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Trichome micromorphology of the Chinese-Himalayan genus *Colquhounia* (Lamiaceae), with emphasis on taxonomic implications

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Abstract: Trichome micromorphology of leaves and young stems of nine taxa (including four varieties) of *Colquhounia* were examined using light and scanning microscopy. Two basic types of trichomes were recognized: eglandular and glandular. Eglandular trichomes are subdivided into simple and branched trichomes. Based on the number of cells and trichome configuration, simple eglandular trichomes are further divided into four forms: unicellular, two-celled, three-celled and more than three-celled trichomes. Based on branching configuration, the branched eglandular trichomes can be separated into three forms: biramous, stellate and dendroid. Glandular trichomes can be divided into two subtypes: capitate and peltate glandular trichomes. Results from this study of morphological diversity of trichomes within *Colquhounia* lend insight into infrageneric classification and species relationships. Based on the presence of branched trichomes in *C. elegans*, this species should be transferred from *Colquhounia* sect. *Simplicipili* to sect. *Colquhounia*. We provide a taxonomic key to species of Chinese *Colquhounia* based on trichome morphology and other important morphological traits.

Key words: *Colquhounia*; glandular hairs; leaf anatomy; Lamioideae; Yunnan

Introduction

Trichomes are widespread on stems, leaves, calyces and other vegetative and reproductive parts of lamiaceous plants and are widely used in taxonomic studies (El-Gazzar & Watson 1968, 1970; Abu-Asab & Cantino 1987; Navarro & Oualidi 2000). Taxonomically, trichomes are useful not only because of the relative ease with which they may be examined but also because of their universal occurrence, particularly in some groups of Lamiaceae (Metcalfe & Chalk 1950; Mathew & Shah 1983; Cantino 1990; Gairola et al. 2009). Moreover, in Lamiaceae, comparative trichome morphology has received much attention in systematic studies and results from those studies have been commonly employed as taxonomically useful characters at different levels of classification (Bruni et al. 1987; Demissew & Harley 1992; Servettaz et al. 1992; Marin et al. 1994; Navarro & Oualidi 2000; Giuliani et al. 2008; Baran et al. 2010).

Colquhounia Wall. was established on the basis of collections from Nepal (Wallich 1822), which is a Chinese-Himalayan genus (Wu 1991; Wu & Wu 1996) of approximately five species (Mabberley 1997; Harley et al. 2004). The genus *Colquhounia* is recognized by the following characteristics: shrub or woody climbing plant; leaves and young branches covered with various types of trichomes; verticillasters few flowered, in spikes or capitula; equally 5–toothed calyces; and nutlets winged at apex (Li & Hedge 1994). Human uses of some species of this genus are varied. Schilling (1988) reported horticultural value of some species of *Colquhounia* based on their colorful flowers and long-lasting anthesis. Additionally, Zhou et al. (2004) and Chhetri et al. (2010) demonstrated that *Colquhounia* has significance in pharmaceutical applications.

In China, there are five species and four varieties recognized from Guizhou, Hubei, Sichuan, Tibet and Yunnan Provinces. These are *C. coccinea* Wall. var. *coccinea*, *C. coccinea* var. *mollis* (Schlecht.) Prain, *C. compta* W.W. Sm. var. *compta*, *C. compta* var. *mekongensis* (W.W. Sm.) Kudo, *C. elegans* Wall. var. *elegans*, *C. elegans* var. *tenuiflora* (Hook. f.) Prain, *C. vestita* Wall, *C. seguinii* Vaniot var. *seguinii*, and *C. seguinii* var. *pilosa* Rehd. Except for *C. coccinea* var. *coccinea*, all taxa can be found in Yunnan, which is considered to be the center of origin of the genus (Wu & Li 1977; Li & Hedge 1994). Based on trichome morphology of leaves and young stems, Wu & Li (1977) classified species of *Colquhounia* into two sections: sect. *Simplicipili* C.Y. Wu & H.W. Li and sect. *Colquhounia* Wall. Section *Simplicipili* is characterized by having simple hairs, whereas the latter has simple trichomes mixed with branched hairs. Xiang et al. (2010) documented nine trichome types in three studied taxa of

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Table 1. Origin of plant material of *Colquhounia* used in this study. Sectional classification follows Wu & Li (1977).

Taxon	Collector & Number	Locality
Sect. *Simplicipili*		
C. elegans var. *elegans*	Chen J *779* (KUN)	China. Yunnan, Mangshi, Hetou Village
C. elegans var. *tenuiflora*	Map PY *07418* (KUN)	China. Xishuangbanna, Menhun, Mannongkan
C. seguinii var. *seguinii*	Xiang CL *065* (KUN)	China. Guizhou, Jiangkou, Mt. Fanjing
C. seguinii var. *pilosa*	Hou KS *74310* (KUN)	China. Yunnan, Lufeng Village
Sect. *Colquhounia*		
C. coccinea var. *coccinea*	Xiang CL *046* (KUN)	China. Yunnan, Yongping
C. coccinea var. *mollis*	Liu ED *6043* (KUN)	China. Yunnan, Mt. Yongde, Wudiqing
C. compta var. *compta*	Xiang CL *HP5134* (KUN)	China. Yunnan, Ninglang, Labo
C. compta var. *mekongensis*	Wu SG*3498* (KUN)	China. Sichuan, Muli County, Shuluo
C. vestita	Liu ED *1721* (KUN)	China. Yunnan, Mt. Yongde, Yanzitou

Colquhounia, but trichome presence and structure in remaining taxa are unknown. In the absence of a comprehensive study of trichome morphology in *Colquhounia*, and considering their importance to taxonomy within the genus, this study aimed to examine and evaluate the trichome morphology and its taxonomic significance in 5 species of *Colquhounia*.

The aims of the present study are: (1) to provide a detailed description of the trichomes of *Colquhounia* and evaluate their micromorphology and diversity in the genus; (2) to elucidate the significance of trichomes at different taxonomic levels, and potential correlations between trichome structure and other taxonomically important traits.

Material and methods

The trichome morphology of five species and four varieties of *Colquhounia*, all found in China, were examined (Table 1). Observations were made on fresh plants collected in Guizhou, Guangxi, Yunnan and Tibet, as well as herbarium specimens deposited in the following herbaria: HITBC, KUN, PE and WUK (the abbreviations follow Holmgren et al. 1981). Herbarium specimens were examined using a hand lens as well as stereo- and light-microscopes. Trichome structure, indumentum types and distribution on stems and both surfaces of basal and cauline leaves were examined and recorded. Field samples were fixed in FAA (Formalin-Acetic acid-70% alcohol, with a ratio of 1:1:18) or maintained living under cultivation. Trichomes on stems and leaf surfaces were also examined under the scanning electron microscopy (SEM).

For SEM examination, the leaves at different stages of development and young stems were fixed for 2 h at 4 °C with 2% glutaraldehyde (in a 0.1 M sodium cacodylate buffer at pH 7.2). After washing in the same buffer and dehydrating in acetone series, the material was mounted on stubs and sputter coated with gold-palladium (Ascensão et al. 1997). Most observations were made using a KYKY-10000B (Science Instrument Company, Beijing, China) SEM with a voltage of 15 KV. Selected specimens used for LM and SEM observation are shown in Table 1.

Results

The types of trichomes observed and their distribution among the taxa studied are summarized in Table 2. Drawings of all types of trichomes investigated are provided in Figs 1–13; selected SEM micrographs of trichome types are shown in Figs 14–27. Two basic types of trichomes were observed: eglandular and glandular.

Eglandular trichomes

All taxa in the genus *Colquhounia* have eglandular trichomes. Based on branching patterns, the eglandular trichomes can be divided into simple eglandular trichomes and branched eglandular trichomes.

Simple eglandular trichomes are uniseriate, unicellular or multicellular. According to the shape and number of cells, the simple eglandular trichomes are further subdivided into four forms: unicellular (ES1), two-celled (ES2), three-celled (ES3) and more than three-celled (ES $>$ 3). The unicellular ES1 trichomes have only one cell but are quite variable in length. Two subtypes are recognized in the present study and both of them have thick walls. One is a pyramidal trichome (Figs 1, 14) and the other is a papillate trichome, which was observed only in *C. coccinea* var. *mollis* (Figs 2, 15). The two-celled ES2 trichomes are usually composed of a cell distended at its base and a long, conical cell. The trichomes distributed on the leaves and stems vary slightly. While both of them are thick-walled, the surface of cells of hairs on the leaves is smooth (Figs 3, 16). However, trichomes on the stems are covered with small protuberances (Figs 4, 17). The three-celled ES3 trichomes are usually long and thick-walled (Figs 5, 18, 20). It is interesting to note that the basal cell of some ES3 trichomes in *C. elegans* var. *elegans* is surrounded with 12 to 16 cells (Figs 6, 19). In addition, the more than three ES $>$ 3 trichomes are much longer than the types described above, which are only present in *C. elegans* (Figs 7, 21).

Branched eglandular trichomes occur commonly in sect. *Colquhounia*, whereas in sect. *Simplicipili*, only *C. elegans* var. *elegans* exhibits this trichome type. Based on branching configuration, branched eglandular trichomes can be subdivided into three subtypes: biramous (EBBi), stellate (EBSt) and dendroid (EBDe). The three subtypes can be differentiated based on the number of branches and the cellular composition. EBBi trichomes fork apically into two unicellular branches (Figs 8, 22). EBSt trichomes lack a main axis or basal

Table 2. Trichome types and their distribution on the leaves and young stems of *Colquhounia*. Sectional classification follows Wu & Li (1977).

Taxon	Distribution	Surface	Eglandular trichomes							Glandular trichomes	
			ES1	ES2	ES3	ES>3	EBBi	EBSt	EBDe	GCa	GPe
Sect. *Colquhounia*											
C. coccinea var. *coccinea*	Tibet [Bhutan, India, Nepal]	sparsely tomentose	+	–	–	–	+	+	+	+	–
C. coccinea var. *mollis*	Yunnan [Bhutan, India, Myanmar, Nepal,Thailand]	densely tomentose	+	–	–	–	+	+	–	+	–
C. vestita	Yunnan	densely tomentose	–	+	–	–	–	–	+	–	–
C. compta var. *compta*	Yunnan	tomentose	+	–	+	–	+	+	–	–	–
C. compta var. *mekongensis*	Sichuan, Yunnan	tomentose	–	–	+	–	–	+	–	–	–
Sect. *Simplicipili*											
C. elegans var. *elegans*	Yunnan [Myanmar, Thailand]	densely hairy	–	+	+	+	+	+	+	+	–
C. elegans var. *tenuiflora*	Yunnan [Cambodia, Laos, Myanmar, Vietnam]	sparsely hairy	–	+	+	+	–	–	–	+	–
C. seguinii var. *seguinii*	Guangxi, Guizhou, Hubei, Sichuan, Yunnan [Myanmar]	strigose/villous	+	+	+	–	–	–	–	+	+
C. seguinii var. *pilosa*	Sichuan, Yunman	villous	+	+	+	–	–	–	–	–	+

Notes: + Present; – Absent; ES1 = simple eglandular unicelluar, ES2 = two-celled, ES3 = three-celled, ES>3 = more than three-celled; EBBi = branched eglandular biramous, EBSt = stellate, ESDe = dendriod; GCa = glandular capitate, GPe = peltate.

pad of tissue and have four to ten branches diverging from a common point. Some branches consist of only one cell (Figs 9, 23), while others are multicellular mixed with unicellular branches (Figs 10, 24). EBDe trichomes have a tree-like branching form, with a definite main axis and four to seven branches distantly spaced along the axis (Figs 11, 25).

Glandular trichomes

Two types of glandular trichomes were observed in *Colquhounia*: capitate (GCa) and peltate (GPe). The GCa trichomes were observed on both leaf surfaces (Figs 25–26) and distributed sporadically on the stems (Fig. 17). Morphologically, the GCa trichomes consist of a basal cell, a stalk cell and one to two head cells forming a secretory cavity (Fig. 12). As reported by Werker et al. (1993) in *Ocimum* L. (Lamiaceae), when head cells stop secreting and the cavity is filled with secreted materials, the secretory cavity collapses (Fig. 26).

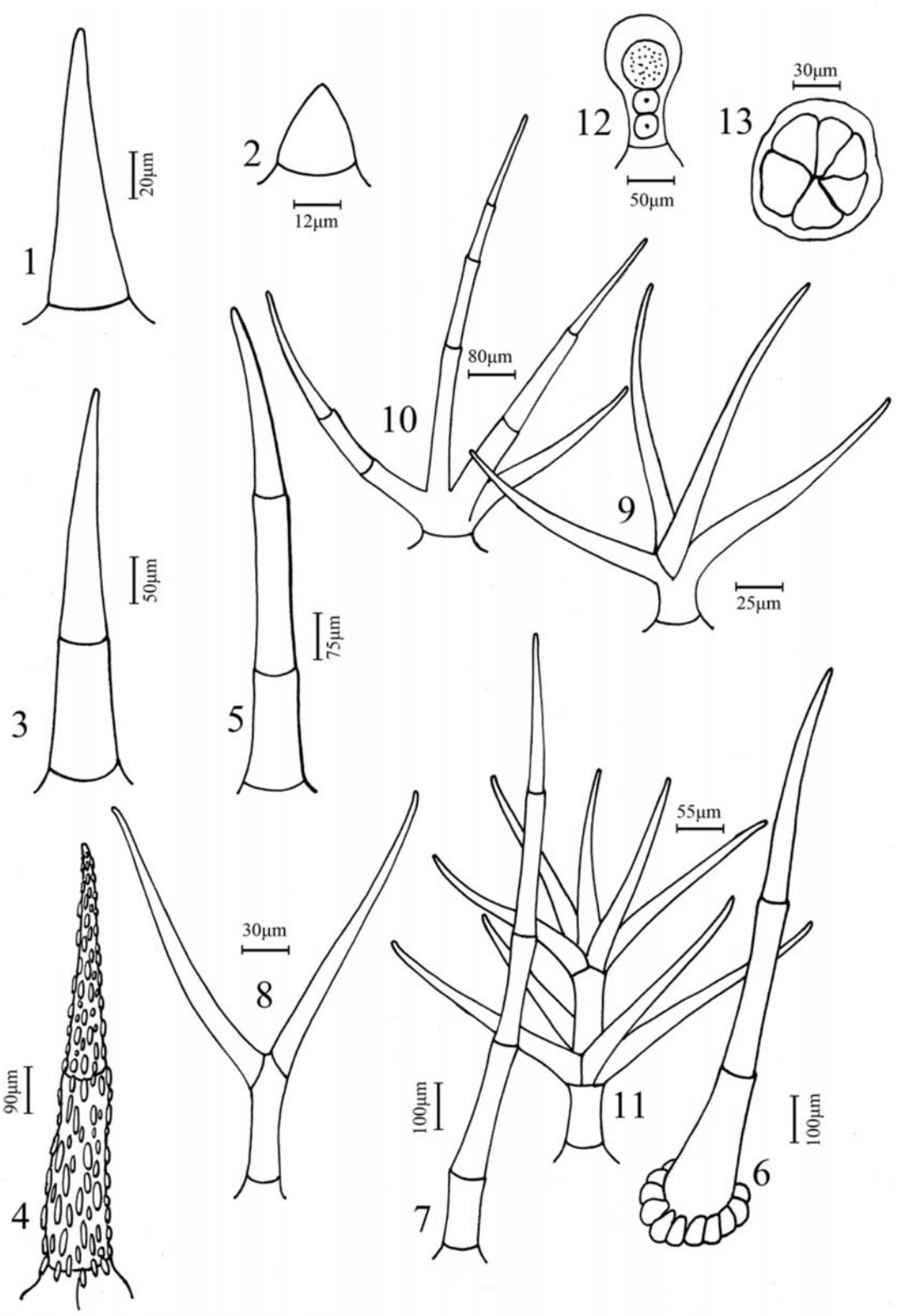
Peltate glandular trichomes (Fig. 13), which usually are composed of a basal cell, a short stalk cell and a large multicellular head that consists of 6 cells, were found only on the abaxial surface of leaves of *C. seguinii*. On mature leaves, the peltate glandular trichomes are apparently embedded among epidermal cells and thus can be described as sessile (Fig. 27).

Discussion

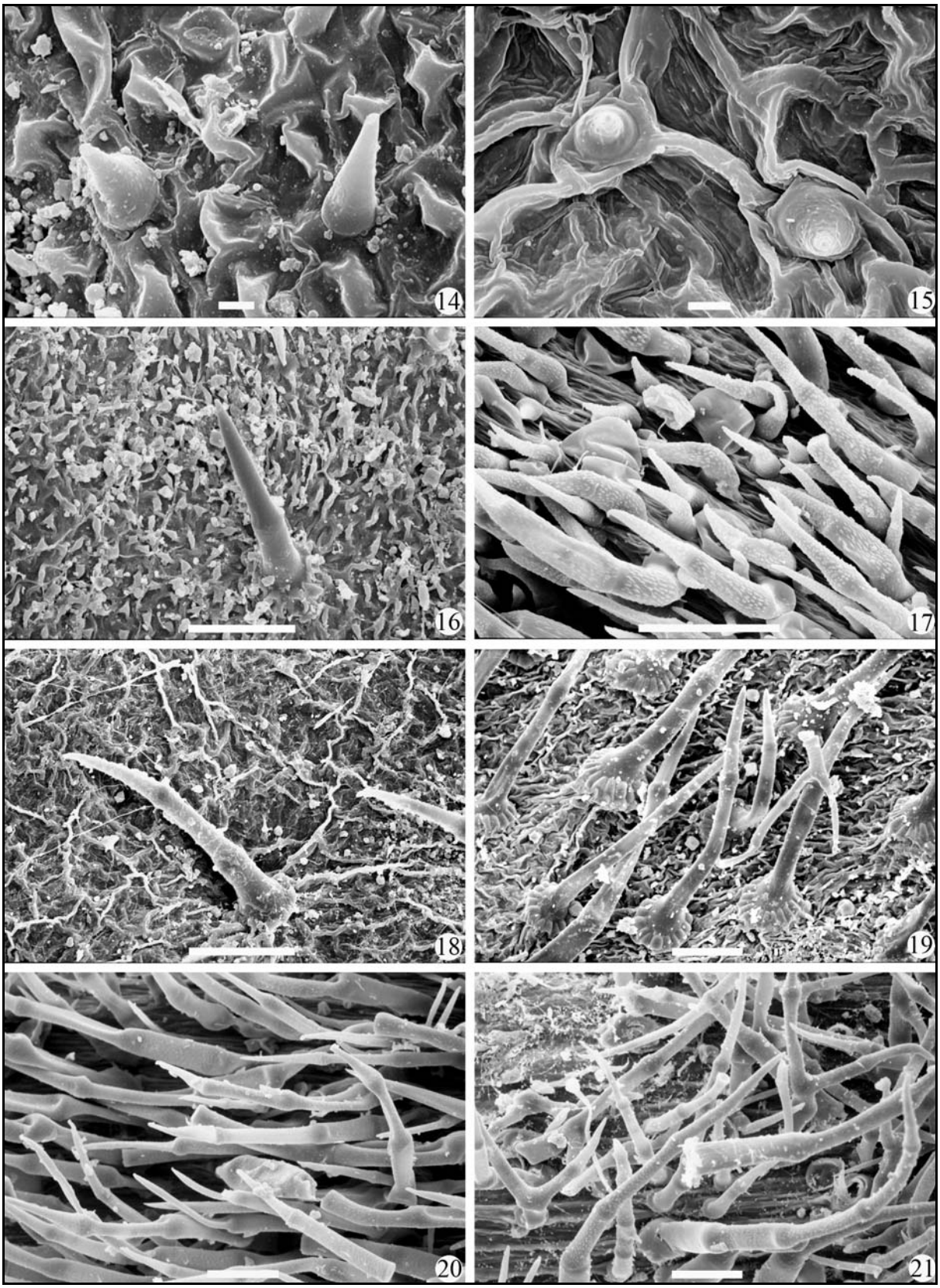
The types and distribution of trichomes show considerable variation among species and varieties of *Colquhounia*, and therefore are potentially valuable for different levels of classification.

At the sectional level, based on the presence or absence of branched hairs, Wu & Li (1977) divided *Colquhounia* into two sections: sect. *Simplicipili* and sect. *Colquhounia*. The former included *C. elegans* var. *elegans*, *C. elegans* var. *tenuiflora*, *C. seguinii* var. *seguinii*, and *C. seguinii* var. *pilosa*; the latter was represented by *C. coccinea* var. *coccinea, C. coccinea* var. *mollis, C. compta* var. *compta, C. compta* var. *mekongensis* and *C. vestita*. According to this classification, taxa in sect. *Colquhounia* have branched hairs, or branched hairs mixed with simple hairs on their leaves or young stems, whereas taxa in sect. *Simplicipili* have only simple trichomes. Results of the present study, however, slightly contradict Wu & Li's classification (1977). Three types of branched hairs (EBBi, EBSt and EBDe) were observed in *C. elegans*, which suggests that it is reasonable to transfer *C. elegans* from sect. *Simplicipili* to sect. *Colquhounia.* As a result, sect. *Simplicipili* will include only one species, *C. seguinii.*

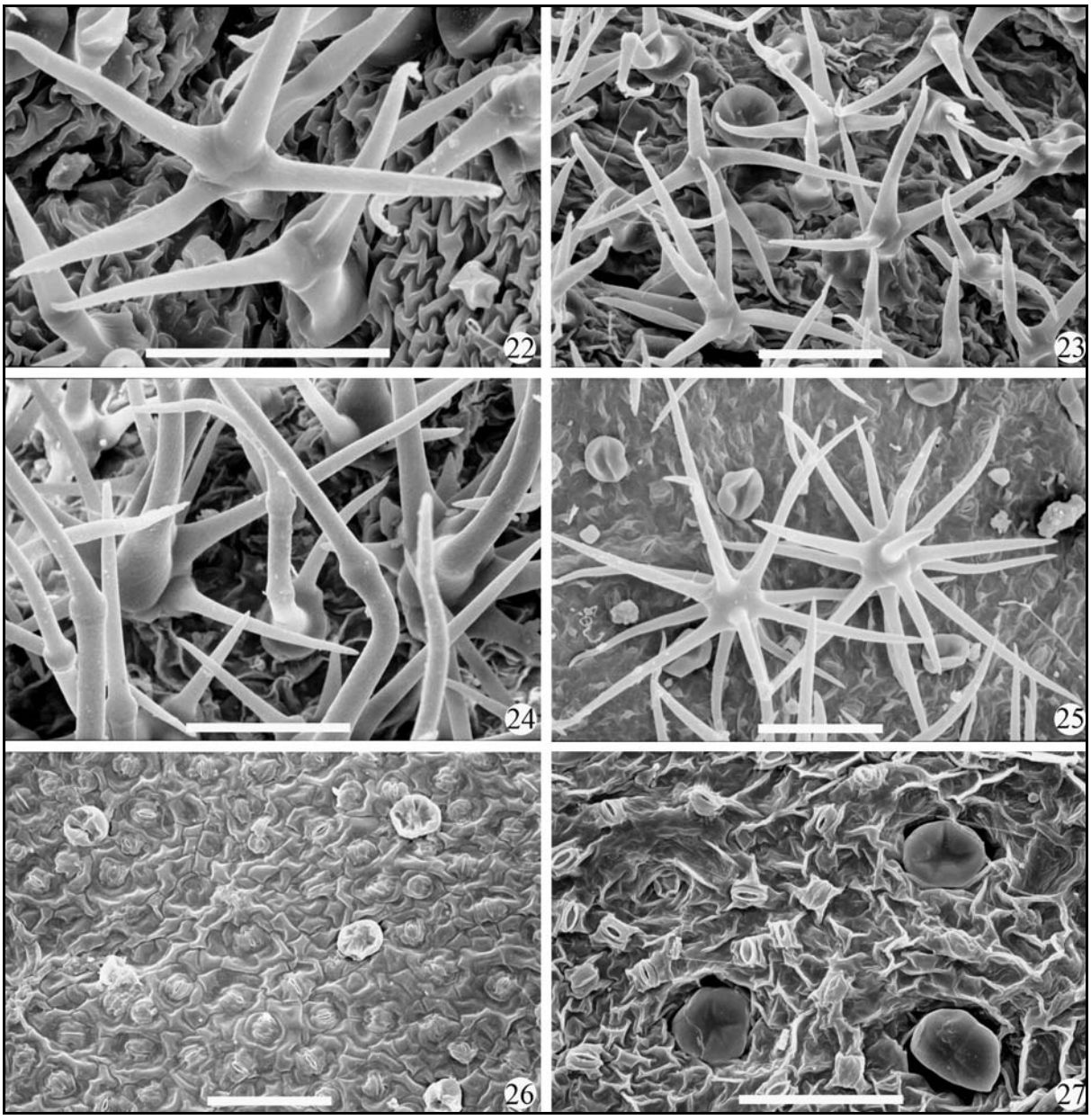
In addition to lacking branched hairs, *C. seguinii* differs from all other species of *Colquhounia* in many other aspects. With respect to habit, *C. seguinii* is a woody liana while the remaining species of *Colquhounia* are erect shrubs. Geographically, *C. seguinii* is widely distributed in different elevations varying from 200 m to 2,700 m in Guangxi, Guizhou, Hubei, Sichuan, Yunnan as well as Myanmar. Thus, *C. seguinii* is the only species of *Colquhounia* that is found below 1,000 m elevation (Li & Hedge 1994). Another distinct feature of *C. seguinii* is the presence of peltate glandular trichomes that are sunken into epidermal cells, which was not observed in any other species of *Colquhounia*. Similar peltate trichomes have been reported in *Ocimum*



Figs 1–13. Drawings of eglandular and glandular trichomes. 1–2 – unicellur trichome, on the leaves of *C. seguinii*; 3 – two-celled trichome with smooth walls, on the leaves of *C. elegans* var. *elegans*; 4 – two-celled trichome with protuberances on the wall, on the stems of *C. seguinii*; 5 – three-celled trichome, on the leaves of *C. seguinii* var. *pilosa*; 6 – three-celled trichome, of which basal cell is surrounded by 12 to 16 cells, on the leaves of *C. elegans* var. *elegans*; 7 – more than three-celled trichome, on the leaves of *C. elegans* var. *elegans*; 8 – biramous trichome, on the leaves of *C. coccinea* var. *mollis*; 9 – stellate trichome with unicellular branches, on the leaves of *C. coccinea* var. *mollis*; 10 – stellate trichome with multi-cellular branches, on the leaves of *C. compta* var. *mekongensis*; 11 – dendroid trichome, on the leaves of *C. elegans* var. *elegans*; l2 – capitate glandular trichome, apical view, on the leaves of *C. elegans* var. *tenuiflora*; 13 – peltate glandular trichome, on the leaves of *C. seguinii* var. *seguinii*.



Figs 14–21. SEM micrographs of simple trichomes. 14 – *C. seguinii*, pyramidal, thick-walled and unicellular trichomes; 15 – *C. coccinea* var. *mollis*, papillate trichomes; 16 – *C. elegans* var. *elegans*, two-celled trichome with smooth wall; 17 – *C. seguinii*, two-celled trichome with protuberances on wall; 18 – *C. seguinii* var. *pilosa*, three-celled trichomes; 19 – *C. elegans* var. *elegans*, three-celled trichome, of which basal cell is surrounded by 12 to 16 cells; (20) – *C. elegans* var. *elegans,* three-celled trichome distributed on the stem; 21 – *C. elegans* var. *elegans,* more than three-celled trichome [scale bar = 10 μm (14–15); scale bar = 100 μm (16–21)].



Figs 22–27. SEM micrographs of branched eglandular and glandular trichomes. 22 – *C. coccinea* var. *mollis*, biramous trichome; 23 – *C. coccinea* var. *mollis*, stellate trichomes with unicellular branches; 24 – *C. compta* var. *mekongensis*, stellate trichomes with multicellular branches; 25 – *C. elegans* var. *elegans*, dendroid trichomes; 26 – *C. elegans* var. *tenuiflora*, capitate glandular trichomes; 27 – *C. seguinii* var. *seguinii*, peltate glandular trichomes (scale bar = 100 μm).

(Werker et al. 1993) and *Hyptis* Jacq. (Rudall 2007) in Lamiaceae.

The morphology and distribution of trichomes and other features also have taxonomic significance at the species level. *Colquhounia coccinea*, for example, is morphologically similar to *C. compta* in that both species are shrubs with ovate to elliptic-ovate leaf blades and axillary cymes. They differ in that *C. coccinea* has scarlet corollas, bigger leaves (7–11 cm) covered with sparsely rust-colored stellate hairs on the abaxial leaf surface, and cymes of many flowers [vs. *C. compta* that has dark red corollas, smaller leaves (4–5 cm), densely gray tomentose indumenta on leaves and young branches, and few-flowered cymes]. However, these characteristics vary widely in different habitats and thus cannot be considered diagnostic for discriminating between two species. Perhaps a better feature to distinguish the two taxa is GCa. Results from the present study show that GCa are present in *C. coccinea* but absent in *C. compta.*

At the subspecies level, trichome morphology provides significantly diagnostic characteristics for delimitation of *C. compta* var. *compta* and *C. compta* var. *mekongensis*. Both of the two varieties are distributed in Yunnan province of China and have similar habitat preferences (dry thickets in open valleys). Identification keys to distinguish among them have tended to be based on the shape of calyx teeth as well as the color and size of their flowers. *Colquhounia compta* var. *compta* has 2.5 cm long, dark gray-red corollas, narrowly triangular

calyx teeth and entire upper lips (of corollas) whereas *C. compta* var. *mekongensis* has longer (approximate 3 cm) and dark red corolla, triangular-subulate calyx teeth and emarginate upper corolla lips. Unfortunately, both sets of diagnostic features are often observed on the same plant. Therefore, other stable characteristics to differentiate between these two varieties should be sought. In this study, ES1 and EBBi were observed in *C. compta* var. *compta* but not in *C. compta* var. *mekongensis*. Consequently, the presence of ES1 and EBBi could be considered a better diagnostic characteristic between the two varieties.

Based on patterns of trichomes and other morphological characteristics, Chinese species of *Colquhounia* may be distinguished using the following dichotomous key:

Key to the species of *Colquhounia* from China

1 Liana; leaves and young stems with simple eglandular trichomes only. (sect. *Simplicipili*) ..... *C. seguinii*
– Shrub; leaves and young stems with branched eglandular trichomes, or these mixed with simple eglandular trichomes. (sect. *Colquhounia*) 2
2 Leaf surfaces with capitate glandular trichomes 3
– Leaf surfaces without capitate glandular trichomes 4
3 Branches tomentose with rust-colored trichomes; unicellular eglandular trichomes present; verticillasters with 6–20 flowers ..... *C. coccinea*
– Branches densely hirsute with retrorse rust-colored trichomes; unicellular eglandular trichomes absent; verticillasters with less than 6 flowers ..... *C. elegans*
4 Stem and abaxial leaf surfaces densely white-lanate-tomentose; dendroid eglandular trichomes present; stellate eglandular trichomes absent ..... *C. vestita*
– Stem and abaxial leaf surfaces densely gray-tomentose; dendroid eglandular trichomes absent; stellate eglandular trichomes present ..... *C. compta*

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