

天仙子族(茄科)的花粉形态补充研究及其系统学意义

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摘要: 在扫描电镜下研究了茄科天仙子族 7 属及颠茄属、茄参属和枸杞属 3 属共 10 属 23 种植物的花粉形态学特征。结果表明:天仙子族的花粉粒形状为球形、近球形、扁球形和长球形;萌发孔类型有无萌发孔、不规则的拟孔、3 沟、4 沟、3~4 沟、散沟和 3 孔沟;外壁纹饰为小刺状、瘤状、各式条纹状、条纹-穴状、条纹-网状、皱波状、细网状和网状。沟膜近光滑、具小颗粒、具小刺状突起或具瘤状突起。各属植物的花粉形态在萌发孔的有无、萌发孔的类型和外壁纹饰等方面有较大的差异,可以作为探讨属间分类和系统关系的重要依据。天仙子族植物花粉萌发孔的演化趋势为:无萌发孔→3、4 沟→3 孔沟。无萌发孔的山莨菪属是原始类群,三孔沟的马尿泡和天仙子等属是进化类群。还讨论了与前人研究结果不同之处和可能的原因。

关键词: 花粉形态;天仙子族;茄科;系统学意义

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Supplemental study on the pollen morphology of the tribe Hyoscyameae (Solanaceae) and its systematic significance

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Abstract: Pollen grains of 23 species in seven genera of the tribe Hyoscyameae (Solanaceae) and three related genera (*Atropa*, *Mandragora*, *Lycium*) were investigated under SEM. The pollen grains are globose, subglobose, oblate or prolate in shape. Germination apertures were absent or present and are irregularly poroid, 3-colpate, 4-colpate, 3-or 4-colpate, pantocolpate or 3-colporate. The exine ornamentation was spinulose, tuberculate, variously striate, striate-foveolate, striate-reticulate, rugose-sinuate, minutely reticulate or reticulate. The colpal membrane was nearly smooth but with granular, spinulose or tuberculate protuberances. The pollen grains show great variation between genera in the Hyoscyameae in the presence and type of a germination aperture and exine ornamentation. These may be important characters in revealing phylogenetic relationship in the tribe. The evolutionary trend in germination apertures ranges from absent or presence to 3-or 4-colpate then to 3-colporate. *Anisodus*, which lacks germination apertures, is considered to be primitive, while genera with 3-colporate pollen grains, such as *Przewalskia* and *Hyoscyamus* are believed to be advanced.

Key words: pollen morphology; tribe Hyoscyameae; Solanaceae; systematic significance

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1 Introduction

Pollen morphology can be useful for the analyzing taxonomic relationships in a wide variety of plant families. Recent studies in the Solanaceae have shown pollen morphology to be of considerable systematic significance, both at the generic and specific levels.

The tribe Hyoscyameae (Hunziker, 2001) comprises approximately 40 species in 7 genera: *Anisodus* Link (4 species) in China, Bhutan, India and Nepal; *Archihyoscyamus* A. M. Lu (1 species) in Western Asia (Kurdistan); *Atropanthe* Pascher (1 species) endemic to China; *Hyoscyamus* L. (about 23 species) widely distributed in Northern Africa, Asia and Europe; *Physochlaina* G. Don (about 11 species) in Asia; *Przewalskia* Maxim. (1 species) endemic to China at high elevation on the Qinghai-Tibetan Plateau; and *Scopolia* Jacq. (2 species) in Asia and Europe. The center of diversity of the tribe is in eastern Asia, with many species native to China. The Hyoscyameae forms the only tribe in the family centered in the northern hemisphere. The diversity has been linked to the Himalayan uplift (Lu & Chang, 1986).

The delimitation of the tribe Hyoscyameae has been debated widely (Bentham, 1876; Tetenyi, 1987; D'Arcy, 1991; Hoare & Knapp, 1997; Olmstead *et al.*, 1999; Hunziker, 2001). The focus of this argument has been on the affinity of *Atropa* to the traditionally recognized Hyoscyameae. Traditional classifications (Kuang & Lu, 1978; Tetenyi, 1987; D'Arcy, 1991) treated *Atropa* as separate from the Hyoscyameae on the basis of the fleshy, indehiscent fruits in *Atropa* and the unusual circumscissile capsules in the other genera.

The pollen grains of only a few taxa of Hyoscyameae have been examined in previous studies (Basak, 1967; Punt & Clarke, 1980; Sandina *et al.*, 1982; Diez & Ferguson, 1984; Chang & Lu, 1984; Lu & Chang, 1986; Ying *et al.*, 1993; Hoare & Knapp, 1997) and it has not been evaluated for its taxonomic utility within a subtribe, the tribe or within the Solanaceae as a whole.

The present paper reports on the pollen grains of 10 genera, including 23 species of Hyoscyameae and three related genera of Solanaceae (*Atropa*, *Mandrag-*

ora, *Lycium*) to assess its utility in providing a better understanding of the systematic relationships of the species within the Hyoscyameae and with other genera in the family.

2 Materials and Methods

Pollen grains were removed from collections deposited in the herbarium of the Institute of Botany, the Chinese Academy of Sciences (PE), Nijmegen Botanical Garden, Nijmegen University (NL), and the Natural History Museum (P), Paris, France (Appendix). For scanning electron microscope (SEM) examination, the pollen grains were collected from dry specimens, mounted on stubs with double-sided adhesive tape, then coated with gold for 3–4 min. Observations were made with a Hitachi S-800 (SEM). The pollen terminology follows Erdtman (1952).

3 Results

Characteristics of the pollen grains studied of members of the Hyoscyameae and related taxa are given in Table 1.

The pollen grains are spheroidal, subspheroidal, oblate or prolate in shape. Germination apertures are absent or present and irregularly poroid, 3-colpate, 4-colpate, 3- or 4-colpate, pantocolpate or 3-colporate. The exine sculpture is spinulose, tuberculate, variously striate, striate-foveolate, striate-reticulate, rugose-sinuate, minutely reticulate or reticulate. The colpal membrane is nearly smooth but with granular, spinulose or tuberculate protuberances. Features of the pollen grains for the various genera are as follows.

1 *Scopolia* (Plate I; 1-3)

Pollen grains spheroidal, 3-colpate or rarely pantocolpate, exine sculpture densely rugose.

2 *Anisodus* (Plate II; 13-16)

Pollen grains subspheroidal or spheroidal, nonaperturate, exine irregularly tuberculate or poroid.

3 *Atropanthe* (Plate II; 17-18)

Pollen grains spheroidal, 3-colpate, colpi long, exine curved striate.

Table 1 Characters of pollen grains in the tribe Hyoscyameae and related taxa of the Solanaceae under SEM

Species	Shape	Aperture	Exine sculpture
<i>Scopolia japonica</i>	Spheroidal	Shortly 3-colpate or pantocolpate	Rugose
<i>Anisodus luridus</i>	Subspheroidal	Nonaperturate or occasionally poroid	Tuberculate, tubercles unequal in size, densely granulate on surface
<i>A. tanguticus</i>	Spheroidal	Nonaperturate or poroid	Tuberculate, tubercles unequal in size
<i>Atropanthe sinensis</i>	Spheroidal	3-colpate	Curved striate
<i>Przewalskia tangutica</i>	Spheroidal	3-colporate	Reticulate
<i>Physochlaina praealta</i>	Subspheroidal to prolate	3-colporate	Shortly striate, occasionally punctate, indistinctly tuberculate on striae
<i>P. physaloides</i>	Spheroidal	4-colpate	Rather densely spinose and irregularly foveolate or punctate together
<i>P. infundibularis</i>	Spheroidal	3-colpate and 4-colpate	Densely spinose and sparsely foveolate together
<i>P. capitata</i>	Subspheroidal to prolate	Indistinctly 3-colpate	Rugose, irregularly spinulate and punctate together
<i>H. desertorum</i>	Prolate	3-colporate	Striate and sparsely punctate together
<i>H. pusillus</i>	Prolate	3-colporate	Striate and sparsely punctate together
<i>H. bipinnatisectus</i>	Subspheroidal	3-colporate	Striate and sparsely punctate together
<i>H. muticus</i>	Spheroidal	3-colporate; colpi long, nearly reaching polar area	Striate and indistinctly foveolate together
<i>H. senecionis</i>	Spheroidal	3-colporate, colpi long nearly reaching polar area	Striate and sparsely punctate together
<i>H. aureus</i>	Prolate	3-colporate	Striate-foveolate, striae low
<i>H. albus</i>	Prolate	3-colporate	Indistinctly striate to rugose, and sparsely punctate together
<i>H. niger</i>	Prolate	3-colporate, colpi long, nearly reaching polar area	Finely reticulate, muri wide and sparsely verrucate together, luminae small, unequal in size
<i>H. reticulates</i>	Prolate	3-colporate, colpi long, nearly reaching polar area.	Finely reticulate, muri wide and sparsely verrucate together, luminae small, unequal in size
<i>Archihyoscyamus leptocalyx</i>	Prolate	3-colporate	Striate, irregularly punctate among striae, sparsely granular on surface of striae
<i>Atropa belladonna</i>	Subspheroidal or oblate	3-colporate	Striate-reticulate, nearly smooth on striate surface
<i>Mandragora caulescens</i>	Spheroidal	Nonaperturate	Spinulate and tuberculate
<i>M. chinghaiensis</i>	Spheroidal	Nonaperturate	Spinulate and tuberculate
<i>Lycium barbarum</i>	Prolate	3-colporate	Striate, irregularly foveolate among striae, irregularly granular at puncta bottom

4 Przewalskia (Plate I; 4-6)

Pollen grains spheroidal, 3-colporate, exine reticulate.

5 Physochlaina (Plate III; 19-30)

Pollen grains spheroidal, subspheroidal to prolate, 3-colpate, 3- or 4-colpate, exine spinose or rugose.

6 Hyoscyamus (Plate IV; 31-36; Plate V; 37-45; Plate VI; 46-51; Plate VII; 55-60)

Pollen grains spheroidal to prolate, 3-colporate, exine striate or rugose.

7 Archihyoscyamus (Plate VI; 52-54)

Pollen grains prolate, 3-colporate, exine striate.

8 Mandragora (Plate II; 10-12)

Pollen grains spheroidal, nonaperturate, exine

sparsely spinulate and tuberculate.

9 Atropa (Plate I; 7-9)

Pollen grains subspheroidal or oblate, 3-colporate, exine densely tuberculate.

10 Lycium (Plate VII; 61-63)

Pollen grains prolate, 3-colporate, exine striate.

Based on aperture, the pollen grains of Hyoscyameae and related genera may be placed in four groups.

(1) Nonaperturate; *Mandragora*; (2) Nonaperturate or occasionally irregularly poroid; *Anisodus*; (3) 3-colpate, 4-colpate or pantocolpate; *Scopolia*, *Atropanthe* and *Physochlaina* (except *P. praealta*); (4) 3-colporate; *Przewalskia*, *Hyoscyamus*, *Archihyoscyamus*, *Physochlaina praealta*, *Atropa* and *Lycium*.

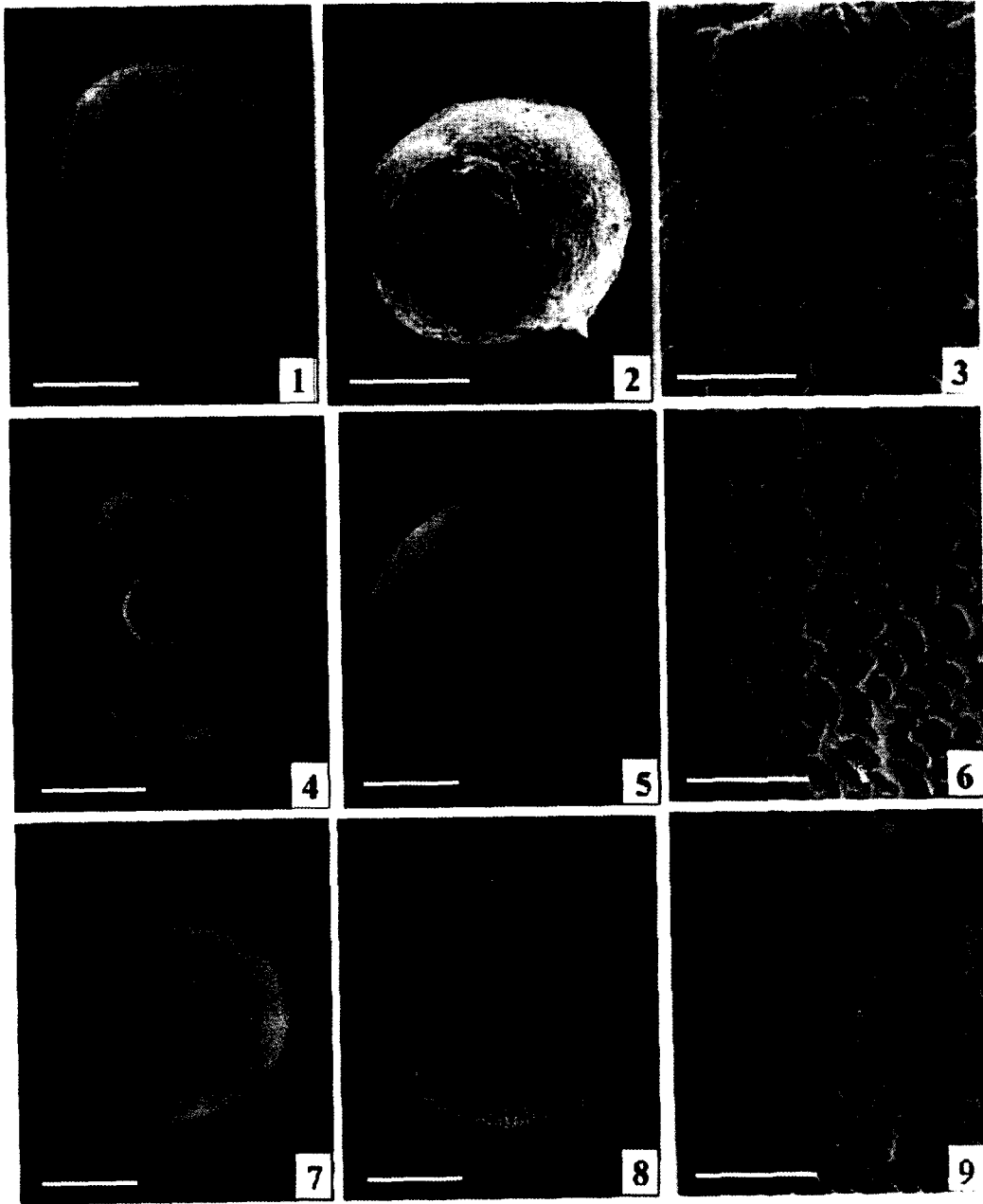


Plate I 1-3. *Scopolia japonica*; 4-6. *Przewalskia tangutica*; 7-9. *Atropa belladonna*; 1,4; bar=17.7 mm; 2; bar=20 mm; 5,7,8; bar=16 mm; 3,6,9; bar=20 mm.

Based on exine sculpture, the pollen grains of Hyoscyameae and related genera can be divided into four types as follows: (1) Rugose or tuberculate; *Scopolia*, *Anisodus*; (2) Striate, curved striate, striate-foveolate, striate-reticulate, striate-rugose; *Atropanthe*, *Physochlaina praealta* *Hyoscyamus* (except *H. niger* and *H. reticulatus*), *Archihyoscyamus*, *Atropa* and *Lycium*; (3) Spinose; *Physochlaina* (except *P. praealta*), *Mandragora*; (4) Finely reticulate, reticulate; *Przewalskia*,

Hyoscyamus niger and *H. reticulatus*.

4 Discussion and Conclusions

Pollen grains of Hyoscyameae vary greatly among the genera in the presence or absence and type of germination aperture and exine sculpture. These features can therefore be important in considering the phylogenetic relationships of the tribe.

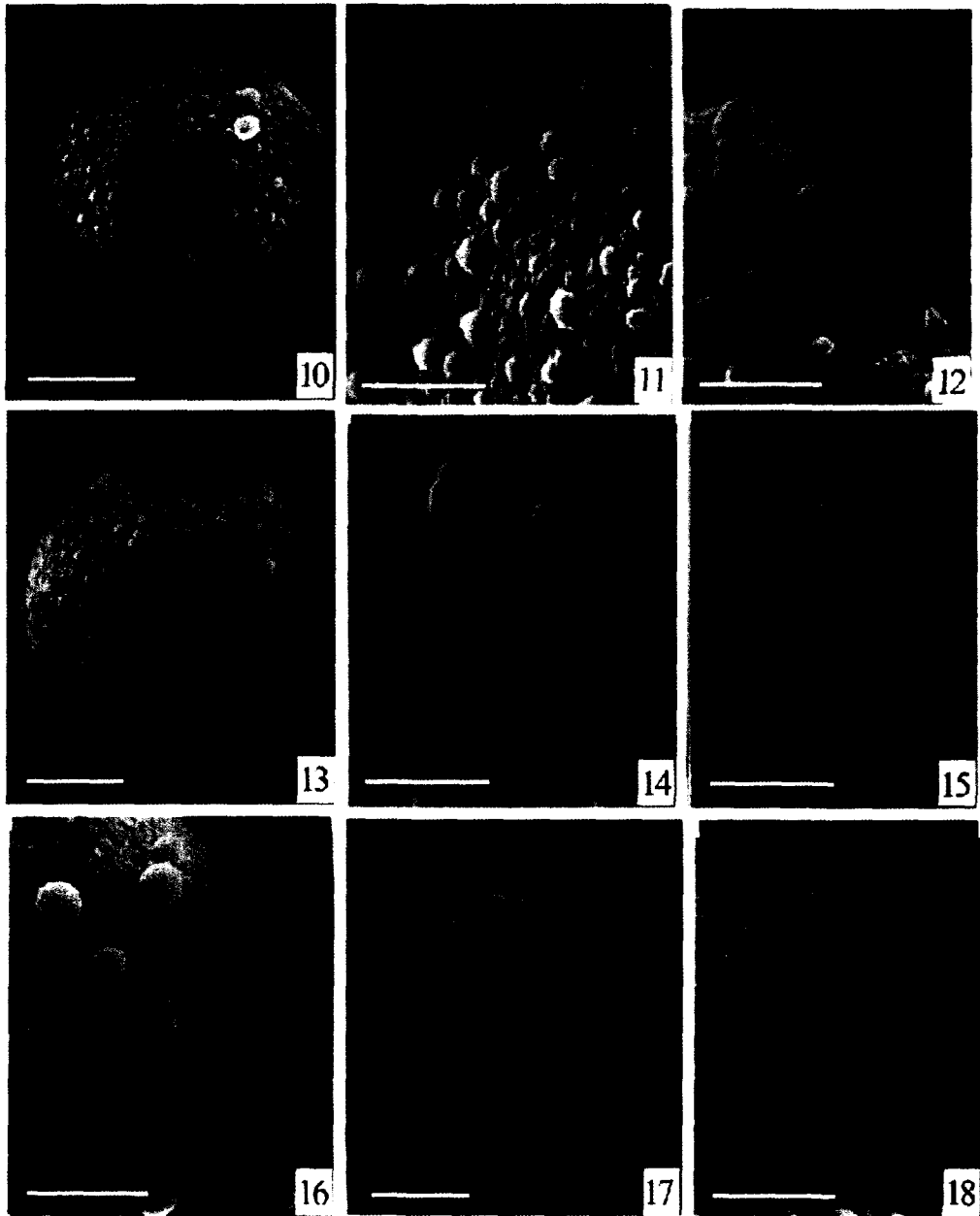


Plate II 10-11. *Mandragora caulescens*; 12. *Mandragora chinghaiensis*; 13-14. *Anisodus luridus*; 15-16. *Anisodus tanguticus*; 17-18. *Atropanthe sinensis*. 10; bar = 17.7 μ m; 11, 12, 14, 16, 18; bar = 20 μ m; 13, 17; bar = 16 μ m; 15; bar = 20 μ m.

The exine sculpture of *Anisodus* and *Scopolia* is tuberculate, but the pollen grains of *Anisodus* are nonaperturate or occasionally irregularly poroid (Hoare & Knapp, 1997), while in *Scopolia*, the pollen grains are 3-colpate or pantocolpate. Morphologically, the flowers of both genera are radial symmetrical, their stamens are equal in length and inserted at the base of the corolla tube, indicating that the two genera have a close relationship. *Anisodus*, however, is more primitive than *Scopolia*.

The nonaperturate and tuberculate exine pollen grains of *Scopolia carniolicoides* (Chang & Lu, 1984) are identical with the pollen grains of *Anisodus*, but different from other species of *Scopolia*. Data from pollens therefore support the incorporation of *S. carniolicoides* in *Anisodus* (D'Arcy & Zhang, 1992).

The 3-colpate apertures of *Atropanthe* are similar to those in some species of *Physochlaina*. But in *Atropanthe*, the colpi are long and converge in the polar area

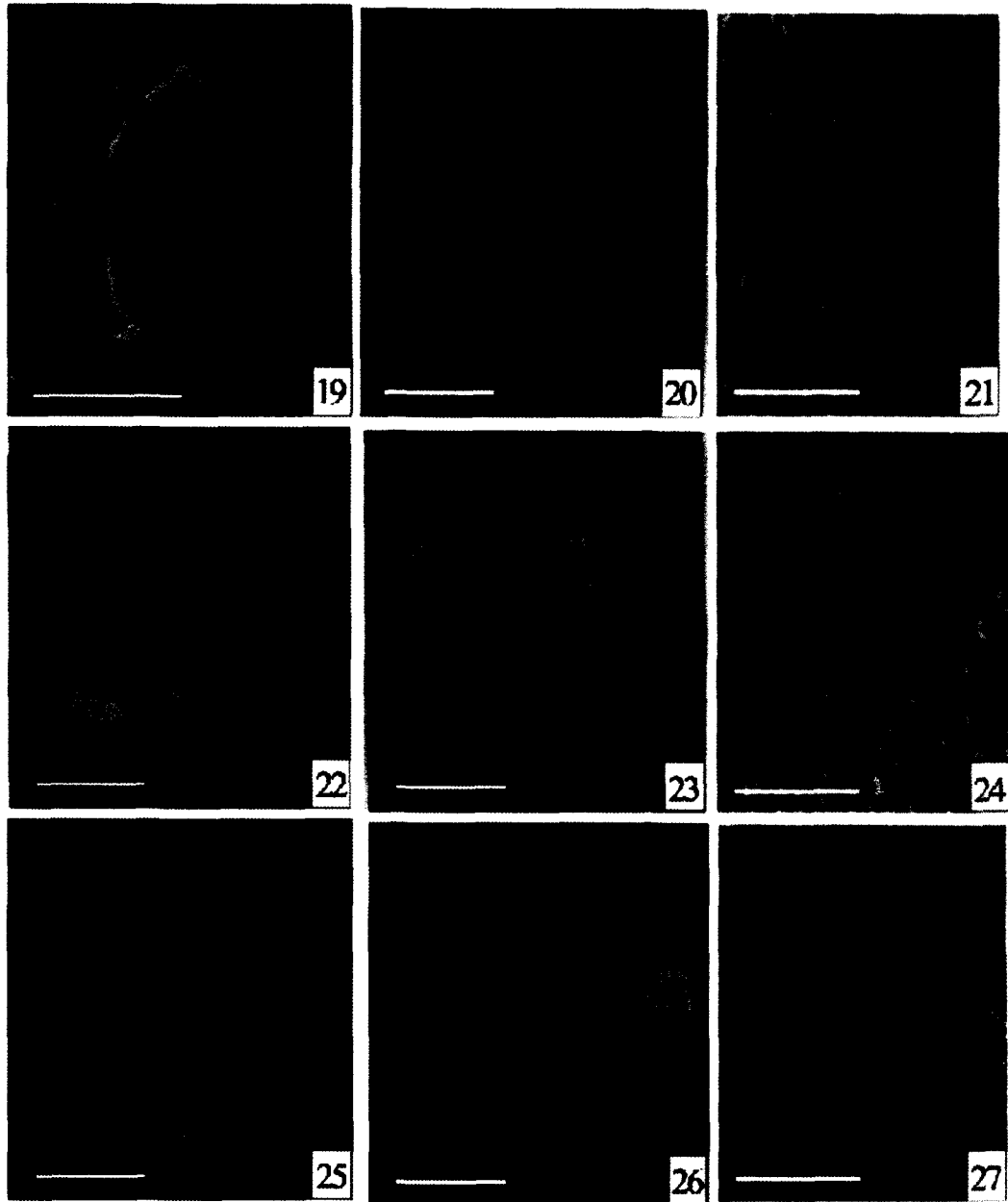


Plate III 19-21. *Physochlaina praealta*; 22-24. *Physochlaina physaloides*; 25-27. *Physochlaina infundibularis*.
19; bar=24 mm; 20, 22, 23, 25, 26; bar=17.7 mm; 21, 24, 27; bar=20 mm.

and the exine sculpture is curved striate, which is different from that of *Anisodus* and *Scopolia*. The flowers of *Atropanthe*, *Anisodus* and *Scopolia* are solitary, but in *Atropanthe* the corolla is distinctly zygomorphic and the stamens are unequal in length. Combined with characteristics of the pollen morphology, we considered the genus *Atropanthe* to be more advanced than *Anisodus* and *Scopolia*.

Przewalskia is quite different from other genera of

Hyoscyameae in morphological and palynological features. *Przewalskia* is endemic to Qinghai, Gansu, Sichuan and Xizang (Tibet) provinces, China, growing in cold, arid environments at 3 200—5 000 m. The axillary flowers are solitary or 2 or 3 together and pedunculate or not. The short stamens are adnate to the base of the corolla tube, not attached to the corolla throat. The aperture is 3-colporate, which is the same as in *Hyoscyamus*. The exine sculpture, however, is reticulate and dif-

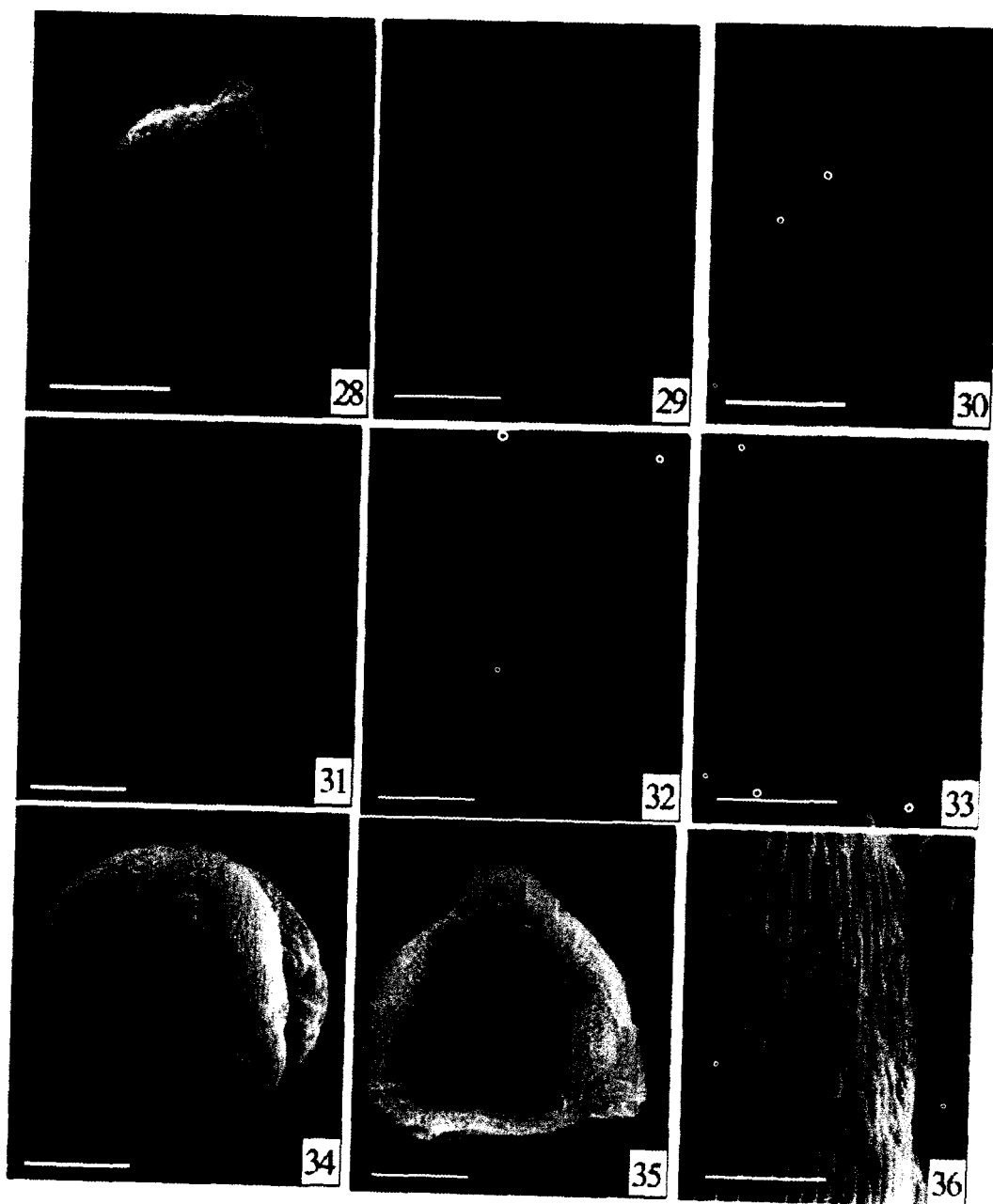


Plate IV 28-30. *Physochlaina capitata*; 31-33. *Hyoscyamus niger*; 34-36. *Hyoscyamus pusillus*. 28, bar=20 mm;
29, 34; bar=17.7 mm; 31, 32, 35; bar=16 mm; 30, 33, 36; bar=20 mm.

ferent from that of *Hyoscyamus*, which is striate. We considered *Przewalskia* to be a distinct, advanced taxon.

In *Hyoscyamus* the pollen grains are identically 3-colporate and with a variously striate, or occasionally finely reticulate exine sculpture. The differences in detail can be used for delineating species. Morphologically, the flowers are distinctly secund, sessile or subsessile, and the lower ones axillary and solitary with the upper ones forming a dense racemose or subscorpioid

cyme. The stamens are inserted near the middle of the corolla tube. *Hyoscyamus* can be considered rather advanced in these features.

The pollen grains of *Archihyoscyamus* are 3-colporate, the same as in *Hyoscyamus*, but the exine sculpture is striate, irregularly punctate among the striae and sparsely granular on surface of the striations. This obvious difference from *Hyoscyamus* supports the recognition of *Archihyoscyamus* (Lu, 1997).

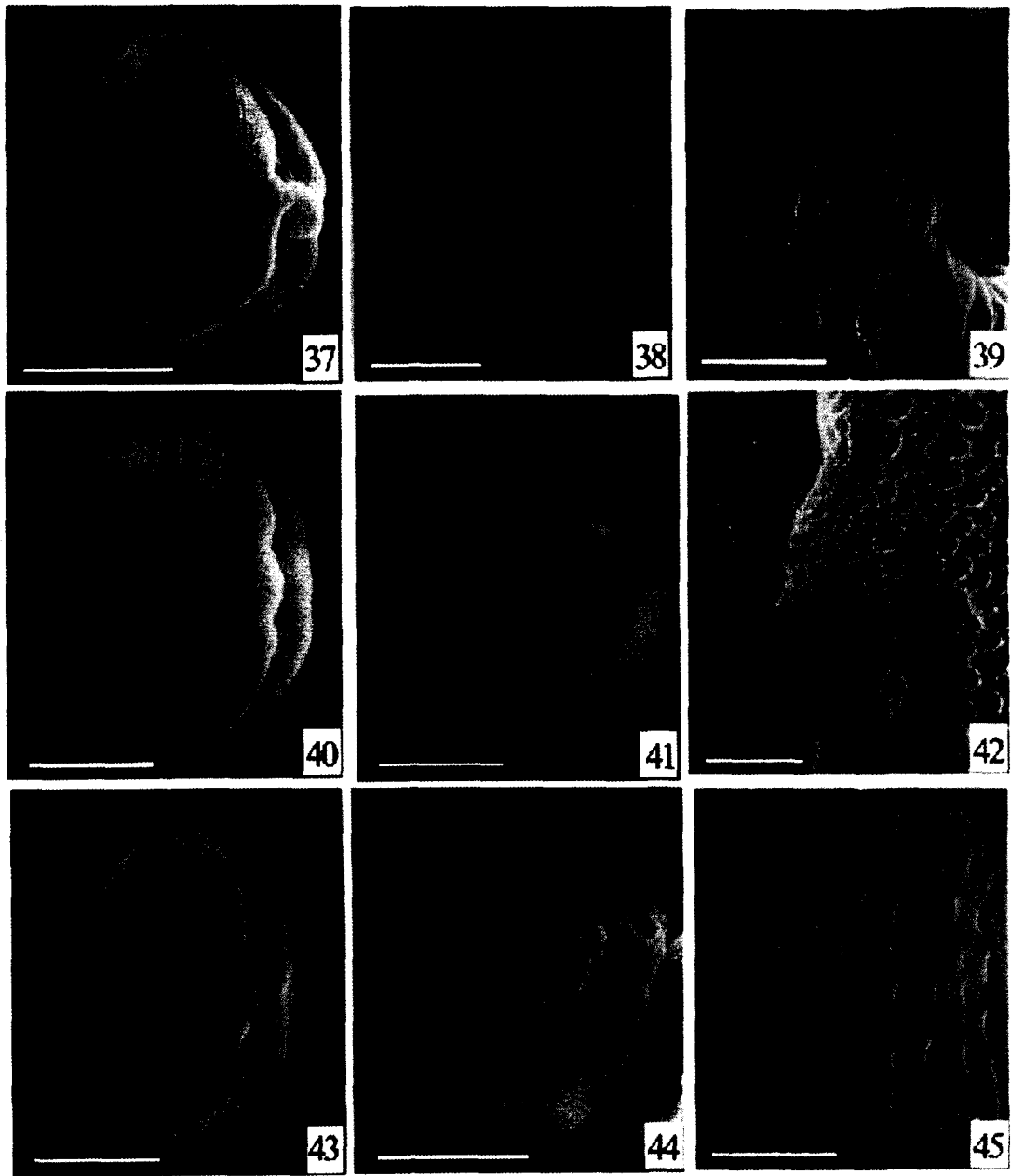


Plate V 37-39. *Hyoscyamus desertorum*; 40-42. *Hyoscyamus reticulatus*; 43-45. *Hyoscyamus aureus*. 37,44; bar=24 mm;
40,41,43; bar=20 mm; 38; bar=17.7 mm; 39,45; bar =20 mm; 42; bar=15.8 mm.

The apertures of *Physochlaina* are usually 3-colpate or 4-colpate. The exine sculpture is spinose or spinulate, and obviously different from other genera in the Hyoscyameae. In *P. praealta*, however, the apertures are 3-colporate and the exine sculpture is shortly striate, which is similar to that of *Hyoscyamus* and may indicate that *P. praealta* is transitional between *Physochlaina* and *Hyoscyamus*.

The pollen grains of *Atropa* are similar to that of

Hyoscyamus and supports treating it as a member of the Hyoscyameae. In *Mandragora*, the nonaperturate pollen is identical with *Anisodus*, but the exine sculpture is spinulate and tuberculate, which is different from *Anisodus*. In *Lycium*, the exine sculpture is striate, irregularly foveolate among the striae and irregularly granular at the bottom of the punctae. These features differ from members of the Hyoscyameae. *Lycium* therefore has a distant relationship with Hyoscyameae.

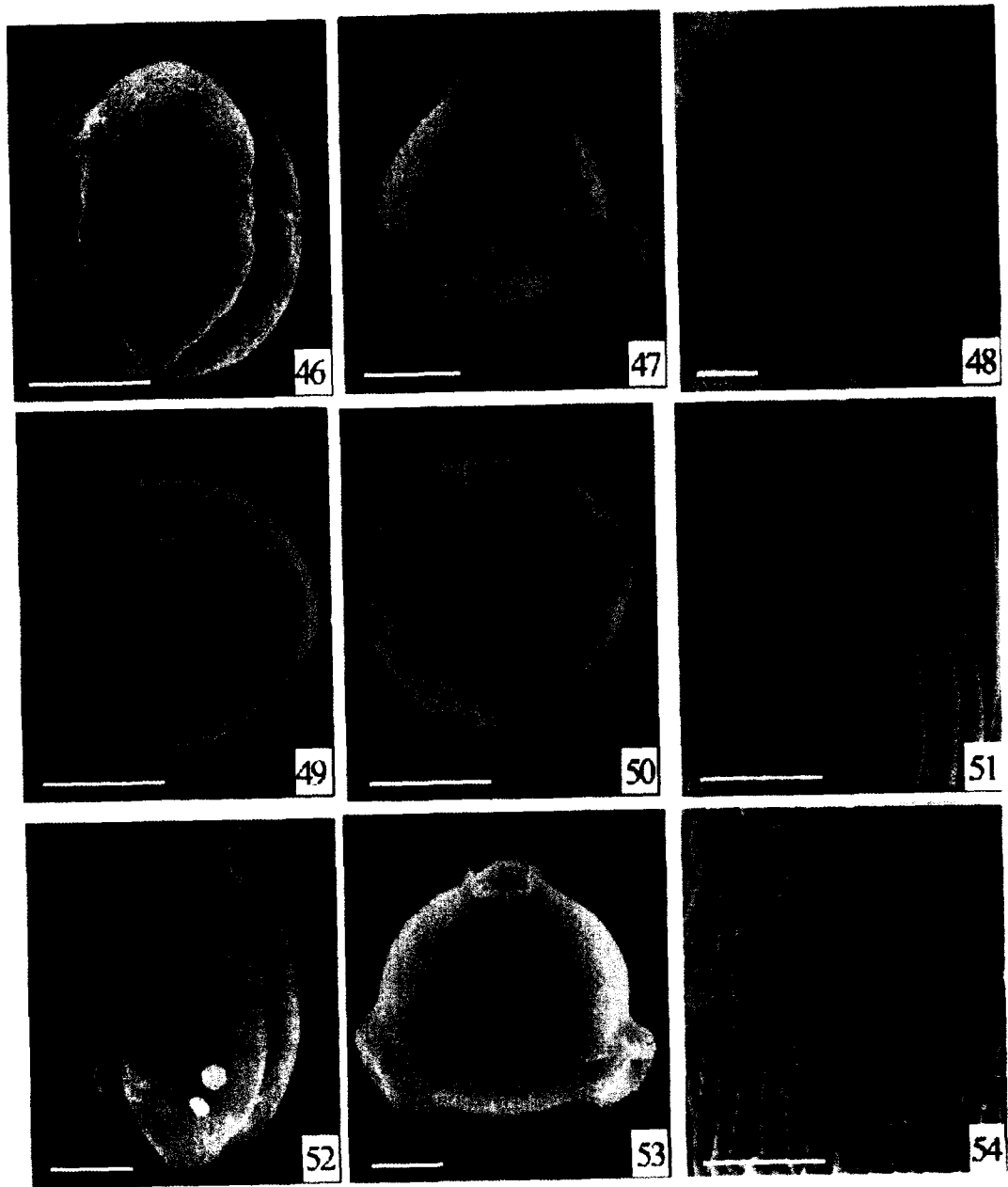


Plate VI 46-48. *Hyoscyamus albus*; 49-51. *Hyoscyamus senecionis*; 52-54. *Archihyoscyamus leptocalyx*. 46,49,50; bar=20 mm; 47; bar=16 mm; 52; bar=13.6 mm; 53; bar=12 mm; 48; bar=10 mm; 51,54; bar=20 mm.

Chang & Lu (1984) examined the pollen grains of 12 species in 6 genera in the subtribe Hyoscyameae. In the largest genus, *Hyoscyamus*, they only studied two species, making it difficult to determine the full extent of diversity and variation within the tribe. The present research found differences in the exine sculpture from the previous report by Chang & Lu (1984), details of which are given in table 2.

In the present study, the exine sculpture of *Atro-*

panthe sinensis is curved striate, while not shortly clavate. In *Physochlaina praealta*, the exine sculpture is shortly striate, not reticulate. In *P. physaloides*, the exine sculpture is densely spinose, not striate-reticulate. In *Hyoscyamus pusillus*, the exine sculpture is striate, not reticulate (Table 2). The differences may be due to the relatively few species studied by Chang & Lu (1984).

The evolutionary trend in the germination aperture of the pollen grains in the Hyoscyameae may be in the

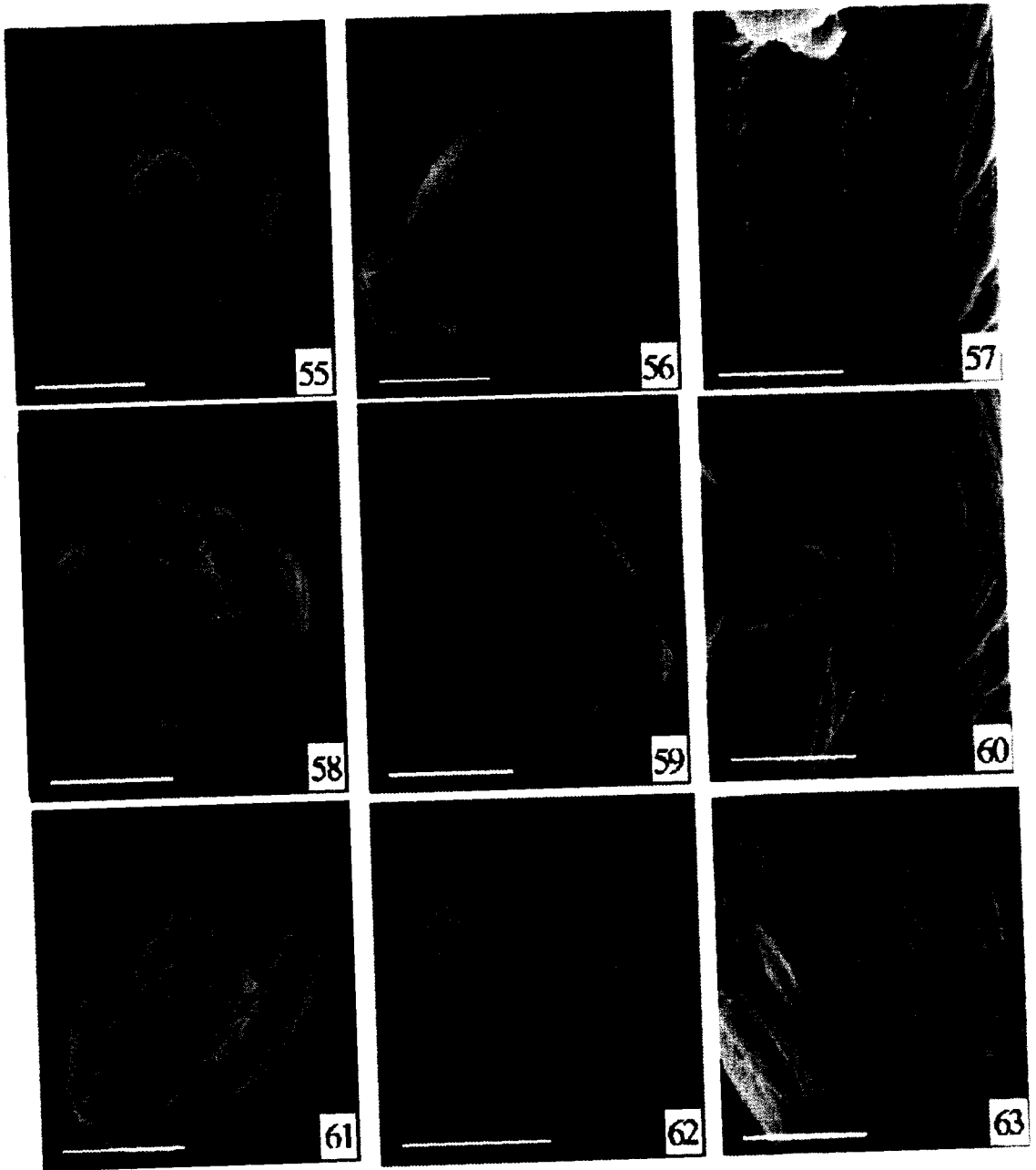


Plate VII 55-57. *Hyoscyamus bipinnatifidus*; 58-60. *Hyoscyamus muticus*; 61-63. *Lycium barbarum*. 55,56; bar=17.7 mm;
58,59,61; =20 mm; 62; bar=24 mm; 57,60,63; bar=20 mm.

direction from absence of germination aperture to presence of 3-or 4-colpate, to 3-colporate germination aperture. *Anisodus*, which has nonaperturate pollen grains, should be primitive, while genera with 3-colporate pollen grains, such as *Przewalskia* and *Hyoscyamus*, should be advanced. This evolutionary trend is basically consistent with the interpretation from morphology.

Appendix: List of taxa examined

1. *Scopolia japonica*

Japan; Honshu, T. Yahara *et al.*, 5936, 1980-04-26(PE)

2. *Anisodus luridus*

China; Cult. In Northwest-Plateau Inst. Bot. CAS, Lu Anming 01, 1974-07-28(PE)

3. *A. tanguticus*

The Netherlands; Cult in Bot. Gard. Nijmegen Univ. no. 96/124(NL) *

4. *Atropanthe sinensis*

The Netherlands; Cult in Bot. Gard. Nijmegen Univ. no. 891007 (NL)

5. *Przewalskia tangutica*

China; Sangxiang, Xizang, Fu Guoxun 184, 1960-06-6(PE)

6. *P. praealta*

China; Malashan, Xizang, Wu Zhengyi *et al.*, 75-456, 1975-07-0(PE)

Table 2 Differences in exine sculpture between this study and previous report by Chang & Lu (1984) in the tribe Hyoscyameae

Species	Exine sculpture (Chang & Lu, 1984)	Exine sculpture (present study)
<i>Atropanthe sinensis</i>	Irregularly shortly clavate	Curved striate
<i>Physochlaina praealta</i>	Reticulate	Shortly striate, occasionally punctate, striae indistinctly tuberculate
<i>P. physaloides</i>	Striate-reticulate	Rather densely spinose and irregularly foveolate or punctate
<i>Hyoscyamus pusillus</i>	Reticulate	Striate and sparsely punctate

7. *P. physaloides*

Mongolia; collecting place unknown, A. A. Hatob 17533, 1944(PE)

8. *Physochlaina infundibularis*

China; Huashan, Shaanxi, Yao Fuhan *et al.*, sine no. (PE)

9. *P. capitata*

China; Gongliu, Xinjiang, Zhou Taiyan *et al.*, 650279, 1965-05-10(PE)

10. *H. desertorum*

Collecting place and date unknown, H. Gombavlt 4983(P)

11. *Hyoscyamus pusillus*

China; Xinyuan, Xinjiang, collector unknown 69112-009, 1969-07-27(PE)

12. *H. bipinnaticase*

Iran; South part, Th. Kotschy sine no. 1842-06-10(P)

13. *H. muticus*

Iran; South part, R. F. Hohenacker 1845, 1842-03-13(P)

14. *H. seneciosis*

Iran; North part, J. Bornmuller 7648, 1902-06-08(P)

15. *Hyoscyamus aureus*

Cyprus; collector and no. unknown, 1880, date unknown(P)

16. *H. albus*

Syria; F. F. Maristed'ALEP en, collector unknown 1947, date unknown(P)

17. *H. niger*

China; Fukang, Xinjiang, collector unknown 4256, 1959-09-19(PE)

18. *H. reticulates*

Iran; East part, P. Sintenis, sine no. 1894, date unknown(P)

19. *Archihyoscyamus leptocalyx*

Kurdistan; P. Sintenis 1000, 1909-05-16(P)

20. *Atropa belladonna*

China; Cult. In Nanjing Bot. Garden, Yue Junsan 0358, 1954-06-05(PE)

21. *Mandragora caulescens*

China; Zhongdian, Yunnan, T. T. Yu 11327, 1937-05-17(PE)

22. *M. chinghaiensis*

China; Seda, Sichuan, collector unknown 06584(PE)

23. *Lycium barbarum*

China; Cult. In Bot. Gard. Inst. Bot. CAS, Zhang Zhiyun & Wen Jie 001, 2002-06-05(PE)

* NL; Botanical Garden, Nijmegen University, Nijmegen, Netherlands.

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