

毛冠菊属系统位置的核形态证据

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Systematic position of *Nannoglottis* Maxim. s.l. (Asteraceae) : karyomorphological data

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Abstract This paper describes for the first time the karyomorphology of 4 populations of 2 species of *Nannoglottis* Maxim. s.l. The two species both show the resting nuclei of the complex chromosome type and the mitotic prophase chromosomes of the interstitial type. The karyotype formula of *N. gynura* is $2n = 18 = 14m + 2sm + 2st$ (SAT) in two populations while that of *N. carpesioides* is $2n = 18 = 14m + 2sm(2SAT) + 2st$ in two populations. The two species under study represent two sections of *Nannoglottis* s.l. *N. gynura*, the only species of sect. *Stenolepis*, is considered as the most primitive member of the genus. Accordingly, the basic chromosome number of the genus might be $x = 9$. Karyomorphological data indicate that *Nannoglottis* should be placed in the tribe Astereae rather than in the Inuleae and the Senecioneae.

Key words *Nannoglottis* Maxim.; Karyomorphology; Tribal classification

Nannoglottis Maxim. s.l., a small genus of the Asteraceae, is endemic to the Plateau Qinghai-Xizang (Tibet). This genus, as circumscribed by Ling & Chen (1965) to include the genera *Stereosanthus* Franch. and *Vierhapperia* Hand.-Mazz., comprises two sections and eight species. In terms of its tribal classification and systematic position, *Nannoglottis* has been one of the problematic genera in the Asteraceae (Ling & Chen 1965).

Nannoglottis s. s. is a monotypic genus, including only *N. carpesioides*. Its habit and leaves resemble those of *Carpesium* L. Therefore, the genus was originally classified in the tribe Inuleae by Maximovicz (1881), but was considered as an abnormal genus because of its trimorphous flowers. Hoffmann (1894) transferred it to the subtribe Senecioninae of the tribe Senecioneae as an isolated genus. Several years later, Franchet (1896) established another genus, *Stereosanthus* Franch., which includes four species. He proposed that *Stereosanthus* might represent an intermediate type between the Inuleae and the Senecioneae. Handel-Mazzetti (1937) acknowledged the above two genera and established an additional monotypic genus *Vierhapperia* Hand.-Mazz., which he placed in the tribe Astereae.

After examining the type specimens and other collections of *Nannoglottis*, *Stereosanthus* and *Vierhapperia*, Ling & Chen (1965) suggested that *Stereosanthus* and *Vierhapperia* be incorporated into *Nannoglottis*. They based this classification on the observation that the three genera share similar flower forms and the same achene and pappus structures. According to Ling & Chen (1965), though differences in disposition of involucre bracts and length of ligules are good criteria for dis-

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criminating species, they are not sufficient for generic delimitation. Furthermore, they argued that *Nannoglottis s. l.* should be classified in the Senecioneae and treated as a primitive genus in the subtribe Senecioninae.

Nordenstam (1977) tentatively proposed that *Nannoglottis s. l.* be excluded from the Senecioneae and transferred to the Astereae as Handel-Mazzetti (1937) treated the reduced *Vierhapperia*. This suggestion was followed by Jeffrey & Chen (1984), Jeffrey (1992), Zhang & Bremer (1992) and Bremer (1994), although they had not found more data to support this treatment and usually treated it as an isolated genus of the Astereae. However, in his systematic treatment of Chinese Asteraceae, Ling (1997) insisted that *Nannoglottis* should be placed in the Senecioneae, in a subtribe of its own, *Nannoglottisinae*. In addition, he thought that *Nannoglottisinae* might be closely related to his subtribe *Tussilaginatae s. s.* (including only two genera, *Petasites* and *Tussilago*) based on the trimorphous flowers commonly found in these two subtribes (Ling 1997). At the same time, Ho *et al.* (1997) thought that *Nannoglottis* might have evolved from *Senecio* of the Senecioneae. All these suggestions for the tribal classification and systematic position of *Nannoglottis* are related to three separate tribes: the Inuleae, the Senecioneae and the Astereae.

The karyomorphological information is one line of important evidence for clarifying the controversial systematic issues of the Asteraceae (Solbrig 1977). But the karyomorphological data of *Nannoglottis* have never been reported due to the difficulty of obtaining materials. In this paper, 4 populations of 2 species, which represent two sections of *Nannoglottis s. l.*, were karyomorphologically investigated. Based on the karyomorphological data, the tribal classification of *Nannoglottis* was discussed.

1 Materials and Methods

The two species and their origins were listed in the Table 1. All voucher specimens are deposited in the Northwest Plateau Institute of Biology, the Chinese Academy of Sciences (HNWP).

Table 1 Origins and vouchers of the studied species

Species	Locality	Voucher Specimens (in NWPB)
<i>Nannoglottis carpesioides</i>	Xunhua, Qinghai, alt. 2000 m	Liu Jiarr-quan 538
	Huzhu, Qinghai, alt. 2100 m	Liu Jiarr-quan 551
<i>N. gynura</i>	Yushu, Qinghai, alt. 3400 m	H. B. G. 1942
	Yushu, Qinghai, alt. 3600 m	H. B. G. 2335

The roots were pretreated with a mixture of 0.05% colchicine and 0.002 mol/L hydroxyquinoline for eight hours, and then fixed overnight in Carnoy's fluid (absolute alcohol glacial acetic acid = 3:1). After being macerated in 1 mol/L hydrochloric acid at 60 °C for five minutes, they were stained and squashed with Carbol Fuchsin. The karyomorphological classifications of the resting and mitotic prophase followed Tanaka (1971). The symbols for the description of karyotypes followed Levan *et al.* (1964). The indices of relative length (IRL) suggested by Kuo (1972) were adopted. The asymmetry of karyotypes was classified according to Stebbins (1971).

2 Results

2.1 *Nannoglottis carpesioides* Maxim. (Table 2)

The resting nuclei were of the complex chromosome type (Fig. 1:1). The karyomorphological type of the mitotic prophase chromosomes belonged to the interstitial type (Fig. 1:2).

The metaphase chromosomes (Fig. 1:3) of both populations were counted to be $2n = 18$, rang-

ing in length from 4.10 μm to 6.70 μm . Their karyotypes (Fig. 1:4,5) were similar, and were formulated as $2n = 18 = 14m + 2sm(2SAT) + 2st$, belonging to Stebbins' 2A type.

2.2 *Nannoglottis gynura* (C. Winkl.) Ling et Y. L. Chen (Table 2)

The resting nuclei and the mitotic prophase chromosomes were the complex chromosome type and the interstitial type respectively, similar to those of *N. carpesioides*. Both populations (Fig. 1:7) had the chromosome number of $2n = 18$, ranging in length from 4.15 μm to 7.22 μm . Their karyotypes (Fig. 1:6~8) were both formulated as $2n = 18 = 14m + 2sm + 2st(2SAT)$, belonging to Stebbins' 2A type.

Table 2 Parameters of mitotic metaphase chromosomes of 4 populations of 2 species in *Nannoglottis*

<i>Nannoglottis carpesioides</i>					<i>N. gynura</i>				
Liu Jiarrquan 538					H. B. G. 1942				
NO	RL	AR	T	IRL	No	RL	AR	T	IRL
1	7.03 + 7.95 = 14.98	1.13	m	1.35	1	7.18 + 8.03 = 15.21	1.12	m	1.37
2	5.67 + 8.07 = 13.74	1.42	m	1.24	2	5.22 + 6.91 = 12.13	1.32	m	1.09
3	4.92 + 6.88 = 11.80	1.40	m	1.06	3	4.41 + 7.10 = 11.51	1.61	m	1.04
4	5.03 + 5.95 = 10.98	1.18	m	0.99	4	4.89 + 6.43 = 11.32	1.31	m	1.02
5	4.57 + 6.23 = 10.97	1.36	m	0.99	5	4.20 + 6.43 = 10.63	1.53	m	0.96
6	2.55 + 7.14 = 9.69	2.80	sm*	0.87	6	2.30 + 8.08 = 10.38	3.51	st*	0.93
7	4.43 + 4.89 = 9.52	1.10	m	0.84	7	4.97 + 5.16 = 10.13	1.03	m	0.91
8	3.88 + 5.41 = 9.29	1.39	m	0.84	8	3.06 + 6.92 = 9.98	2.26	sm	0.90
9	1.78 + 7.50 = 9.28	4.21	st	0.84	9	3.60 + 5.40 = 9.00	1.50	m	0.81
Liu Jiarrquan 551					H. B. G. 2335				
NO	RL	AR	T	IRL	No	RL	AR	T	IRL
1	5.94 + 7.31 = 13.25	1.23	m	1.19	1	5.88 + 7.90 = 13.09	1.34	m	1.24
2	5.45 + 7.46 = 12.91	1.37	m	1.16	2	5.45 + 7.41 = 12.86	1.36	m	1.16
3	5.84 + 6.51 = 12.35	1.11	m	1.11	3	5.18 + 7.33 = 12.51	1.42	m	1.12
4	5.06 + 6.76 = 11.82	1.34	m	1.06	4	4.46 + 7.12 = 11.58	1.60	m	1.04
5	5.73 + 5.74 = 11.47	1.01	m	1.03	5	4.97 + 6.24 = 11.21	1.26	m	1.00
6	4.78 + 5.12 = 9.90	1.11	m	0.89	6	1.88 + 7.66 = 9.54	4.07	st*	0.86
7	2.57 + 7.33 = 9.90	2.85	sm*	0.89	7	4.72 + 4.96 = 9.48	1.10	m	0.85
8	3.80 + 5.84 = 9.64	1.54	m	0.87	8	2.84 + 6.50 = 9.34	2.29	sm	0.84
9	2.08 + 6.65 = 8.73	3.20	st	0.77	9	3.54 + 5.25 = 8.79	1.48	m	0.79

RL: relative length. AR: arm ratio. T: type. IRL: index of relative length.

* indicating the satellite chromosomes

3 Discussion

The two species of *Nannoglottis* s.l. under study have common karyomorphological characteristics and similar karyotypes. *N. carpesioides* was the only species of *Nannoglottis* s. s. (Maximovicz 1881) while *N. gynura* was ascribed to *Stereosanthus* by Franchet (1896) and Handel.-Mazzetti (1937). Their similar chromosome data support Ling & Chen (1965) reducing *Stereosanthus* as a congeneric name of *Nannoglottis*.

Nannoglottis s.l. comprises two sections: sect. *Stenolepis* and sect. *Nannoglottis*. The former section includes only one species: *N. gynura*, and this species was considered as the most primitive member of the genus (Ling & Chen 1965). The latter section consists of seven species, including *N. carpesioides*. Although a further study of more species is needed, this research indicates $x = 9$ might be the base chromosome number of *Nannoglottis* s.l.



Fig. 1~5. *Nannoglottis capesoides* (1~4. Liu Jiarr-quan 538; 5. Liu Jiarr-quan 551).
 Fig. 6~8. *N. gynura* (6~7. H. B. G. 1942; 8. H. B. G. 2335). (1~3, 6. $\times 2000$; 4~5, 7~8. $\times 3000$)

As stated in the introduction, the tribal classification and systematic position of *Nannoglottis* have long been disputed. The base chromosome numbers of the Inuleae and the Senecioneae are $x =$

10. All genera postulated to be related to *Nannoglottis* in the Inuleae and the Senecioneae have the base chromosome numbers of $x = 10$ or $x = 30$ derived from $x = 10$ (Table 3). The chromosome data reject the suggestions for the tribal classification of *Nannoglottis* in the Inuleae and the Senecioneae, and the close relationships of *Nannoglottis* to some genera (e. g. *Carpesium*, *Senecio*, *Tussilago* and *Petasites*) of these two tribes (Ling 1997, Ho *et al.* 1997, Ling & Chen 1965, Franchet 1896, Hoffmann, 1894; Maximovicz 1881).

Table 3 A comparison of the base chromosome numbers of *Nannoglottis* and related taxa

Taxon	Base number	Reference
<i>Nannoglottis</i>	$x = 9$	Present research
<i>Astereae</i>	$x = 9$	Semple 1995
<i>Aster</i>	$x = 9$	Anderson 1974
<i>Erigeron</i>	$x = 9$	Semple 1995
<i>Inuleae</i>	$x = 10$	Anderberg 1991
<i>Carpesium</i>	$x = 10$	Anderberg 1991
<i>Senecioneae</i>	$x = 10$	Robinson <i>et al.</i> 1997
<i>Senecio</i>	$x = 10$	Robinson <i>et al.</i> 1997
<i>Petasites</i>	$x = 30$	Robinson <i>et al.</i> 1997
<i>Tussilago</i>	$x = 30$	Robinson <i>et al.</i> 1997

The common $x = 9$ of *Nannoglottis* and the Astereae indicates that *Nannoglottis* might have a close affinity with the Astereae. In addition, Astereae evolved in Eurasia, possibly in the region adjacent to the Indian Ocean (Xiang & Semple 1996). *Nannoglottis* is distributed in this region. Therefore, from the phytogeographical viewpoint, it is imaginable that *Nannoglottis* may have evolved with the Astereae from a common ancestor. Our results support the suggestion of Jeffrey & Chen (1984), Jeffrey (1992), Zhang & Bremer (1992) and Bremer (1994) that *Nannoglottis* should be treated in the Astereae. However, based on the current available data, it is still difficult to speculate about the systematic position of *Nannoglottis* in the Astereae. Gross-morphologically, *Nannoglottis* is

unique in the Astereae except that its style branches are similar to those of most genera in this tribe. In addition, st chromosomes were detected in *Nannoglottis* but not in all investigated genera of the Astereae (unpublished data). Both the tribal classification of *Nannoglottis* and its systematic position in the Astereae need to be confirmed and determined from other lines of evidence especially from the molecular data. The tribal classifications and systematic positions of many problematic genera of the Asteraceae (e. g. *Adenocaulon*, *Corymbium* and *Eremothamus*) have been successfully determined by molecular methods (Jansen & Kim 1996).

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References

- Anderberg A A, 1991. Taxonomy and phylogeny of the tribe Inuleae (Asteraceae). *Pl Syst Evol*, 176: 75 ~ 123
- Anderson L C, Kyhos D W, Mosquin T *et al.*, 1974. Chromosome numbers in Compositae, : *Haplopappus* and other Astereae. *Amer J Bot*, 61: 665 ~ 671
- Bremer K, 1994. Asteraceae. Cladistics and Classification. Portland: Timber Press
- Cronquist A, 1955. Phylogeny and taxonomy of the Compositae. *Amer Midl Naturalist*, 53: 478 ~ 511
- Franchet A R, 1896. Compositae novae e flora sinensi. *Journ de Bot*, 10: 368 ~ 386
- Handel.-Mazzetti H, 1937. Neue und bemerkenswerte chinesische Compositen, besonders aus dem Berliner Herbar. *Notizbl Bot Gart u Mus Berl-Dahl*, 13: 607 ~ 661
- Hoffman O, 1894. Compositae. In: Engler & Prantl eds. *Die Nat ublichen Pflanzenfamilien*. Englelmann: Leipzig Nachtrage. 4(5): 289
- Ho T-N(何廷农), Liu Sh-W(刘尚武), Lu X-F(卢学峰), 1997. From Bei-Qilianshan floristic analysis to deter-

- mine the northeastern margin of Tangut flora. *Acta Biol Plat Sin*(高原生物学集刊), 13: 69 ~ 82
- Jansen R K, Kim K J, 1996. Implications of chloroplast DNA data for the classification and phylogeny of the Asteraceae. In: Hind D J N & Beentje H J eds. *Compositae: Systematics. Proceedings of the International Compositae Conference*, Kew, 1994. Royle Botanic Gardens, Kew. 1: 317 ~ 339
- Jeffrey C, 1992. The tribe Senecioneae (Compositae) in the Mascarene Islands with an annotated world check-list of the genera of the tribe. *Notes on Compositae*. Kew Bull, 47: 49 ~ 109
- Jeffrey C, Chen Y L, 1984. Taxonomic studies on the tribe Senecioneae (Compositae) in the eastern Asia. *Kew Bull*, 39: 205 ~ 446
- Karis P O, 1993. Morphological phylogenetics of the Asteraceae -Asteroideae, with notes on character evolution. *Pl Syst Evol*, 186: 69 ~ 93
- Kim K J, Jansen P K, Wallace R S *et al.*, 1992. Phylogenetic implications of *rbcL* sequence variation in the Asteraceae. *Ann Miss Bot Gard*, 79: 428 ~ 445
- Kuo S R, 1972. Karyotype analysis of some formosan gymnosperms. *Taiwania*, 17: 66 ~ 80
- Levan A, Fredga K, Sandberg A A, 1964. Nomenclature for centromeric position on chromosomes. *Hereditas*, 52: 201 ~ 220
- Ling R(林 鏊), Chen Y L(陈艺林), 1965. Genera nova vel minus cognita familiae compositarum, *Cavea W. W. Smith et Small et Nannoglottis Maxim.* *Acta Phytotax Sin*(植物分类学报), 10(1): 91 ~ 103
- Ling Y R(林有润), 1997. On the preliminary study of the systematics and floristics of Compositae from China. *Bull Bot Res* (Harbin)(植物研究), 17(1): 6 ~ 27
- Maximowicz C J, 1881. Diagnoses plantarum novarum Asiaticarum LV. *Bull Acad Sci St Petersburg*, 27: 480 ~ 495
- Nordenstam B, 1977. Senecioneae and Liabeae —systematic review. In: Heywood V H *et al.* eds. *The Biology and Chemistry of the Compositae*. London: Academic Press 2: 799 ~ 830
- Ornduff R, Mosquin T, Kyhos D H *et al.*, 1967. Chromosome number in Compositae. Senecioneae. *Amer J Bot*, 54: 205 ~ 213
- Robinson H, Carr G D, King R M *et al.*, 1997. Chromosome numbers in Compositae: Senecioneae. *Ann Miss Bot Gard*, 84: 893 ~ 906
- Robinson H, 1983. A generic review of the tribe Liabeae (Asteraceae). *Smithsonian Contr Bot*, 54: 1 ~ 69
- Semple J C, Chmielewski J G, Chinnappa C C, 1983. Chromosome number determinations in *Aster* L. (Compositae), with comments on cytogeography, phylogeny and chromosome morphology. *Amer J Bot*, 70: 1432 ~ 1443
- Semple J C, 1995. A review of hypotheses on ancestral chromosomal base numbers in the tribe Astereae and the genus *Aster*. In: Hind D J N & Pope G V eds. *Advances in Compositae Systematics*. Royle Botanic Garden, Kew. 153 ~ 165.
- Solbrig C, 1977. Chromosome review of the Compositae. In: Heywood V H *et al.* eds. *The Biology and Chemistry of the Compositae*. London: Academic Press. 1: 265 ~ 278
- Stebbins G L, 1971. *Chromosomal Evolution in Higher Plants*. London: Edward Arnold.
- Tanaka R, 1971. Types of resting nuclei in Orchidaceae. *Bot Mag Tokyo*, 84: 118 ~ 122
- Xiang C S, Semple J C, 1996. Molecular systematic study of *Aster* sensu lato and related genera (Asteraceae: Astereae) based on chloroplast DNA restriction site analyses and mainly North American taxa. In: Hind D J N & Beentje H J eds. *Compositae: Systematics. Proceedings of the International Compositae Conference*, Kew, 1994. Royle Botanic Gardens, Kew. 1: 393 ~ 423
- Zhang X P, Bremer K, 1992. A cladistic analysis of the tribe Astereae (Asteraceae) with notes on their evolution and subtribal classification. *Pl Syst Evol*, 184: 259 ~ 283

摘要 首次记载了毛冠菊属 2 种 4 居群的核形态资料。两种植物的染色体间期和前期染色体为复杂型和中间型。狭舌毛冠菊两居群的染色体数目与核型公式为 $2n = 18 = 14m + 2sm + 2st$ (2SAT); 毛冠菊两居群的染色体数目与核型公式为 $2n = 18 = 14m + 2sm$ (2SAT) + 2st。它们分别代表了整个毛冠菊属的两组植物,并包含了形态学上最原始的种类,因此,该属的染色体基数可能为 $x = 9$ 。核形态证据表明毛冠菊属放在紫菀族比放在旋覆花族和千里光族中更为合理。

关键词 毛冠菊属;核形态;族的归属

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