的特有类群,其生态习性、营养器官和蒴果形态高度相似,但花部器官却显示出一定的分化和多样性。分子系统学证据显示,该属实际上是一个多系群。根据形态性状特异性组合,结合分子系统学证据,该文将广义的斜蒴苣苔属拆分为3个属,包括狭义的斜蒴苣苔属(*Loxocarpus* sensu stricto)及姚氏苣苔属(*Yaoa*)和斜钟花属(*Paraloxocarpus*)2新属。该文提供了3个属的检索表和描述,对相关的21种做出新组合。

关键词　东南亚;新属;新组合;斜蒴苣苔属;姚氏苣苔属;斜钟花属;苦苣苔科

中图分类号:Q949　　**文献标志码**:A　　**doi**:10. 7525/j. issn. 1673-5102. 2025. 06. 003

Two New Genera of Gesneriaceae from Southeast Asia

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Abstract　The genus *Loxocarpus* R. Br. sensu lato is the endemic group of Southeast Asia and Sundaland. The species in *Loxocarpus* exhibit differentiation and diversity in floral organs with similar habits and morphology in vegetative organs and fruits. However, evidence from molecular phylogenies indicates that *Loxocarpus* sensu lato is polyphyletic. According to correlated morphological characters combined with molecular data, we separated *Loxocarpus* sensu lato into three genera, including *Loxocarpus* sensu stricto and two new genera, i.e. *Yaoa* and *Paraloxocarpus*. In the present study, the three genera were described with a key to them, and 21 new combinations were proposed.

Key words　Southeast Asia; new genera; new combinations; *Loxocarpus*; *Yaoa*; *Paraloxocarpus*; Gesneriaceae

斜蒴苣苔属(*Loxocarpus* R.Br.)(原中文名为肿蒴苣苔属)隶属苦苣苔科(Gesneriaceae)苦苣苔亚科(Didymocarpoideae),是古热带植物区、印度-马来西亚亚区的马来西亚地区[1]和巽他古陆(Sundaland)的特有属。英国植物学家Brown[2]根据斜蒴苣苔(*Loxocarpus incanus* R.Br.)建立了斜蒴苣苔属。该属发表后被大多数学者接受,属下种类陆续增加[3-16]。目前,斜蒴苣苔属有23种2变种[13,17-18]。该属早期曾被降级和组合为广义长蒴苣苔属(*Didymocarpus*)内的斜蒴苣苔组(*Didymocarpus* Wall. sect. *Loxocarpus* (R. Br.) Benth.)[19-21]。另有学者[22-23]将其移到另一个属(*Roettlera* Vahl),也作为该属下的一个组*Roettlera* Vahl sect. *Loxocarpus* (R.Br.) Fritsch。由于*Roettlera* Vahl的属名晚于其他类群的相同属名,属晚出异物同名,*Roettlera* Vahl被改名为*Henckelia* Sprengel[24-25](这里中文属名新拟为舌柱苣苔属),组名也相应改为舌柱苣苔属斜蒴苣苔组(*Henckelia* sect. *Loxocarpus* (R.Br.) A.Weber & B.L. Burtt)[26-27]。随后,在不完全的分子系统学研究基础上,舌柱苣苔属又被分解成3个属,即钟花苣苔属(*Codonoboea* Ridl.)、斜蒴苣苔属(*Loxocarpus* R.Br.)和舌柱苣苔属(*Henck-*

基金项目:国家自然科学基金项目(31970239,32170228)。
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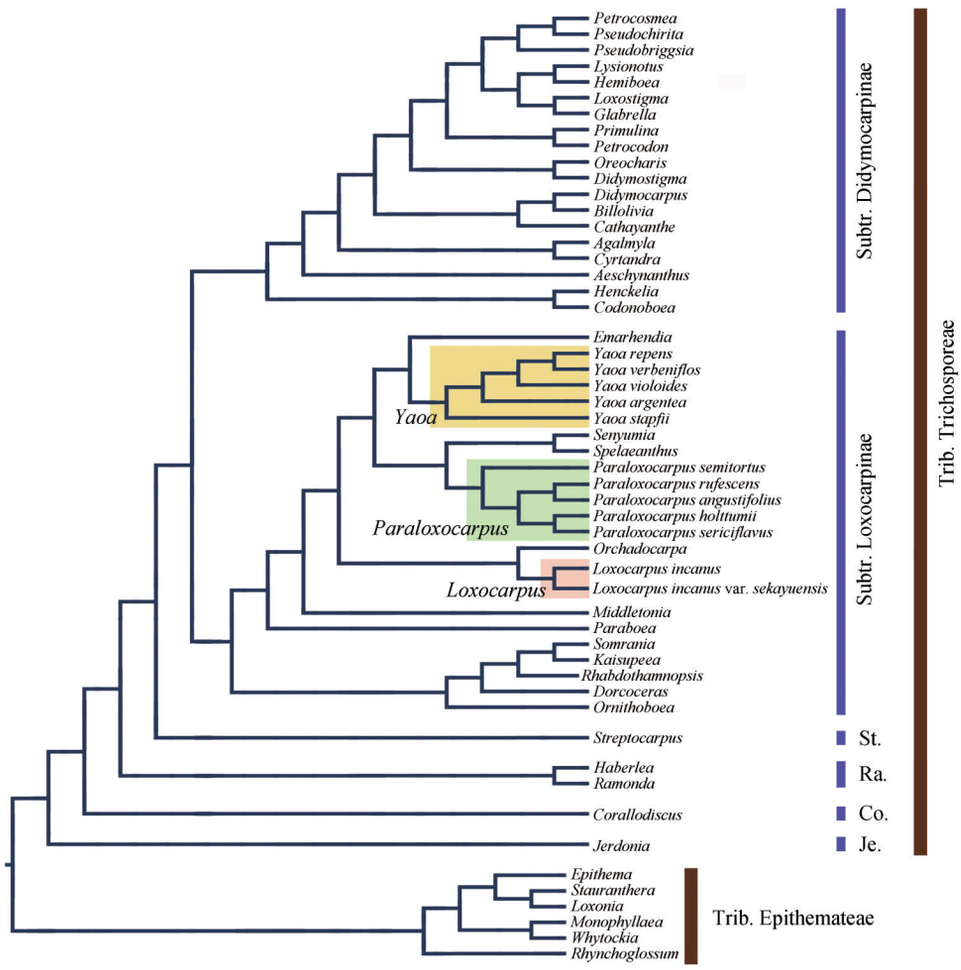
收稿日期:2025年4月17日。

elia Sprengel)[13,17]。值得注意的是,马来半岛的斜蒴苣苔属与印度南部和斯里兰卡特产的舌柱苣苔属的一些种在营养体和花序,甚至花与果的形态上显示出高度的相似性[26-28]。两者同为热带雨林区砂岩和花岗岩地带的小型莲座状植物,常具发达的根茎和不定根,营养体和花序轴常密被白色(稀淡黄或淡褐色)的绢状柔毛或绒毛,花序常少数,花小具短筒,蒴果短而横生,蝎尾状[13,17]。舌柱苣苔属的一些种在形态上主要为唇柱苣苔型柱头,即二唇形,但仅下唇发育,下唇倒三角形至舌状,先端常2裂,区别于斜蒴苣苔属的点状、头状或盾状柱头[17,28]。Ridley[29]指出斜蒴苣苔属的种子靠雨冲式散布。该属和舌柱苣苔属的蒴果成熟时仅上侧室背开裂,形成槽状或舟状的溅水槽或碗状的溅水杯,种子小且多数聚集于朝上的侧膜胎座上[13,27,30]。这种靠雨滴散布种子的蝎尾状蒴果除了上述2属外,还出现在苦苣苔亚科的横蒴苣苔属(*Beccarinda* Kuntze)、半蒴苣苔属(*Hemiboea* C.B. Clarke)、筒花苣苔属(*Briggsiopsis* K.Y.Pan)[31]、盾叶苣苔属(*Metapetrocosmea* W.T.Wang)[32]、钟花苣苔属(*Codonoboea* Ridl.)[33]、腺唇苣苔属(*Emarhendia* Kiew, A.Weber & B.L.Burtt)[34]、厚蒴苣苔属(*Ridleyandra* A.Weber & B.L.Burtt)[27, 30]和镰果蛛毛苣苔(*Paraboea incudicarpa* B.L.Burtt)[35]等属种中。综上所述,不同属之间无论是形态上的相似性,还是种子散布方式的相似性,都是苦苣苔亚科不同分类群在相似生境中平行进化或趋同进化的结果[36]。这些性状的演化虽然极大地丰富了苦苣苔科植物的多样性,但也为该科的系统分类带来许多困惑。近年来,随着分子系统学的迅速发展,苦苣苔科大多数类群的系统发育关系逐渐清晰[13,16-17,26,37]。

分子系统学进一步的研究显示,长蒴苣苔属、舌柱苣苔属和钟花苣苔属3个属与斜蒴苣苔属关系较远,分别属于2个不同的亚族,而且斜蒴苣苔属本身也被证明是多系群[13,18,37-39](图1)。在斜蒴苣苔属被Middleton等[17]恢复之前,Yao[13]第1个以分子系统学为主开展该属的分类学修订研究。该研究选择斜蒴苣苔组20个种,以主要分布于马来西亚的果实扭曲的31个亚洲类群为外类群,利用叶绿体片段*trnL-F*和核基因片段ITS的DNA序列,基于最大简约法和贝叶斯方法进行系统发育重建。该分子系统发育研究结果显示,斜蒴苣苔组和舌柱苣苔属其他类群的系统发育关系较远,该类植物以中等支持率(moderate support)与其他4个属(*Orchadocarpa*、*Emarhendia*、*Senyumia*、*Spelaeanthus*)聚为一支(BS=67~93,PP=68~88,作者分别以不同取样组合和单一或2个DNA片段构建了许多分子系统发育树),支持恢复斜蒴苣苔属。另外,在该系统发育研究中,斜蒴苣苔类分支由3个次级分支组成,每个次级分支中的斜蒴苣苔属类群以较高支持率自成一小支,进而以较高支持率分别与*Orchadocarpa*、*Emarhendia*和*Senyumia*/*Spelaeanthus*聚在一起。根据该分子系统发育和形态学研究结果,Yao[13]确认斜蒴苣苔属包括23物种和2变种,但也明确指出该属是并系类群(实为多系),并没有进一步划分成更小的单系群。在随后的分类学修订中,Yao[13]对斜蒴苣苔属包括的23个种,列出检索表,并逐一配图(或照片)描述。Puglisi等[18]进一步扩大了对斜蒴苣苔亚族(Loxocarpinae)的取样(包括64个内类群和4个外类群),利用核基因ITS和叶绿体基因*trnL-trnF*与*ndhF-trnL*^{UAG}的DNA序列进行系统发育重建,进一步验证斜蒴苣苔属是一个多系类群,但支持率并不太高(BS<50;PP=100)。根据扩大取样后的分子系统发育研究结果,作者对其他类群进行分类处理的同时,特别指出斜蒴苣苔属是一个多系类群,需要进一步研究后再行处理[18]。斜蒴苣苔属植物尽管在营养器官、花序和蒴果方面相似性较高,但在花部器官,尤其在花冠和雌蕊上,形态分化明显[13,18,37],这和分子系统发育的支系分化高度一致。显然,斜蒴苣苔属下分支各具形态分化特征,从某种程度而言,这具有很强的系统发育意义和指示性[13,18,37]。

针对这个科学问题,在前人的研究基础上,笔者于2019和2020年分别前往马来西亚、印度尼西亚北部和泰国南部,对斜蒴苣苔属、腺唇苣苔属(*Emarhendia* Kiew, A.Weber & B.L.Burtt)、溶洞苣苔属(*Spelaeanthus* Kiew, A.Weber & B.L.Burtt)、粉雾苣苔属(*Senyumia* Kiew, A.Weber & B.L.Burtt)和其他苦苣苔科植物进行了详细的野外考察和研究。鉴于此,本文根据花冠、花柱和柱头的形态,以及特定的性状组合,将广义的斜蒴苣苔属(*Loxocarpus*)拆分为与分子系统发育树3个分支相对应的3个狭义属,即狭义的斜蒴苣苔属(*Loxocarpus* sensu stricto)及姚氏苣苔属(*Yaoa*)与斜钟花属(*Paraloxocarpus*)2个新属,并对相关的21种做出新组合处理。



Co. Subtr. Corallodiscinae；Je. Subtr. Jerdoniiae；Ra. Subtr. Ramondinae；St. Subtr. Streptocarpinae（自 Yao[13]；Puglisi 等[18]）。

Co. Subtr. Corallodiscinae; Je. Subtr. Jerdoniiae; Ra. Subtr. Ramondinae; St. Subtr. Streptocarpinae (from Yao[13]; Puglisi *et al.*[18]).

图 1　广义斜蒴苣苔属及其相关类群的系统发育树

Fig.1　Phylogenetic tree of *Loxocarpus* sensu lato and related groups

分属检索表

1. 花冠近辐状或宽钟形；冠檐长约为冠筒的2~6倍，多少扁面状；冠筒的宽度大于其长度；花丝上半部通常增粗 …… **1. 姚氏苣苔属 *Yaoa***

1. 花冠筒状钟形或斜钟形；冠檐短于或约等长于冠筒，二唇形或近整齐；冠筒的长度大于其宽度，稀长宽约相等；花丝上半部不增粗 …… 2

2. 花冠筒状钟形；冠筒直伸，口部于上唇两裂片之间具有一个沟槽或凹凸结构；花柱于花后枯萎，旋卷，全部或大部分脱落；柱头盾状 …… **2. 斜蒴苣苔属 *Loxocarpus***

2. 花冠斜钟形；冠筒侧面观呈S形，口部平滑，无沟槽；花柱于花后直伸或稍弯曲，全部或大部分宿存，柱头点状或头状 …… **3. 斜钟花属 *Paraloxocarpus***

Key to three genera

1. Corolla subrotate or broad-campanulate; corolla limb ca. 2–6 times as long as the tube, more or less flat-faced; the width of corolla tube more than its length; filaments usually thickened in distal half…… **1. *Yaoa***

1. Corolla tubular-campanulate or oblique-campanulate; corolla limb shorter than, rarely ca. as long as the tube, labiate or subregular; the length of corolla tube more than its width; filaments not thickened in distal half…… 2

2. Corolla tubular-campanulate; tube straight, the mouth with a groove or concavity (concavo-convex structure) between the two upper lobes; style withered, spirally twisted, wholly or mostly caduceus after anthesis; stigma peltate …… **2. *Loxocarpus***

2. Corolla oblique-campanulate; tube S-shaped in lateral view, the mouth smooth, without any groove; style straight or slightly curved, wholly or mostly persistent after anthesis; stigma punctiform or capitate…… **3. *Paraloxocarpus***

1 姚氏苣苔属(新属)Yaoa Z. Y. Li & Y. Z. Wang, gen. nov.

该新属的植株形态和习性与狭义的斜蒴苣苔属相似,但花冠近辐状或宽钟状,具较长和扁面的檐部(斜蒴苣苔属的花冠筒状钟形,具较短的二唇形的檐部),冠筒的宽度大于其长度(后者冠筒长度大于其宽度),花冠口部平滑(后者口部于上方两裂片之间具一沟槽),花丝通过上半部增粗(后者上半部不增粗),花柱于花后全部或大部分宿存,直伸或稍弯曲(后者于花后枯萎、旋卷,全部或大部分脱落),容易区分。

The new genus is similar to *Loxocarpus* R. Br. sensu stricto in the habit, but it can be easily distinguished from the latter by its subrotate or broad-campanulate corolla with much longer and more or less flat-faced limb (vs. tubular-campanulate corolla with shorter labiate limb in *Loxocarpus*), the width of corolla tube more than its length (vs. the length of corolla tube more than its width), corolla mouth smooth, without any groove (vs. with a groove between the two upper lobes), filaments usually thickened in distal half (vs. not thickened in distal half), and style straight or slightly curved, and wholly or mostly persistent after anthesis (vs. style withered, spirally twisted, and wholly or mostly caduceus after anthesis).

属名*Yaoa*以马来西亚林业研究所(Forest Research Institute Malaysia)的植物学家姚子良(Yao Tze Leong)命名。

模式:姚氏苣苔Yaoa verbenifolos(C.B.Clarke)Z.Y.Li & Y.Z.Wang

多年生草本,植株通常小型,莲座状,被无腺或具腺毛。茎退化成根茎(rootstock),或延长和匍匐,节上常具不定根。叶互生,常聚生于根茎顶端或生于茎上,具柄;叶片卵形、椭圆形、倒卵形、长圆形或宽条形,边缘具锯齿、小圆齿、波状或全缘,脉羽状。聚伞花序腋生,具梗,具1~15花;苞片条形、披针形或倒披针形。花萼5深裂,裂片不相等,宿存。花冠淡紫色、紫堇色或蓝色,近辐状或宽钟状,斜升、开展或俯垂,具短而宽的筒部和斜的檐部;筒的长度小于宽度,口部圆形,稀横长圆形,平滑而无沟槽;檐长于筒,多少扁面状(flat-faced),上唇2深裂,下唇3浅裂至3深裂。雄蕊2,贴生于花冠远轴侧的近基部,雄蕊先熟(protandrous);花丝常上半部增粗;花药乳黄色、黄色,稀深紫堇色(银毛姚氏苣苔(*Y. argentea*),双斑姚氏苣苔(*Y. stapfii*)),肾形,近顶端,稀腹面连着,药室极叉开,顶端汇合,位于花冠口部或外伸;退化雄蕊2或3,贴生花冠近轴侧的近基部。蜜腺不存在或不明显环状。子房斜圆锥状或狭圆锥状,被无腺或具腺毛;花柱外伸,整体或大部分于花后宿存;柱头点状(punctiform)、头状或盾状。蒴果横生,圆锥状、狭圆锥状、角状(corniculate)或细圆筒状(堇叶姚氏苣苔(*Y. violoides*),海岸姚氏苣苔(*Y. littoralis*),多序姚氏苣苔(*Y. segelamensis*)),长(5~)8~20(~30) mm,直或稍弯曲,仅近轴侧室背开裂,形成槽状或舟状溅水槽(splash gutter),稀为碗状溅水杯(splash cup)。种子椭圆状或狭椭圆状,具网状突起。

11种,分布于马来西亚的沙捞越(Sarawak)州和沙巴(Sabah)州,以及文莱(Brunei)和印度尼西亚北部。

1.1 银毛姚氏苣苔(新拟)Yaoa argentea (B. L. Burtt) Z. Y. Li & Y. Z. Wang, comb. nov. 图版:Yao (2012)[13], Pl 2c & Pl 3a-b.

Loxocarpus argenteus B. L. Burtt in Notes Roy. Bot. Gard. Edinburgh 31(1): 47. 1971; *Henckelia argentea* (B.L. Burtt) B.L. Burtt in Beitr. Biol. Pflanzen 70(2-3): 339. 1997 (publ. 1998). Type: Malaysia, Borneo, Sarawak, Kuching (First) Division, Bako National Park, Telok Asam, Path to main padang, and at Bukit Tambi, 1962-05-17, *B. L. Burtt & P. J. B. Woods B 1840* (holotype E; isotype SAR).

特产于马来西亚的沙捞越州。

1.2 黄毛姚氏苣苔(新拟)Yaoa burttii (T. L. Yao) Z. Y. Li & Y. Z. Wang, comb. nov. 图版:Yao[13], Pl 10.

Loxocarpus burttii T.L. Yao in Gard. Bull. Singapore 67(2): 289, f. 1, 2. 2015. Type: Malaysia, Borneo, Sarawak, Miri District, Lambir Hills National Park, below BKT. Lambir, sandstone cliff, c. 1500 feet, 1978-09-24, *B.L. Burtt B11597* (holotype E; isotypes KEP, SAR).

特产于马来西亚的沙捞越州东部。

1.3　角蒴姚氏苣苔(新拟)Yaoa conicapsularis (C. B. Clarke) Z. Y. Li & Y. Z. Wang, comb. nov.

Didymocarpus conicapsularis C. B. Clarke in A. DC. & C. DC., Monogr. Phan. 5(1): 100. 1883. *Roettlera conicapsularis*(C.B.Clarke) Kuntze, Revis. Gen. Pl. 2: 476. 1891, nom. illegit. *Loxocarpus conicapsularis*(C.B.Clarke) B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 24(1): 45. 1962. *Henckelia conicapsularis* (C. B. Clarke) B. L. Burtt in Beitr. Biol. Pflanzen 70(2-3): 342. 1997 (publ. 1998). Type: Indonesia, Karimantan, *J.E. Teysmann 11215* (holotype FI; isotype BO).

分布于马来西亚的沙巴州、沙捞越州,以及印度尼西亚北部。

1.4　疏毛姚氏苣苔(新拟)Yaoa coodei(B. L. Burtt) Z. Y. Li & Y. Z. Wang, comb. nov.

Henckelia coodei B. L. Burtt in Coode et al., Checkl. Fl. Pl. Gymn. Brunei: 437. 1996. Type: Brunei, Temburong District, Temburong River at Wong Nguan rapids, 120 m, mixed lowland, 1990-03-05, *M.J.E. Coode 6617*(holotype K; isotype BRUN).

分布于马来西亚沙捞越州和沙巴州及文莱东部。

1.5　海岸姚氏苣苔(新拟)Yaoa littoralis(T. L. Yao) Z. Y. Li & Y. Z. Wang, comb. nov.

Loxocarpus littoralis T.L. Yao in Gard. Bull. Singapore 67(2): 293, f. 1. 2015. Type: Malaysia, Borneo, Sarawak, Kuching District, Tanjung Po, in deep shade on dripping wet rocks near the sea, 1955-10-05, *W.M.A. Brooke 10614*(holotype L).

特产于马来西亚的沙捞越州。

1.6　匍匐姚氏苣苔(新拟)Yaoa repens(B. L. Burtt) Z. Y. Li & M. Q. Han, comb. nov. 图版: Yao[13], Pl 7a-e.

Loxocarpus repens B. L. Burtt in Bot. J. Linn. Soc. 85(1): 24. 1982, non *Henckelia repens* (Bedd.) A. Weber & B.L. Burtt (1997, publ. 1998). *Henckelia procumbens* B.L. Burtt in Beitr. Biol. Pflanzen 70(2-3): 353. 1997 (publ. 1998). Type: Malaysia, Borneo, Sarawak, Fourth Division, Gunong Mulu Nat. Park, C. 1350 m, in upper montane forest, 1962-06-14, *B.L. Burtt & P.J.B. Woods, B2097* (holotype E; isotypes, KEP, SAR, WU).

分布于马来西亚的沙巴州、沙捞越州,以及文莱和印度尼西亚北部。

1.7　多序姚氏苣苔(新拟)Yaoa segelamensis (T. L. Yao) Z. Y. Li & Y. Z. Wang, comb. nov. 图版: Yao[14], Fig. 3.

Loxocarpus segelamensis T.L. Yao in Gard. Bull. Singapore 67(2): 293. 2015. Type: Malaysia, Borneo, Sarawak, Marudi District, Baram, Sungai Segelam, around Long Selatong Lepo Ga, on rocky ridge, 1977-07-24, *S.C. Chin 2797*(holotype KLU).

特产于马来西亚的沙捞越州东部。

1.8　条叶姚氏苣苔(新拟) Yaoa taeniophyllus (B. L. Burtt) Z. Y. Li & Y. Z. Wang, comb. nov.

Henckelia taeniophylla B. L. Burtt in Coode et al., Checkl. Fl. Pl. Gymn. Brunei: 438. 1996. *Loxocarpus taeniophyllus* (B.L. Burtt) Y.L. Yao in Edinburgh J. Bot. 70(3): 394. 2013. Type: Brunei, Temburong, Bangar, northern slope of Bkt. Bangar, 10-100 m, 1964-01-18, *M. Hotta 13263* (holotype KYO; isotype E).

特产于文莱东部。

1.9　双斑姚氏苣苔(新拟)Yaoa stapfii(Kraenzl.) Z. Y. Li & F. P. Liu, comb, nov.

Didymocarpus stapfii Kraenzl. in Mitt. Inst. Allg. Bot. Hamburg 7: 89. 1923. *Loxocarpus stapfii* (Kraenzl.) B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 24(1): 46. 1962. *Henckelia stapfii* (Kraenzl.) B. L. Burtt in Beitr. Biol. Pflanzen 70(2-3): 356. 1997 (publ. 1998). Type: Indonesia, Kalimantan, Bukit Mehipit, Urwald, 500 m, 1824-12-08, *H. Winkler 661* (holotype HBG; isotype E).

分布于马来西亚的沙捞越州,以及印度尼西亚的西加里曼丹省与廖内省(林加岛)。

1.10　姚氏苣苔(新拟)Yaoa verbeniflos(C. B. Clarke) Z. Y. Li & Y. Z. Wang, comb. nov. 图版: Yao[13], Pl 11a-d.

Didymocarpus verbeniflos C.B. Clarke in A. DC. & C. DC., Monogr. Phan. 5(1): 99. 1883. *Roettlera verbeniflos* (C.B. Clarke) Kuntze, Revis. Gen. Pl. 2: 475. 1891, nom. illegit. *Loxocarpus verbeniflos* (C.B. Clarke) B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 22(4): 310. 1958. *Henckelia verbeniflos* (C.B. Clarke) B.L. Burtt in Beitr. Biol. Pflanzen 70(2-3):

358. 1997 (publ. 1998). Type: Malaysia, NE Borneo, Ins. Sandakan, *1877, F.W. Burbidge s.n.* (holotype K, K000450484; isotype BM).

分布于马来西亚的沙巴州、沙捞越州和纳闽岛(拉布安岛)及文莱。

1.11 堇叶姚氏苣苔(新拟)Yaoa violoides(C. B. Clarke) Z. Y. Li & Y. Z. Wang, comb. nov. 图版: Yao[13], Pl 12a-c.

Didymocarpus violoides C.B. Clarke in A. DC. & C. DC., Monogr. Phan. 5(1): 97. 1883. *Roettlera violoides* (C.B. Clarke) Kuntze, Revis. Gen. Pl. 2: 477. 1891, nom. illegit. *Henckelia violoides* (C.B. Clarke) B.L. Burtt in Coode et al., Checkl. Fl. Pl. Gymn. Brunei: 438. 1996. *Loxocarpus violoides* (C.B. Clarke) T. L. Yao in Edinburgh J. Bot. 70(3): 394. 2013. Type: NE of Borneo, Lobong Peak, 5 000 ft. *T. Lobb s.n.* (holotype K, K000450484).

分布于马来西亚的沙捞越州和沙巴州及文莱。

2 斜蒴苣苔属 Loxocarpus R. Br., Cyrtandreae: 120. 1839.

模式:斜蒴苣苔 Loxocarpus incanus R.Br.

多年生草本,植株莲座状,密被银白色绢状柔毛。茎退化成短的、老时木质化的根茎,节上常具不定根。叶互生,但通常簇生,具柄;叶片稍肉质,宽卵形至椭圆形,边缘具多数细锯齿,脉羽状,但在腹面通常不明显。聚伞花序腋生,具梗,1~4(~5)回分枝,具3~29(~52)朵花,但小形植株有时仅具1~2朵花;苞片条形。花萼5深裂,常具短筒。花冠筒状钟形,稍俯垂,淡紫色、紫堇色或蓝色;檐部短于筒部,二唇形,上唇2深裂,下唇较长,3深裂;筒直伸,其长度大于宽度,口部横长圆形,于上唇两裂片之间具一沟槽。雄蕊2,贴生于花冠远轴侧的基部,雄蕊先熟;花丝上半部不增粗;花药乳黄色,肾形,腹面连着,药室极叉开,顶端汇合,内藏;退化雄蕊3,贴生于花冠近轴侧的基部。蜜腺不存在。子房圆锥状,密被绢状柔毛;花柱在花药开裂后明显外伸,于花后枯萎、旋卷并整体或大部分脱落;柱头盾状。蒴果横生,卵状圆锥形,长3.5~7.0 mm,直,仅近轴侧室背开裂,形成碗状溅水杯,基部具隆起的基突(basal hump)。种子椭圆状至狭椭圆状,具网状突起。

1种,2变种,广布于马来半岛。

属名 *Loxocarpus* 源于希腊文,loxos 意为"斜的",carpos意为"果"。

2.1 斜蒴苣苔 Loxocarpus incanus R. Br., Cyrtandreae: 120. 1839.

Loxocarpus alatus A. DC. in DC., Prodr. 9: 277. 1845, nom. illeg. *Didymocarpus incanus* (R. Br.) C.B. Clarke in A. DC. & C. DC., Monogr. Phan. 5(1): 98. 1883. *Henckelia browniana* A. Weber in Beitr. Biol. Pflanzen 70(2-3): 341. 1997 (publ. 1998). Type: Malaysia, Malay Peninsula, Penang, 1832, N. Wallich 809 (lectotype BM, designated by Banka & Kiew 2009; isolectotype K). *Loxocarpus minimus* Ridl. in J. Straists Branch Roy. Asiat. Soc. 86: 302. 1922. *Henckelia minima* (Ridl.) A. Weber in Beitr. Biol. Pflanzen 70(2-3): 350. 1997 (publ. 1998) Type: Malaysia, Malay Peninsula, Negri Sembilan, Bukit Tangga, 1920-12-22, *H.N. Ridley s. n.* (holotype K, K000450475).

2.1.1 斜蒴苣苔(原变种)Loxocarpus incanus R. Br. var. incanus. 图版: Weber[16], Fig. 18e; Banka & Kiew[30], Fig. 1e & Fig. 2c, d; Yao[13], Pl 5a-b; Puglisi et al.[18], Fig. 1c & Fig. 3a.

广布于马来半岛。

2.1.2 狭叶斜蒴苣苔(新拟)Loxocarpus incanus R. Br. var. sekayuensis(Banka &Kiew) T. L. Yao in Edinburgh J. Bot. 70(3): 394. 2013. 图版: Banka & Kiew[30], Fig. 1g & Fig. 2f; Yao[13], Pl 5c.

Henckelia sekayuensis Banka & Kiew in Edinburgh J. Bot. 66(2): 254. 2009. Type: Malaysia, Malay Peninsular, Teregganu, Sekayu Recreational Forest, 1986-08-29, *S. Anthonysamy SA 638* (holotype KEP).

分布于马来西亚的吉兰丹州和登嘉楼州。

3 斜钟花属(新属)Paraloxocarpus Z. Y. Li & Y. Z. Wang, gen. nov.

该新属的植株形态和习性与狭义的斜蒴苣苔属(*Loxocarpus* R. Br.)相似,但花冠斜钟形,口部平滑而无沟槽(斜蒴苣苔属的花冠筒状钟形,冠筒侧面观呈S形,口部于上方两裂片之间具一沟槽),花柱于花后全部或大部分宿存,直伸或稍弯曲(后者花柱于花后枯萎、旋卷,全部或大部分脱落),柱头

点状或头状(后者盾状)。

The new genus is similar to *Loxocarpus* R. Br. in the plant rosette herbs, but differs from the latter by having oblique-campanulate corolla, the tube S-shaped in lateral view, the mouth without any groove (in *Loxocarpus* corolla tubular-campanulate, the mouth with a groove between the two upper lobes), style straight or slightly curved, and wholly or mostly persistent after anthesis (vs. withered, spirally twisted, and wholly or mostly caduceus after anthesis), and stigma punctiform or capitate (vs. peltate).

模式:斜钟花 Paraloxocarpus semitortus(C.B. Clarke) Z.Y.Li & Y.Z.Wang

多年生草本,植株通常莲座状,被银白色、淡黄至褐色的毛。茎常退化为根茎,节上常具不定根,较少具直立茎(直茎斜钟花(*P. caulescens*)和梅氏斜钟花(*P. meijeri*))。叶互生于茎上或簇状生于根茎上,具柄;叶片卵形、椭圆形、近圆形至狭倒卵形或狭披针形,边缘具细锯齿、细圆齿至全缘。聚伞花序腋生,具梗,不分枝或1~4回分枝,具1~15朵花;苞片条形、披针形或椭圆形。花萼5深裂几达基部。花冠斜钟状,通常俯垂,白色、淡紫色、紫堇色、紫色或蓝色;檐部短于或约等长于筒部,二唇形,上唇2深裂,下唇3深裂或3裂达中部;筒的长度超过宽度,侧面呈S形,口部圆形或横长圆形,平滑而无沟槽。雄蕊2,贴生于花冠远轴侧的基部,内藏,稀外伸,雄蕊先熟,花丝上半部不增粗,直伸,稀膝曲状(蓝喉斜钟花(*P. caeruleus*));花药乳黄色、黄色,稀褐色或深紫堇色,肾形,腹面连着,药室极叉开,顶端汇合;退化雄蕊3或2,贴生于花冠近轴侧的基部。腺体不存在、环状(何氏斜钟花(*P. holttumii*),斜钟花(*P. semitortus*)),或为子房背侧的一个突起(蓝喉斜钟花(*P. caeruleus*)、锈毛斜钟花(*P. rufescens*))。子房斜圆锥状或狭圆锥状,密被无腺或具腺毛;花柱内藏或外伸,整体或大部分于花后宿存;柱头点状或头状。蒴果横生,圆锥状至狭圆锥状或角状,长4~10 mm,直或弯曲,仅近轴侧室背开裂,形成舟状溅水槽。种子宽至狭椭圆状,具网状突起。

10种,分布于马来西亚和印度尼西亚(东、西、中加里曼丹省、苏门答腊和林加岛)。

属名*Paraloxocarpus*源于希腊文,para意为"近似",*Loxocarpus*意为"斜蒴苣苔属"。

3.1　狭叶斜钟花(新拟)Paraloxocarpus angustifolius(Ridl.) Z. Y. Li & Y. Z. Wang, comb. nov. 图版:Banka & Kiew[30], Fig. 1d; Yao[13], Pl 1b & Pl 2a-b.

Loxocarpus angustifolius Ridl. in J. Linn. Soc. Bot. 38: 319. 1908. *Henckelia stenophylla* A. Weber in Beitr. Biol. Pflanzen 70(2-3): 357. 1997 (publ. 1998). Type: Malaysia, Malay Peninsula, Pahang, Kuala Teku, 1905-07-09, *L. Wray & H.C. Robinson 5504* (holotype BM; isotype SING).

特产于马来西亚的彭亨州。

3.2　蓝喉斜钟花(新拟)Paraloxocarpus caeruleus (Ridl.) Z. Y. Li & Y. Z. Wang, comb. nov. 图版: Weber & Burtt[26], Fig. 6f; Banka & Kiew[30], Fig. 1f & Fig. 2i; Yao[13], Pl 3c.

Didymocarpus caeruleus Ridl. in J. Linn. Soc. Bot. 32: 513. 1896. *Loxocarpus caeruleus* (Ridl.) Ridl. in J. Straits Branch Roy. Asiat. Soc. 44: 62. 1905. *Henckelia caerulea* (Ridl.) A. Weber in Beitr. Biol. Pflanzen 70(2-3): 341. 1997 (publ. 1998). Type: Malaysia, Malay Peninsula, Perak, Burkit Larut, 1881-09, *H. N. Ridley 2476* (lectotype K, designated by Banka & Kiew[30]).

分布于马来西亚的马来半岛地区。

3.3　直茎斜钟花(新拟)Paraloxocarpus caulescens(B. L. Burtt) Z. Y. Li & Y. Z. Wang, comb. nov. 图版:Weber & Burtt[26], Fig. 6d.

Loxocarpus caulescens B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 22(4): 44. 1962. *Henckelia caulescens* (B.L. Burtt) A. Weber & B.L. Burtt in Beitr. Biol. Pflanzen 70(2-3): 342. 1997 (publ. 1998). Type: Indonesia, Sumatra, Taram, East of Pajakumbuh, 500–1 000 m, sandstone region of River Tjampo, along steep slope on rocks with bryophytes, 1957-08-24, *W. Meijer 6893* (holotype L; isotypes E,K,L).

分布于印度尼西亚的苏门答腊和廖内群岛(Kepulauan Riau)。

3.4　何氏斜钟花(新拟)Paraloxocarpus holttumii(M. R. Hend.) Z. Y. Li & Y. Z. Wang, comb. nov. 图版:Weber & Burtt[26], Fig. 6c; Banka & Kiew[30], Fig. 1a & Fig. 2a; Yao[13], Pl 4a-c.

Loxocarpus holttumii M.R. Hend. in Gard. Bull.

Straits Settlem. ser. 3, 4: 412. 1929. *Henckelia ericii* A. Weber in Beitr. Biol. Pflanzen 70(2-3): 344. 1997 (publ. 1998). *Codonoboea holttumii* (M. R. Hend) C. L. Lin in Gard. Bull. Singapore 62(2): 263. 2011. Type: Malaysia, Malay Peninsula, Johor, Gunung Panti, 1926-02014, *R. E. Holttum 18097* (holotype SING).

特产于马来西亚的柔佛州。

3.5 梅氏斜钟花(新拟)Paraloxocarpus meijeri (B. L. Burtt) Z. Y. Li & Y. Z. Wang, comb. nov.

Loxocarpus meijeri B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 22(4): 44. 1962. *Henckelia meijeri* (B.L. Burtt) A. Weber & B.L. Burtt in Beitr. Biol. Pflanzen 70(2-3): 350. 1997 (publ. 1998). Type: Indonesia, Sumatra, Taram, east of Pajarkumbu, sandstone ridge of River Tjambo, 500–1 000 m, 1957-08-28, *W. Meijer 7083* (holotype L.).

特产于印度尼西亚的苏门答腊西部。

3.6 锈毛斜钟花(新拟)Paraloxocarpus rufescens (C. B. Clarke) Z. Y. Li & Y. Z. Wang, comb. nov. 图版: Yao[13], Pl 8a-e.

Didymocarpus rufescens C.B. Clarke in A. DC. & C. DC., Monogr. Phan. 51(1): 99. 1883. *Roettlera rufescens* (C.B. Clarke) Kuntze, Revis. Gen. Pl. 2: 477. 1891, nom. illegit. *Loxocarpus rufescens* (C.B. Clarke) B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 22(4): 309. 1958. *Henckelia rufescens* (C.B. Clarke) B.L. Burtt in Beitr. Biol. Pflanzen 70(2-3): 355. 1997 (publ. 1998). Type: Malaysia, Borneo, Ragiato di Sarawak, Sul Picco di Santubong, 1866-07, O. Beccari 2130 (holotype, FI-B). *Didymocarpus johannis-winkleri* Kraenzl. in Mitt. Inst. Allg. Bot. Hamburgh 7: 89. 1927. Type: Indonesia, West-Borneo, aufdem Bukit Mehipit, Urwald, Felsen, alt. 900 m, 1924-12-29, *H.K.A. Winkler 1150* (holotype HBG).

分布于马来西亚沙捞越州,以及印度尼西亚的西加里曼丹省和特米昂岛(Pulau Temiang)。

3.7 斜钟花(新拟)Paraloxocarpus semitortus (C. B. Clarke) Z. Y. Li & Y. Z. Wang, comb. nov. 图版: Weber & Burtt[26], Fig. 6e; Banka & Kiew[30], Fig. 1b & Fig. 2b; Yao[13], Pl 9a-c.

Didymocarpus semitortus C.B. Clarke in A. DC. & C. DC., Monogr. Phan. 5(1): 99. 1883. *Roettlera semitorta* (C.B. Clarke) O. Kuntze, Revis. Gen. Pl., 2: 477. 1891, nom. illegit. *Loxocarpus semitortus* (C.B. Clarke) Ridl. in J. Straits Branch Roy. Asiat. Soc. 44: 61. 1905. *Henckelia semitorta* (C.B. Clarke) A. Weber in Beitr. Biol. Pflanzen 70(2-3): 356. 1997 (publ. 1998). Type: Malaysia, Malay Peninsula, Johor, Gunung Ledang (Mt. Ophir, Malacca), *W. Griffith 3836* (lectotype K, designated by Banka & Kiew[30]).

特产于马来西亚的柔佛州。

3.8 绢毛斜钟花(新拟)Paraloxocarpus sericeus (Ridl.) Z. Y. Li & Y. Z. Wang, comb. nov.

Didymocarpus sericeus Ridl. in J. Linn. Soc. Bot. 32: 513. 1896. *Loxocarpus sericeus* (Ridl.) B. L. Burtt in Notes Roy. Bot. Gard. Edinburgh 31(1): 49. 1971. *Henckelia sericea* (Ridl.) A. Weber in Beitr. Biol. Pflanzen 70(2-3): 356. 1997 (publ. 1998). Type: Indonesia, Lingga(Island), *Nong Chie*(native collector), *s.n.*(Holotype SING, SING 0100354).

特产于印度尼西亚的林加岛。

3.9 黄毛斜钟花(新拟)Paraloxocarpus sericiflavus (Kiew & Banka) Z. Y. Li & Y. Z. Wang, comb. nov. 图版: Banka & Kiew[30], Fig. 1c & Fig. 2g-h; Yao[13], Pl 9d-e & Pl 10a-b.

Henckelia sericiflava Kiew & Banka in Edinburgh J. Bot. 66(2): 256.2009. *Loxocarpus sericiflavus* (Kiew & Banka) T.L. Yao in Edinburgh J. Bot. 70(3): 394. 2013. Type: Malaysia, Malay Peninsula, Johor, Gunung Panti, 1936-12-05, E. J. H. Corner SFN 32538 (holotype SING). *Henckelia anthonysamyi* Banka in Edinburgh J. Bot. 66(2): 249. 2009. Type: Malaysia, Malay Peninsula, Johor, Kahang Timor, Sungai Yong, 1987-05-28, *S. Anthonysamy SA 681* (holotype KEP; isotype E).

特产于马来西亚的柔佛州。

3.10 紫斜钟花(新拟)Paraloxocarpus tunkui (Kiew) Z. Y. Li & Y. Z. Wang, comb. nov. 图版: Banka & Kiew[30], Fig. 1i & Fig. 2h.

Loxocarpus tunkui Kiew in Malay. Nat. J. 41: 221. 1987. *Henckelia tunkui*(Kiew) A. Weber in Beitr. Biol. Pflanzen 70: 357. 1997 (publ. 1998). Type: Malaysia, Malay Peninsula, Pahang, Sungai Gerugal, 1989-06-18, *B.H. Kiew KBH 86–10*(holotype KEP; isotype SING).

分布于马来西亚的彭亨州和柔佛州。

4　系统位置未定种

Loxocarpus pauzii T.L. Yao in Blumea 57(2): 134. Fig. 1. 2012. —Type: Malaysia, Malay Peninsula, Kelantan, Gunung Stong State Parh, Stong Waterfall, alt. 315 m, 2008-07-26, *T.L. Yao et al. FRI 65371* (holotype KEP; isotypes E, L). 图版：Yao[13], Pl 6a-k; Yao et al.[15], Fig.1.

该种外形奇特，具有短筒的扁面花冠，接近姚氏苣苔属，但花丝上半部不增粗；聚伞状花序2~4回分枝，具11~42花，又近似狭义的斜蒴苣苔属(*Loxocarpus*)，但蒴果狭圆锥形(后者蒴果卵状圆锥形，开裂后呈碗状)，顶端具喙状的宿存花柱(后者花柱于花后旋卷，整体或大部分脱落)，柱头点状(punctiform)而非盾状。该种花冠上唇不分裂，叶片和种子形状及分子系统树的位置[13, 15]都不同于本文中的3个属，该种特产于马来西亚的吉兰丹州，其系统位置需做进一步研究。

综上所述，广义斜蒴苣苔属(*Loxocarpus* R.Br. sensu lato)自建立以来，经历了被合并、恢复、再降级和再恢复的过程[2,10-11,13,17,21]。这一过程反映了人们对这些类群认知的不断深入。在前人研究的基础上，尤其是Yao[13]以分子系统学为主开展的该属分类学修订，本文通过在马来西亚、印度尼西亚及泰国南部的野外考察，进一步从形态学入手，深入详细地观察和分析了该属在分子系统发育中的3个分支(分别与近缘属聚在一起，见图1)的形态分化。本研究发现，该属的3个独立分支尽管在营养器官、花序和蒴果方面具有较高的相似性，但在花冠和雌蕊上展现出显著的形态分化，各自均具有独特的形态特征。因此，本文将这些类群划分为3个属，即斜蒴苣苔属、姚氏苣苔属和斜钟花属。

目前，分子系统学研究已经全面进入全基因组时代，利用转录组和全基因组海量的DNA序列资料及基因组不同层次的变异特征所开展的系统发育重建能够准确地揭示所研究类群的系统地位和系统发育关系[40]。在此基础上，人们对形态性状及其变异的认识就能够更加真实地反映其形态演化的历史，消除平行或趋同演化带来的干扰。目前，这3个属的分子系统学研究仅基于2~3个DNA片段的序列，分子系统树的支持率普遍不高，还有待于全面的系统发育基因组学研究。另外，这些类群的野外调查还不够全面，对一些种类的认识还缺乏第一手资料。例如，本文中的*Loxocarpus pauzii* T.L. Yao，外形十分奇特，由于缺乏足够证据，本文暂时搁置对该种的分类学处理。未来，将在详细的野外调查和广泛取样基础上，开展基于转录组或全基因组序列资料的系统发育重建，进而对这些类群开展更加深入的形态学观察和形态性状及其变异式样的比较分析，更加精准地把握这些类群在形态演化上各自的共衍征，从而全面了解广义斜蒴苣苔属的系统发育关系和分类学问题。

致谢　奥地利维也纳大学植物研究所的Anton Weber博士、中国科学院植物研究所的金效华博士和覃海宁博士、中央民族大学的刘博博士提供资料，在此一并致谢。

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