



Collectanea Botanica 34: e003

enero-diciembre 2015

ISSN-L: 0010-0730

<http://dx.doi.org/10.3989/collectbot.2015.v34.003>

# The upper reaches of the largest river in Southern China as an “evolutionary front” of tropical plants: Evidences from Asia-endemic genus *Hiptage* (Malpighiaceae)

M.-X. REN (任明迅)<sup>1,2</sup>

<sup>1</sup> Key Laboratory of Protection and Development Utilization of Tropical Crop Germplasm Resources (Hainan University), Ministry of Education, CN-570228 Haikou, China

<sup>2</sup> College of Horticulture and Landscape Architecture, Hainan University, CN-570228 Haikou, China

Author for correspondence: M.-X. Ren (rensanshan@hotmail.com)

Editors: J.-Q. Liu & N. Garcia-Jacas

Received 28 October 2014; accepted 16 December 2014

## Abstract

THE UPPER REACHES OF THE LARGEST RIVER IN SOUTHERN CHINA AS AN “EVOLUTIONARY FRONT” OF TROPICAL PLANTS: EVIDENCES FROM ASIA-ENDEMIC GENUS *Hiptage* (MALPIGHIACEAE).—The biodiversity hotspot at the Guizhou–Yunnan–Guangxi borders is a distribution centre of tropical plants in China. It spans the whole upper reaches of Zhujiang River, the largest river in Southern China. In this paper, I aimed to explore the roles of the river in the spread and diversification of tropical plants in this area, using the Asia-endemic genus *Hiptage* Gaertn. (Malpighiaceae) as an example. Two diversity and endemism centres of *Hiptage* are recognized: Indo-China Peninsula and upper reaches of Zhujiang River (UZJ). The area-adjusted endemism index further indicates UZJ as the most important distribution region of endemic species since UZJ has a very small area (~210,000 km<sup>2</sup>) but six out of the total seven species are narrow endemics. UZJ is located at the northern edge of distribution ranges of *Hiptage*, which resulted mainly from the north-west–south-east river systems of UZJ promoting northward spreads of this tropical genus. The highly-fragmented limestone landscapes in this region may promote habitat isolation and tends to be the main driving factor for origins of these endemic species. *Hiptage* is also distinctive for its highly-specialized pollination system, mirror-image flowers, which probably facilitates species diversification via floral and pollination isolation. Other studies also found UZJ as a major diversification centre of the tropical plant families Gesneriaceae and Begoniaceae. Thereafter, it is concluded that UZJ is an “evolutionary front” of tropical plants in China, which contributes significantly to the origin and maintenance of the unique biodiversity in the area.

Key words: adaptation; biodiversity; endemic plant; endemism centre; karst; mirror-image flowers; pollination; speciation.

## Resumen

EL CURSO SUPERIOR DEL RÍO MÁS GRANDE DEL SUR DE CHINA COMO UN «FRENTE EVOLUTIVO» DE PLANTAS TROPICALES: EVIDENCIA DEL GÉNERO ENDÉMICO DE ASIA *Hiptage* (MALPIGHIACEAE).—El hotspot de biodiversidad en las fronteras de las provincias Guizhou–Yunnan–Guangxi es un centro de distribución de plantas tropicales en China. Se extiende por toda la cuenca alta del río Zhujiang, el mayor río del sur de China. En este artículo, se explora el papel del río en la propagación y la diversificación de las plantas tropicales en este área, usando el género endémico de Asia *Hiptage* Gaertn. (Malpighiaceae) como ejemplo. Se reconocen dos centros de diversidad y endemismo de *Hiptage*: la Península Indochina y el curso superior del río Zhujiang (UZJ). El índice de endemismo ajustado al área indica UZJ como la región más importante de distribución de especies endémicas, ya que, aunque UZJ tiene un área muy pequeña (~210.000 km<sup>2</sup>), seis de un total de siete especies son estrechamente endémicas. UZJ está situado en el extremo norte del área de distribución de *Hiptage*, lo que resultó principalmente de la disposición noroeste-sureste de los sistemas fluviales de UZJ, que facilitaron la expansión y diferenciación hacia el norte de este género tropical. Los paisajes de piedra caliza altamente fragmentados en esta región han contribuido al aislamiento de hábitat y pueden ser el principal factor para el origen de estas especies endémicas. *Hiptage* también se distingue por su sistema de polinización altamente especializado, con flores de imagen espejular, lo que probablemente facilita la diversificación de las especies a través del aislamiento de la polinización. Otros estudios también encontraron que UZJ es un importante centro de diversificación de las familias de plantas tropicales Begoniaceae y Gesneriaceae. Por consiguiente, se concluye que UZJ es un «frente evolutivo» de plantas tropicales en China, lo que contribuye de manera significativa al origen y mantenimiento de la biodiversidad única en la zona.

Palabras clave: adaptación; biodiversidad; centro de endemismo; especiación; flores de imagen espejular; karst; planta endémica; polinización.

## 摘要

南中国最大河流珠江的上游地区是热带植物的一个“进化前沿”；来自金虎尾科亚洲特有属风筝果属 (*Hiptage*) 的证据。——中国西南的云南-贵州-广西交界区是全球性的生物多样性热点地区，也是中国热带植物的分布中心。这一区域横跨南中国最大河流—珠江的整个上游地区。这里，我试图以典型的热带植物类群金虎尾科 (Malpighiaceae) 亚洲特有的风筝果属 (*Hiptage* Gaertn.) 为例，从河流的作用来解释这一地区热带植物的扩散与物种分化及其生物多样性热点地区的形成。风筝果属具有两个物种多样性与特有中心：一个位于中南半岛南部，一个则是珠江上游地区。面积校正后的特有性指数进一步证实，珠江上游地区是风筝果属最集中的特有种分布地区，其大约210,000 km<sup>2</sup>的面积上有7个种，其中6个为狭域分布的地方特有种。珠江上游地区位于风筝果属整个分布区域的北缘；风筝果属植物能扩散到这一地区，主要得益于该地的河流走向基本都呈西北-东南走向。西北-东南走向的河道可以促进东南亚暖湿气流北进，从而允许风筝果属等热带植物得以扩散至珠江上游地区的红水河、南盘江以及右江等地。这些地方分布着高度破碎化的岩溶地貌，又进一步促进了局部生境隔离与物种分化。此外，风筝果属还具有极其特化的传粉系统“镜像花柱” (mirror-image flowers)，可能加速了繁殖隔离与物种分化。其它研究也发现，珠江上游地区是一些典型热带植物类群如苦苣苔科和秋海棠科的物种多样化中心。因此，珠江上游地区（滇黔桂交界区）很可能就是中国热带植物的一个“进化前沿”，对这一地区独特生物多样性的形成与维持具有重要作用。

关键词：生物多样性；特有植物；特有中心；适应；岩溶地貌；镜像花柱；传粉；物种形成。

## Cómo citar este artículo / Citation

Ren, M.-X. 2015. The upper reaches of the largest river in Southern China as an “evolutionary front” of tropical plants: Evidences from Asia-endemic genus *Hiptage* (Malpighiaceae). *Collectanea Botanica* 34: e003. doi: <http://dx.doi.org/10.3989/collectbot.2015.v34.003>

## Copyright

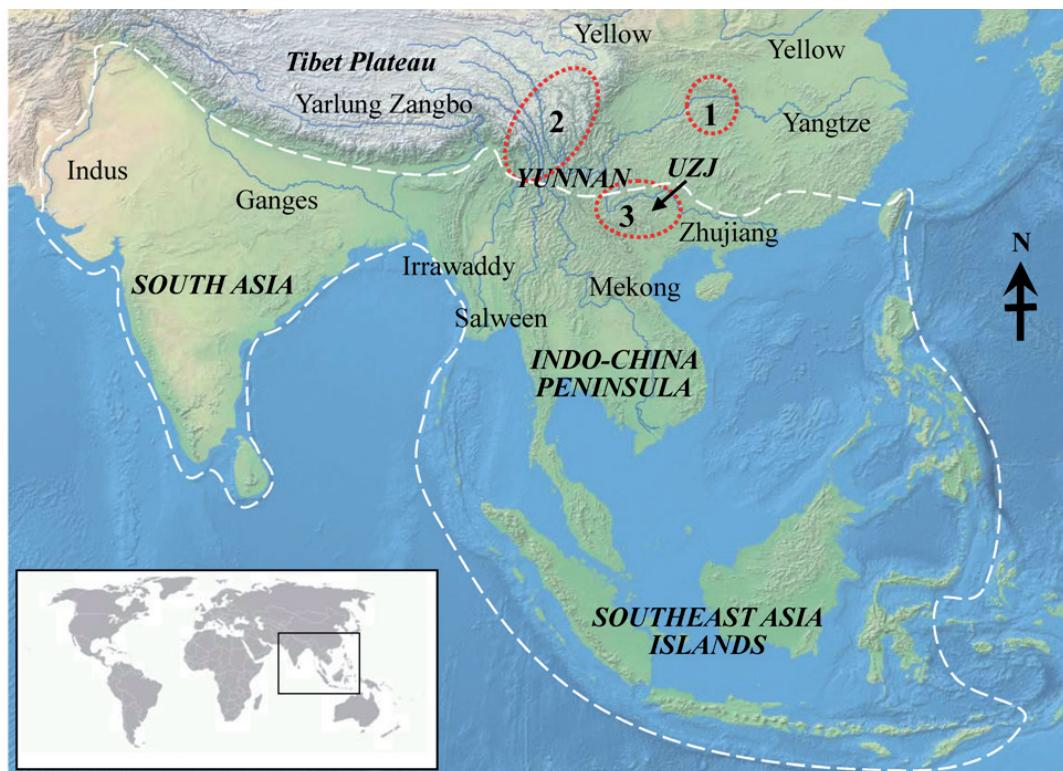
© 2015 CSIC. Este es un artículo de acceso abierto distribuido bajo los términos de la licencia Creative Commons Attribution-Non Commercial (by-nc) Spain 3.0.

## INTRODUCTION

China is one of the richest countries in plant biodiversity, harbouring more than 30,000 seed plants (Liu *et al.*, 2003; López-Pujol *et al.*, 2006). Such “mega-biodiversity” (Mittermeier *et al.*, 1997; Liu *et al.*, 2003; Tang *et al.*, 2006) has been often attributed to the highly complicated ecological and evolutionary history of China and East Asia. For example, China has complex topographies and almost all types of biomes from tropical to boreal, which provides abundant suitable habitats for various plants (Ying, 2001). China is also one of major centres of origin and diversification for vascular plants (Axelrod *et al.*, 1996; Qian, 2002), and particularly the southern part of this vast country is the home for both relict and recently evolved plants (Ying & Zhang, 1984; López-Pujol *et al.*, 2011).

In Southern China, three regions are widely recognized as major “biodiversity hotspots” and they are roughly equal to the country’s “centres of plant endemism” (Ying & Zhang, 1984; Ying *et al.*, 1993; Ying, 1996; López-Pujol *et al.*, 2011). All these three hotspots are located in mountain areas

with large rivers (Fig. 1) but they differ significantly in plant composition and origin. The biodiversity hotspot at central China locates at the boundaries of Hubei, Hunan, and Guizhou provinces, and Chongqing City, including the Three Gorges region on the Yangtze River (Fig. 1). Most endemic plants in this region are palaeoendemics, i.e. the relict species that have survived from the Tertiary (Ying *et al.*, 1993; López-Pujol *et al.*, 2011). The Hengduan Mountains on the eastern fringe of the Tibetan Plateau are also widely recognized as a globally important biodiversity hotspot. It consists largely of recently evolved endemic species (neoendemics) that resulted from the uplift of the Himalayas and surrounding mountains (Chapman & Wang, 2002; Qian, 2002). The third hotspot spans the upper reaches of Zhujiang River (the largest river in Southern China), at the confluence of three Chinese provinces (Guizhou, Yunnan, and Guangxi). This biodiversity hotspot (hereafter UZJ) is dominated by limestone landscapes and river valleys (Figs. 1 and 2). UZJ is also distinctive for its nearly equal proportion of neoendemics and palaeoendemics (Ying *et al.*, 1993; López-Pujol *et al.*, 2011) and



**Figure 1.** Distribution of the genus *Hiptage* and the associated important geographic regions. The white line indicates the distribution range of *Hiptage*, which was divided into five regions with their names in bold and italics. The red dash-lined circles are the three biodiversity hotspots in China: 1, borders of Hubei–Hunan–Guizhou–Chongqing, including Three Gorges Region on the Yangtze River; 2, Hengduan Mountains; 3, borders of Guizhou–Yunnan–Guangxi, roughly equal to the upper reaches of Zhujiang River (UZJ). The background map was provided by Dr. J. López-Pujol.

significantly more tropical species than the other two hotspots. Myers *et al.* (2000) included it as one part of the globally important biodiversity hotspot “Indo-Burma”. Compared to other hotspots, UZJ hotspot received less attention, and the evolutionary histories and maintenance mechanisms of its unusual biodiversity have not been satisfactorily resolved (Ying *et al.*, 1993; Fang *et al.*, 1995).

In this paper, I will use the distribution map of *Hiptage*, an Asia-endemic genus of the typically tropical family Malpighiaceae, with the aims of: (1) to determine the diversity and endemism centre(s) of the genus by calculating species richness and endemism for five different geographic regions; (2) to discuss possible determinants for distribution patterns of *Hiptage* from both environmental and biological factors by comparing widely-recognized hypothesis and updated studies on this genus; (3) to explore the underlying mechanism(s) of origin and maintenance of the tropical plant diversity in UZJ hotspot with an emphasis on the roles of river and associated environmental features.

## MATERIALS AND METHODS

### Basic information of the genus *Hiptage*

*Hiptage* is one of the largest Old World genera of Malpighiaceae, with >25 species usually recognized (Anderson *et al.*, 2006–). This genus is originated as a result of inter-continent long-distance dispersals from tropical America to Asia during the late Oligocene, ~29 Ma (Davis *et al.*, 2002).

*Hiptage* species grows mainly as high-climbing, twining woody lianas in South Asia, Indo-China Peninsula, Indonesia, Philippines, and Southern China including Hainan and Taiwan islands (Chen & Funston, 2008; Ren *et al.*, 2013). Jacobs (1955) also reported one endemic species in Fiji islands, which locates at Southern Pacific. Because of its three-winged peculiar samara, *Hiptage* is probably the Old World genus easiest to recognize. Its flowers are bilaterally symmetrical and basically white but the posterior petal is often yellow in its centre (Fig. 3A). The number and structure of sepal gland(s)



**Figure 2.** Distribution of six *Hiptage* species endemic to upper reaches of Zhujiang River (all included within the red dashed circle). The main topographic features are also illustrated at the bottom.

represent diagnostic traits in the family (Jacobs, 1955; Anderson, 1990; Vogel, 1990; Srivastava, 1992; Chen & Funston, 2008). Normally only the posterior sepal bearing one large gland in *Hiptage* but in some species gland is missing or borne in pairs (Vogel, 1990; Anderson *et al.*, 2006–; Chen & Funston, 2008). Stamens are 10, one of them much longer and bigger than the other nine. All anthers of *Hiptage* dehisce longitudinally (Ren *et al.*, 2013), contrasting to poricidal anthers in most

heteromorphic stamens. Ren *et al.* (2013) found in *H. benghalensis* (L.) Kurz, the most widespread species of the genus, that longitudinal anthers probably are an adaptation to its pollinator *Apis dorsata*, an Asia-endemic pollen-collecting honeybee (Fig. 3B).

*Hiptage* is also distinctive for having mirror-image flowers (Ren *et al.*, 2013). Mirror-image flowers show a sexual polymorphism in which the style deflects either to the left (left-styled flower) or the right



**Figure 3.** Mirror-image flowers (A) and its main pollinator *Apis dorsata* (B) of *Hiptage benghalensis*, the most widespread species of the genus. L, left-styled flower; R, right-styled flower. The sepal gland is indicated by arrows.

(right-styled flower) side of the floral axis, and the bigger stamen deflects to the opposite side of the style (Fig. 3A). Normally insects enter the flower between the style and the big stamen and consequently contact two sexual organs respectively with their left and right side of abdomens (Fig. 3B; Jesson & Barrett, 2002; Ren *et al.*, 2013). Therefore, mirror-image flowers exhibit a highly specialized insect-pollinating mechanism for promoting cross-pollination between left- and right-styled flowers or reducing pollination between flowers on the same plant (Barrett *et al.*, 2000; Jesson & Barrett, 2002; Ren *et al.*, 2013).

#### Species identification

Published floras including *Flora of China* (Chen & Funston, 2008), *Flora of Thailand* (Sirirugsa, 1991), *Flora of Malaysia* (Jacobs, 1955), *Flora of Bhutan* (Grierson, 1991), and *Flora of Taiwan* (Chen, 1993) were used to identify *Hiptage* species and their geographic distributions. *Hiptage* species in India were mainly determined according to Srivastava (1992). All the described species in these floras were checked. The Malpighiaceae website <http://herbarium.lsa.umich.edu/malpigh/> (Anderson *et al.*, 2006–) was also used as a guideline. When there was any mismatching information about taxonomy and distribution, I referred to the newest floras. Finally, 29 species were recognized in this study (Appendix).

#### Distribution regions

According to geographic locations and landscape type, the distribution range of *Hiptage* was classified into five geographic regions: Islands (Philippines, Indonesia, Fiji, Andaman); South Asia (Pakistan, Sri Lanka, Bhutan, Nepal, Bengal, India); Indo-China Peninsula (including Malay Peninsula); upper reaches of Zhujiang River (UZJ); and Yunnan Province (except the area included into UZJ). Yunnan Province was analysed separately because this province is the major distribution centre of tropical plants in China (Zhu *et al.*, 2003). The area occupied by the different regions varies greatly, ranging from a minimum of  $21 \times 10^4 \text{ km}^2$  in UZJ to a maximum of  $410 \times 10^4 \text{ km}^2$  in South Asia (Table 1).

Excepting the islands region, all the other four regions were characterized by large rivers (Fig. 1). Particularly UZJ is a region with numerous rivers and diverse limestone landscapes (karst) (Fig. 2). The mainstream of UZJ are Nanpanjiang River and Hongshuihe River (Fig. 2). UZJ also includes the upper reaches of the tributaries Youjiang and Zuojiang rivers (Fig. 2). These two rivers are very close to the mainstreams, with a nearest distance of ~20 km and ~10 km to Nanpanjiang and Hongshuihe rivers, respectively (Fig. 2), and their topography and habitats are quite the same to the mainstream (Ying *et al.*, 1993; Fang *et al.*, 1995; Hou *et al.*, 2010).

**Table 1.** Geographic distribution patterns of *Hiptage* species. Two diversity and endemism centres are indicated in bold. *NT* is species richness (the number of total species); *SD* (species density) =  $NT/[\ln(\text{area}) + \ln(\text{elevation range})]$ ; *NE* is the number of endemic species; *EI* (endemism index) =  $[NE/(NT - NE)]/[\ln(\text{area}) + \ln(\text{elevation range})]$ .

Region	Distance to the equator (km)	Area ( $\times 10^4$ km $^2$ )	Elevation range (m) <sup>1</sup>	NT	SD	NE	EI
Islands (Philippines, Fiji, Indonesia, Andaman)	0–2100	220	2000	8	0.62	4	0.08
<b>Indo-China Peninsula</b>	<b>130–2500</b>	<b>230</b>	<b>5880</b>	<b>16</b>	<b>1.13</b>	<b>10</b>	<b>0.12</b>
<b>Upper reaches of Zhujiang River (UZJ)</b>	<b>2500–2800</b>	<b>21</b>	<b>2400</b>	<b>7</b>	<b>0.65</b>	<b>6</b>	<b>0.55</b>
Yunnan Province (except UZJ)	2300–3200	30	6600	4	0.33	1	0.03
South Asia (Sri Lanka, India, Bengal, Pakistan)	600–3800	410	1500	8	0.60	2	0.03

<sup>1</sup> Elevation range is calculated as the difference between highest and lowest elevation of the region, which is used to estimate habitat heterogeneity.

## Determination of diversity and endemism centres

The numbers of total species and endemic species were counted for each geographic region. To detect the diversity centre (distribution centre of species richness), area- and habitat-adjusted species density (*SD*) was calculated using the formula  $SD = NT/[\ln(A) + \ln(E)]$ , where *NT* is the species richness (the number of total species of the region), *A* is the area of the region (km $^2$ ), and *E* is the habitat heterogeneity estimated by the elevation range (the difference between the highest and the lowest elevation in the region) according to Tang *et al.* (2006). The data of area and habitat heterogeneity for each geographic region are log-transferred to minimize their impacts on the calculation of species density using a revised method described in Qian (1998) and Tang *et al.* (2006).

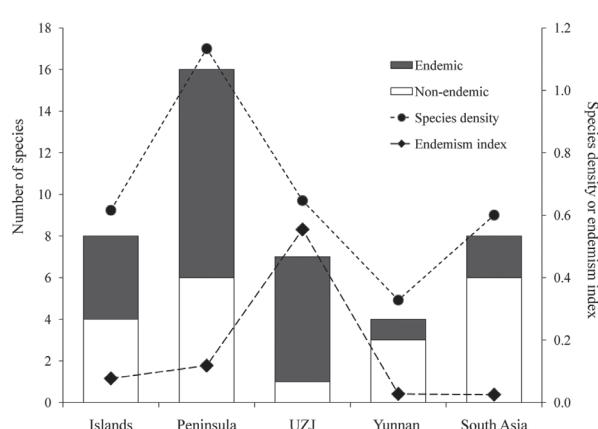
To determine the endemism centre(s), area- and habitat-adjusted endemism index (*EI*) was calculated using the formula  $EI = [NE/(NT - NE)]/[\ln(A) + \ln(E)]$ , where *NT* is the number of total species, *NE* is the number of endemic species, *A* is the area of the region (km $^2$ ), and *E* is the habitat heterogeneity.

To explore the correlation of species diversity and main geographic factors, the Pearson correlation coefficient between species diversity (i.e. number of total species, number of endemic species, endemism index) and three factors [region area, distance to the equator, and habitat heterogeneity (elevation range)] was calculated using SPSS software v17.0.

## RESULTS

Based on the comprehensive surveys on all the described species, twenty-nine species of *Hiptage* were identified in this study (see Appendix). Two regions, Indo-China Peninsula and UZJ, were identified as the main diversity centres because they have the highest values of species density, both  $\geq 0.65$  (Table 1 and Appendix). There were 16 species in Indo-China Peninsula, in which 10 were endemic, mostly in Thailand at the south of the peninsula. In UZJ, six out the total seven *Hiptage* species were endemic (Table 1). These two regions were also recognized as endemism centres because both regions had an endemism index  $> 0.1$  (Fig. 4 and Table 1). UZJ was especially distinctive for its highest endemism, with a value of endemism index about five times of the second, Indo-China Peninsula (Fig. 4 and Table 1). This result made UZJ the distribution centre of endemic species of *Hiptage*. All the *Hiptage* species in UZJ have obviously reduced glands, with only two, one or no sepal gland (Appendix). Such floral trait is found to be a derived character in the family according to a complete generic phylogeny with both morphological and molecular data (Davis & Anderson, 2010).

The endemic species in UZJ were mostly distributed along the rivers and valleys (Fig. 2), with some species occurred at the nearby limestone hills. Three rare endemic species with only one recorded place, i.e. *Hiptage luodianensis* S. K. Chen, *H. fraxinifolia* F. N. Wei, and *H. multiflora* F. N. Wei were found in the valley of Hongshuihe, Zuojiang,



**Figure 4.** Species richness and the area- and habitat-adjusted species density and endemism index of *Hiptage* in five geographic regions.

and Yongjiang rivers, respectively (Fig. 2). The other three species with two or more recorded places, i.e. *H. lanceolata* Arènes, *H. tianyangensis* F. N. Wei, and *H. minor* Dunn were also distributed along the Hongshuihe and Youjiang valleys (Fig. 2).

Statistical analysis revealed that the distributions of species diversity, measured by total number of total species (species richness), number of endemic species and endemism index, were not correlated with the region area, the distance to the equator, or the elevation range (Table 2).

## DISCUSSION

This study pointed out upper reaches of Zhujiang River in South China is not only the northern distribution edge of the tropical genus *Hiptage* but also its diversity and endemism centre. The correlation analyses found no associations of species diversity and endemism with geographic factors

including region size, distance to the equator, and habitat heterogeneity (elevation range) (Tables 1 and 2). These facts suggest the formation of this diversity and endemism centre of *Hiptage* cannot be explained by large-scaled geographic factors and mainly is resulted from recent evolution caused by local topographic features or intrinsic traits of the genus, which I discuss in detail below.

### Rivers and monsoon climate

Not only UZJ but also Indo-China peninsula (another centre of species diversity and endemism of *Hiptage*) are characterized by large rivers (Fig. 1). In Indo-China Peninsula, all the rivers such as Mekong River and Salween River are of north–south direction (Fig. 1). This flow direction can promote the northward spread of *Hiptage* since this tropical genus can only find suitable habitat along the riverside where is far away from typical tropical climate (Anderson *et al.*, 2006–; Ren *et al.*, 2013). The long-distance dispersal of *Hiptage* is mainly achieved via its three-winged fruits, which can help the fruits to disperse over oceans (Davis *et al.*, 2002). UZJ is the most important diversity and endemism centre of *Hiptage* (Figs. 2 and 4, and Table 1) and contains numerous mountains and rivers with north-west–south-east direction (Figs. 1 and 2). These rivers are smaller than Mekong, Salween, and Red rivers but their valleys and slopes are also the home to many narrowly-endemic *Hiptage* species (Ren *et al.*, 2013; Fig. 2).

More importantly, both UZJ and Indo-China Peninsula are close to the Tibetan Plateau and Himalaya (Fig. 1). The Himalayan uplift created tropical monsoon climate in its southern and eastern regions and the role of monsoon climate for species spread and speciation were already widely acknowledged in the nearby Hengduan Mountains

**Table 2.** Correlation between species richness, species density, endemism index, and three geographic factors.

	Geographic factors		
	Distance to the equator	ln(area)	ln(elevation range)
Species richness	$r = -0.6521$ , $P = 0.594$	$r = 0.5402$ , $P = 0.427$	$r = 0.2004$ , $P = 0.525$
Species density	$r = -0.5683$ , $P = 0.970$	$r = 0.4446$ , $P = 0.723$	$r = 0.1531$ , $P = 0.625$
Endemism index	$r = 0.5500$ , $P = 0.341$	$r = -0.6232$ , $P = 0.333$	$r = -0.1576$ , $P = 0.735$

(Fig. 1; Chapman & Wang 2002; López-Pujol *et al.*, 2006). Monsoon climate in Indo-China Peninsula and nearby regions is characterized by strong northward wind in the summer (approximately from April to October), which is also rain season (Wu & Zhang, 1998). In UZJ, the mainstream Hongshuihe River and two main branches (Youjiang and Zuojiang rivers) are all north-west–south-east direction (Fig. 2). This flow direction can bring the monsoon climate northward and promote the spread of *Hiptage* along the river valleys and even to the north bank of Hongshuihe River (Fig. 2). This is why all the *Hiptage* species in UZJ are distributed along the rivers and, when the river (Hongshuihe and Nanpanjiang sections) changes the flow to west–east direction, no *Hiptage* species move northward anymore (Fig. 2).

However, a question remains: why the Red River and the upper reaches of Mekong and Salween rivers (Figs. 1 and 2) have not formed a diversity or endemism centre of the genus *Hiptage*, given that their north–south flow direction also have the potential for species spread? The main reason probably is that the valleys of Mekong and Salween rivers are so wide that the three-winged fruits of *Hiptage* can disperse over a very long distance along the valleys, resulting in strong and continuous gene flow between the lower and upper reaches. Most mountains in this region are also of north–south direction and in good connectivity, which further maintains gene flow connecting upper and middle or lower reaches of rivers. This is why the only one endemic species on the Salween River, *H. yunnanensis* Huang ex S. K. Chen, occurs in the extraordinarily complex Hengduan Mountains in the northwestern Yunnan Province (Fig. 1) far away from the middle and lower reaches of the river. The valley of Red River is by far much wider and shorter than Mekong and Salween rivers, and gene flow along the Red River is strong enough to maintain species connectivity. Therefore it is not surprising that there is no endemic species along Red River, even it is only ~60 km away from UZJ (Fig. 2).

### Highly-fragmented limestone landscapes

Another reason for UZJ as a diversification centre is its vast fragmentary limestone landscapes. Southwestern China has the largest continuous limestone

areas in the world (Clements *et al.*, 2006; Hou *et al.*, 2010), which includes the UZJ and the biodiversity hotspot at borders of Guizhou–Yunnan–Guangxi provinces (Hou *et al.*, 2010). The limestone area here experienced severe erosion due to heavy rainfalls (Zhu *et al.*, 2003; Hou *et al.*, 2010) and is distinctive for its *fengcong* and *fenglin*, i.e. partially or completed isolated karst peaks (Fig. 2). These separate peaks, together with numerous slopes and pits with different orientations, may provide isolated microhabitats for plants (Fang *et al.*, 1995; Zhu *et al.*, 2003; Clements *et al.*, 2006; Hou *et al.*, 2010). Clements *et al.* (2006) attributed the high level of species richness and endemism in Southeast Asian karsts, including Southwestern China, to their high diversity of microhabitats and climatic conditions. This is particularly the case in UZJ and surrounding areas since the limestone landscapes here are highly fragmented and remained relatively stable during the last glacial period of the Pleistocene (Li, 1994; Hou *et al.*, 2010), making this region not only a survival center for relict species, but also an important place for species diversification (Chapman & Wang, 2002; Qian, 2002; López-Pujol *et al.*, 2011).

For *Hiptage*, many endemic species are found exclusively on limestone rocks in UZJ and Indo-China Peninsula (Sirirugsa, 1991). In UZJ, some species such as *H. tianyangensis* and *H. multiflora* occupy the tops or sunny slopes of hills, some species including *H. minor*, *H. lanceolata* and *H. lodianensis* can only grow at the bottom of river valleys, while other species such as *H. fraxinifolia* and *H. benghalensis* are found predominantly in dense forests or shrubs (Chen & Funston, 2008; M. X. Ren, pers. obs.). These local separations of species distributions suggest that habitat differentiation is quite possible between species.

UZJ is also the distribution and endemism centre for other tropical families including Gesneriaceae and Begoniaceae (Li & Wang, 2004; Wei *et al.*, 2004; Hou *et al.*, 2010). For example, many recently-evolved genus and species of Gesneriaceae such as *Allocheilos* W. T. Wang, *Thamnocharis* W. T. Wang, *Tengia* Chun, and *Lagarosolen* W. T. Wang are only found in UZJ and its neighboring areas (Lu *et al.*, 1989; Wei *et al.*, 2004). In Guangxi Province, Wei *et al.* (2004) found 16 out 38 genus of Gesneriaceae that were distributed exclusively in karst regions, while Lu *et al.* (1995) and Hou *et al.* (2010)

even reported ~80% of the endemic genera are only distributed in limestone areas. Furthermore, most endemic species of Gesneriaceae are restricted to the highly-fragmented limestone areas between Youjiang and Zuojiang rivers (Fig. 2; Wei *et al.*, 2004). These facts further suggest the evolutionary diversification of these tropical taxa in UZJ mainly resulted from fragmented limestone landscapes (Li, 1994; Fang *et al.*, 1995; Wei *et al.*, 2004).

### Highly-specialized pollination mechanism

*Hiptage* is characterized with mirror-image flowers with heteromorphic stamens and longitudinal anthers (Fig. 3A; Ren *et al.*, 2013). Mirror-image flowers are a sexual polymorphism in which the style deflects away from the floral axis either to the left (left-styled flower) or the right (right-styled flower) (Jesson & Barrett, 2002; Gao *et al.*, 2006; Ren *et al.*, 2013). Normally the pollinators for mirror-image flowers are large-bodied pollen-collecting honeybees such as *Apis dorsata* (Fig. 3B; Ren *et al.*, 2013). This highly-specialized insect-pollination mechanism can facilitate cross-pollinations between left- and right-styled flowers through two deflected sexual organs touching left and right sides of the pollinator's abdomen respectively (Jesson & Barrett, 2002; Ren *et al.*, 2013). Therefore, the spatial separation of the deflected stigma and anther (herkogamy; Webb & Lloyd, 1986; Ren & Zhang, 2004) must be under selection to adapt to the pollinator's body size to ensure successful pollen transfers between two floral types (Jesson & Barrett, 2002; Gao *et al.*, 2006; Ren *et al.*, 2013).

Due to its accurate pollen transfers and high pollination efficiency, mirror-image flowers have the potential to generate floral isolation and facilitate speciation (Grant, 1994; Armbruster & Muchhala, 2009). *Hiptage* species differ significantly in flower size and length of sexual organs (Chen & Funston, 2008), and it is likely that herkogamy also varies greatly among species. Such differences probably reflect adaptations to different pollinators or different parts of the same pollinator, a phenomenon found in other herkogamous species (Medrano *et al.*, 2005; Kay & Sargent, 2009) or species with similar specialized floral traits (Armbruster & Muchhala, 2009).

Other tropical families with their diversification centre at UZJ also show specialized floral syndromes

and pollination mechanisms. For example, Gesneriaceae are well-known for its highly-specialized floral traits and pollination mechanism (Lu *et al.*, 1989; Fang *et al.*, 1995; Li & Wang, 2004) and also contain species with mirror-image flowers in this region (Gao *et al.*, 2006). Begoniaceae are also distinctive for its unisexual flowers and this trait is probably an adaptation to stressful habitats on limestones (Hou *et al.*, 2010). Species of both families in UZJ region are mostly neoendemics (Lu *et al.*, 1989; Fang *et al.*, 1995; Li & Wang 2004; Hou *et al.*, 2010). Nevertheless, this hypothesis about the association of species diversity and floral specialization in UZJ is in need of further experimental tests.

In conclusion, upper reaches of Zhujiang River can be seen as the “evolutionary front” of tropical plants in China due to its predominant proportion of narrowly-endemic and recently-evolved species of *Hiptage* (Malpighiaceae) and other tropical groups such as Gesneriaceae and Begoniaceae. Environmental factors (rivers with monsoon climate and limestone landscapes) and intrinsic traits of the plants such as highly-specialized pollination systems are responsible for the origin and evolution of the biodiversity in this “evolutionary front”, with the environmental factors more likely being the most significant driving factors. Tropical plants are the main composition of UZJ and its neighbouring regions and should be paid enough attention in the studies of the origin and evolution of this unusual biodiversity hotspot, which is one of globally-important biodiversity hotspots.

### ACKNOWLEDGEMENTS

I thank Dr. X.-Q. Song in Hainan University for his discussion on an early idea of this manuscript. Financial supports are provided by National Natural Science Foundation of China (Grant number: 31170356) and a start-up fund from Hainan University (kyqd1501).

### REFERENCES

- Anderson, W. R. 1990. The origin of the Malpighiaceae—the evidence from morphology. *Memoirs of the New York Botanical Garden* 64: 210–224.
- Anderson, W. R., Anderson, C. & Davis, C. C. 2006-. *Malpighiaceae*. University of Michigan, Ann Arbor. Retrieved September 10, 2014 from <http://herbarium.lsa.umich.edu/malpigh/index.html>

- Armbruster, S. W. & Muchhal, N. 2009. Associations between floral specialization and species diversity: cause, effect, or correlation? *Evolutionary Ecology* 23: 159–179. <http://dx.doi.org/10.1007/s10682-008-9259-z>
- Axelrod, D. I., Al-Shehbaz, I. & Raven, P. H. 1996. History of the modern flora of China. In: Zhang, A. & Wu, S. (Eds.), *Floristic characteristics and diversity of East Asian plants*. China Higher Education Press, Beijing: 43–55.
- Barrett, S. C. H., Jesson, L. K. & Baker, A. M. 2000. The evolution and function of stylar polymorphisms in flowering plants. *Annals of Botany* 85: 253–265. <http://dx.doi.org/10.1006/anbo.1999.1067>
- Chapman, G. P. & Wang, Y. Z. 2002. *The plant life of China. Diversity and distribution*. Springer-Verlag, Berlin & Heidelberg. <http://dx.doi.org/10.1007/978-3-662-04838-2>
- Chen, C. H. 1993. Malpighiaceae. In: Huang, T. C. (Ed.), *Flora of Taiwan* 3 (2nd ed.). Lunwei Printing Company, Taipei: 565–566.
- Chen, S. & Funston, A. M. 2008. Malpighiaceae. In: Wu, Z. Y., Raven, P. H. & Hong, D. Y. (Eds.), *Flora of China* 11 (*Oxalidaceae through Aceraceae*). Science Press, Beijing & Missouri Botanical Garden Press, St. Louis: 132–138.
- Clements, R., Sodhi, N. S., Schilthuizen, M. & Ng P. K. L. 2006. Limestone karsts of Southeast Asia: Imperiled arks of biodiversity. *Bioscience* 56: 733–742. [http://dx.doi.org/10.1641/0006-3568\(2006\)56\[733:LKOSAI\]2.0.co;2](http://dx.doi.org/10.1641/0006-3568(2006)56[733:LKOSAI]2.0.co;2)
- Davis, C. C. & Anderson, W. R. 2010. A complete generic phylogeny of Malpighiaceae inferred from nucleotide sequence data and morphology. *American Journal of Botany* 97: 2031–2048. <http://dx.doi.org/10.3732/ajb.1000146>
- Davis, C. C., Bell, C. D., Mathews, S. & Donoghue, M. J. 2002. Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. *Proceedings of the National Academy of Sciences of the United States of America* 99: 6833–6837. <http://dx.doi.org/10.1073/pnas.102175899>
- Fang, R.-Z., Bai, P.-Y., Huang G.-B. & Wei Y.-G. 1995. 滇黔桂热带亚热带（滇黔桂地区和北部湾地区）种子植物区系 [A floristic study on the seed plants from tropics and subtropics of Dian-Qian-Gui]. *Acta Botanica Yunnanica* S7: 111–150 [in Chinese].
- Gao, J.-Y., Ren, P.-Y., Yang, Z.-H. & Li, Q.-J. 2006. The pollination ecology of *Paraboea rufescens* (Gesneriaceae), a buzz-pollinated tropical herb with mirror-image flowers. *Annals of Botany* 97: 371–376. <http://dx.doi.org/10.1093/aob/mcj044>
- Grant, V. 1994. Modes and origins of mechanical and ethological isolation in angiosperm. *Proceedings of the National Academy of Sciences of the United States of America* 91: 3–10. <http://dx.doi.org/10.1073/pnas.91.1.3>
- Grierson, A. J. C. 1991. Malpighiaceae. In: Grierson, A. J. C. & Long, D. G. (Eds.), *Flora of Bhutan* 2(1). Royal Botanic Garden, Edinburgh: 40–42.
- Hou, M.-F., López-Pujol, J., Qin, H.-N., Wang, L.-S. & Liu, Y. 2010. Distribution pattern and conservation priorities for vascular plants in Southern China: Guangxi Province as a case study. *Botanical Studies* 51: 377–386.
- Jacobs, M. 1955. Malpighiaceae. In: Steenis, C. G. G. J. van (Ed.), *Flora Malesiana* Ser. 1, 5(2). Noordhoff-Kolff, Djakarta: 125–145.
- Jesson, L. K. & Barrett, S. C. H. 2002. Enantioistyly: solving the puzzle of mirror-image flowers. *Nature* 417: 707. <http://dx.doi.org/10.1038/417707a>
- Kay, K. M. & Sargent, R. D. 2009. The role of animal pollination in plant speciation: Integrating ecology, geography, and genetics. *Annual Reviews of Ecology, Evolution, and Systematics* 40: 637–656. <http://dx.doi.org/10.1146/annurev.ecolsys.110308.120310>
- Li, X.-W. 1994. 中国特有种子植物属在云南的两大生物多样性中心及其特征 [Two big biodiversity centres of Chinese endemic genera of seed plants and their characteristics in Yunnan Province]. *Acta Botanica Yunnanica* 16: 221–227 [in Chinese].
- Li, Z. Y. & Wang, Y. Z. 2004. 中国苦苣苔科植物 [*Gesneriaceae of China*]. Henan Scientific and Technical Publishing House, Zhengzhou [in Chinese].
- Liu, J., Ouyang, Z., Pimm, S. L., Raven, P. H., Wang, X., Miao, H. & Han, N. 2003. Protecting China's biodiversity. *Science* 300: 1240–1241. <http://dx.doi.org/10.1126/science.1078868>
- López-Pujol, J., Zhang, F.-M & Ge, S. 2006. Plant biodiversity in China: richly varied, endangered, and in need of conservation. *Biodiversity and Conservation* 15: 3983–4026. <http://dx.doi.org/10.1007/s10531-005-3015-2>
- López-Pujol, J., Zhang, F.-M, Sun, H.-Q., Ying, T.-S. & Ge, S. 2011. Centres of plant endemism in China: places for survival or for speciation? *Journal of Biogeography* 38: 1267–1280. <http://dx.doi.org/10.1111/j.1365-2699.2011.02504.x>
- Lu, Y. X., Huang, G. B. & Liang, C. F. 1989. 广西特有植物研究 [Study on the endemic plants from Guangxi]. *Guizhou 9: 37–58* [in Chinese].
- Medrano, M., Herrera, C. M. & Barrett, S. C. H. 2005. Herkogamy and mating patterns in the self-compatible daffodil *Narcissus longispathus*. *Annals of Botany* 95: 1105–1111. <http://dx.doi.org/10.1093/aob/mci129>
- Mittermeier, R. A., Gil, P. R. & Mittermeier, C. G. 1997. *Megadiversity: Earth's biologically wealthiest nations*. Conservation International (CI), Washington, DC.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. <http://dx.doi.org/10.1038/35002501>
- Niedenzu, F. 1928. Malpighiaceae. In: Engler, A. (Ed.), *Das Pflanzenreich IV*. 141. Verlag von Wilhelm Engelmann, Leipzig: 1–870.
- Qian, H. 1998. Large-scale biogeographic patterns of vascular plant richness in North America: an analysis at the genera level. *Journal of Biogeography* 25: 829–836. <http://dx.doi.org/10.1046/j.1365-2699.1998.00247.x>
- Qian, H. 2002. A comparison of the taxonomic richness of temperate plants in East Asia and North America. *American Journal of Botany* 89: 1818–1825. <http://dx.doi.org/10.3732/ajb.89.11.1818>
- Ren, M. X., Zhang, D. Y. 2004. Herkogamy. In: Zhang, D. Y. (Ed.), *植物生活史进化与繁殖生态学* [*Plant life-history evolution and reproductive ecology*]. Science Press, Beijing: 302–321 [in Chinese].
- Ren, M.-X., Zhong, Y.-F. & Song, X.-Q. 2013. Mirror-image flowers without buzz pollination in the Asia-endemic *Hiptage benghalensis* (Malpighiaceae). *Botanical Journal of the Linnean Society* 173: 764–774. <http://dx.doi.org/10.1111/boj.12101>
- Sirirugsa, P. 1987. Three new species of *Hiptage* (Malpighiaceae) in Thailand. *Nordic Journal of Botany* 7: 277–280. <http://dx.doi.org/10.1111/j.1756-1051.1987.tb00944.x>
- Sirirugsa, P. 1991. Malpighiaceae. In: Smitinand, T. & Larsen, K. (Eds.), *Flora of Thailand* 5(3). The Forest Herbarium, Royal Forest Department, Bangkok: 272–299.

- Srivastava, R. C. 1992. Taxonomic revision of the genus *Hippage* Gaerlner (Malpighiaceae) in India. *Candollea* 47: 601–612.
- Tang, Z., Wang, Z., Zheng, C. & Fang, J. 2006. Biodiversity in China's mountains. *Frontiers in Ecology and the Environment* 4: 347–352. [http://dx.doi.org/10.1890/1540-9295\(2006\)004\[0347:BICM\]2.0.co;2](http://dx.doi.org/10.1890/1540-9295(2006)004[0347:BICM]2.0.co;2)
- Vogel, S. 1990. History of the Malpighiaceae in the light of pollination ecology. *Memoirs of the New York Botanical Garden* 55: 130–142.
- Webb, C. J. & Lloyd, D. G. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms II. Herkogamy. *New Zealand Journal of Botany* 24: 163–178. <http://dx.doi.org/10.1080/0028825X.1986.10409726>
- Wei, Y.-G., Zhong, S.-H. & Wen, H.-Q. 2004. 广西苦苣苔科植物区系和生态特点研究 [Studies on the flora and ecology Gesneriaceae in Guangxi Province]. *Acta Botanica Yunnanica* 26: 173–182 [in Chinese].
- Wu, G. & Zhang, Y. 1998. Tibetan plateau forcing and the timing of the monsoon onset over South Asia and the South China Sea. *Monthly Weather Review* 126: 913–927. [http://dx.doi.org/10.1175/1520-0493\(1998\)126<0913:TPFAT>2.0.CO;2](http://dx.doi.org/10.1175/1520-0493(1998)126<0913:TPFAT>2.0.CO;2)
- Ying, T.-S. 1996. 中国种子植物特有属的分布区学研究 [Aerography of the endemic genera of seed plants in China]. *Acta Phytotaxonomica Sinica* 34: 479–485 [in Chinese].
- Ying, T.-S. 2001. 中国种子植物物种多样性及其分布格局 [Species diversity and distribution pattern of seed plant in China]. *Biodiversity Science* 9: 393–398 [in Chinese].
- Ying, T. S., Zhang, Y. L. & Boufford, D. E. 1993. *The endemic genera of seed plants in China*. Science Press, Beijing.
- Ying, T.-S. & Zhang, Z.-S. 1984. 中国植物区系中的特有现象 – 特有属的研究 [Endemism in the flora of China – Studies on the endemic genera]. *Acta Phytotaxonomica Sinica* 22: 259–268 [in Chinese].
- Zhu, H., Wang, H., Li, B. & Sirirugsa, P. 2003. Biogeography and floristic affinities of the limestone flora in southern Yunnan, China. *Annals of Missouri Botanical Garden* 90: 444–465. <http://dx.doi.org/10.2307/3298536>

**Appendix.** Geographic distribution and main floral traits of the *Hiptage* species.

Species	Main floral feature	Distribution	References
<i>Hiptage benghalensis</i> (L.) Kurz	Flowers fragrant. Sepal gland 1, ~4–5 × 2 mm, thick, oblong, 1/2 decurrent to pedicel. Stamens differing in size, longest 8–12 mm, others 3–5 mm.	<b>South Asia</b> (India, Pakistan, Bengal, Sri Lanka) <b>Islands</b> (Indonesia, Philippines, Andaman) <b>Indo-China Peninsula</b> (Myanmar, Laos, Cambodia, Thailand, Vietnam, Malaysia) <b>Yunnan Province</b> <b>Upper reaches of Zhujiang River</b>	Srivastava, 1992; Chen & Funston, 2008; Ren <i>et al.</i> , 2013
<i>H. candicans</i> Hook. f.	Sepal gland 1, base decurrent to pedicel	<b>South Asia</b> (India) <b>Islands</b> (Indonesia) <b>Indo-China Peninsula</b> (Myanmar, Laos, Thailand) <b>Yunnan Province</b>	Chen & Funston, 2008
<i>H. acuminata</i> Wall. ex A. Juss.	Sepal gland 1, small, 1/4 decurrent to pedicel	<b>South Asia</b> (India, Bengal ) <b>Indo-China Peninsula</b> (Myanmar) <b>Yunnan Province</b>	Chen & Funston, 2008
<i>H. parvifolia</i> Wight & Arn.	Sepal gland 5, ovoid, ~3 mm long	<b>South Asia</b> (India, Sri Lanka) <b>Indo-China Peninsula</b> (Myanmar) <b>Islands</b> (Philippines, Indonesia)	Niedenzu 1928; Srivastava, 1992
<i>H. obtusifolia</i> DC.	Sepal gland 5, ~2 × 0.75 mm	<b>South Asia</b> (India, Bengal) <b>Islands</b> (Andaman, Indonesia, Philippines) <b>Indo-China Peninsula</b> (Thailand)	Srivastava, 1992
<i>H. sericea</i> Hook. f.	Sepal gland 5, oblong 2–3 mm long, 1/4 decurrent to pedicel	<b>South Asia</b> (India) <b>Indo-China Peninsula</b> (Myanmar, Malaysia, Thailand)	Srivastava, 1992
<i>H. jacobsii</i> R. C. Srivast.	Sepal gland 5, ~2 × 1 mm	<b>South Asia</b> (India endemic)	Srivastava, 1992
<i>H. nayaritii</i> R. C. Srivast.	Sepal gland 5, round 2–3 mm long	<b>South Asia</b> (India endemic)	Srivastava, 1992
<i>H. thothathrii</i> N. P. Balakr. & R. C. Srivast.	Sepal gland 5, oblong ~4 × 1 mm	<b>Islands</b> (Andaman endemic)	Srivastava, 1992
<i>H. luzonica</i> Merr.	Sepal gland 1, orbicular	<b>Islands</b> (Philippines endemic)	Jacobs, 1955
<i>H. pubescens</i> Merr.	Sepal gland 1, orbicular, cup shaped with thicken rims, ~1 mm	<b>Islands</b> (Philippines endemic)	Jacobs, 1955
<i>H. myrtifolia</i> A. Gray	Sepal gland 1	<b>Islands</b> (Fiji endemic)	Jacobs, 1955
<i>H. lucida</i> Pierre	Sepal gland 5, very small	<b>Indo-China Peninsula</b> (Vietnam, Thailand)	Sirirugsa,1991
<i>H. triacantha</i> Pierre	Sepal gland 1, oblong ~1.5–3 × 0.7–1 mm, sometimes decurrent to pedicel	<b>Indo-China Peninsula</b> (Thailand endemic)	Sirirugsa,1991
<i>H. bullata</i> Craib	Sepal gland 5, orbicular, <1 mm	<b>Indo-China Peninsula</b> (Thailand endemic)	Sirirugsa,1991
<i>H. glabrifolia</i> Craib	No sepal gland	<b>Indo-China Peninsula</b> (Thailand endemic)	Sirirugsa,1991
<i>H. detergens</i> Craib	Sepal gland 1, ovate, 1–5 mm long	<b>Indo-China Peninsula</b> (Thailand endemic)	Sirirugsa,1991
<i>H. calcicola</i> Sirirugsa	No sepal gland	<b>Indo-China Peninsula</b> (Thailand endemic)	Sirirugsa, 1987; Sirirugsa,1991
<i>H. gracilis</i> Sirirugsa	No sepal gland	<b>Indo-China Peninsula</b> (Thailand endemic)	Sirirugsa, 1987; Sirirugsa,1991
<i>H. condita</i> Craib	No sepal gland	<b>Indo-China Peninsula</b> (Thailand endemic)	Sirirugsa,1991

**Appendix.** Geographic distribution and main floral traits of the *Hiptage* species (cont.).

Species	Main floral feature	Distribution	References
<i>H. monopteryx</i> Sirirugsa	No sepal gland	<b>Indo-China Peninsula</b> (Thailand endemic)	Sirirugsa, 1987; Sirirugsa, 1991
<i>H. burkilliana</i> Arènes	No sepal gland	<b>Indo-China Peninsula</b> (Malaysia)	Jacobs, 1955
<i>H. yunnanensis</i> Huang ex S. K. Chen	Sepal gland 1, small, 1/4–1/2 decurrent to pedicel	<b>Yunnan Province</b> (endemic to the upper reaches of Salween River)	Chen & Funston, 2008
<i>H. fraxinifolia</i> F. N. Wei	Sepal gland 1, not decurrent to pedicel	<b>Upper reaches of Zhujiang River</b>	Chen & Funston, 2008
<i>H. tianyangensis</i> F. N. Wei	Sepal gland 1, not decurrent to pedicel	<b>Upper reaches of Zhujiang River</b>	Chen & Funston, 2008
<i>H. multiflora</i> F. N. Wei	Sepal gland 1, not decurrent to pedicel	<b>Upper reaches of Zhujiang River</b>	Chen & Funston, 2008
<i>H. lanceolata</i> Arènes	No sepal gland	<b>Upper reaches of Zhujiang River</b>	Chen & Funston, 2008
<i>H. minor</i> Dunn	No sepal gland	<b>Upper reaches of Zhujiang River</b>	Chen & Funston, 2008
<i>H. luodianensis</i> S. K. Chen	Sepal gland 2	<b>Upper reaches of Zhujiang River</b>	Chen & Funston, 2008