STUDIES OF THE POLLEN MORPHOLOGY AND TAXONOMY OF THE TRIBES LOTEAE AND CORONILLEAE (LEGUMINOSAE: PAPILIONOIDEAE) 1. ANTHYLLIS L. AND RELATED GENERA

M. J. Diez * & I. K. Ferguson **

* Departamento de Biologia Vegetal y Ecologia, Universidad de Sevilla, Apdo. 1095, 41080 Sevilla, Spain. ** The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, England

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Resumen. Se estudia la morfología del polen de 25 taxones con los microscopios óptico y electrónicos. El polen es 3, 4 (-5), 6 (-7) -zonocolporado, de contorno circular, elíptico o rectangular en visión ecuatorial, de tamaño pequeño a grande, $PxE = 20-60 \times 18-60$ µm. Los colpos son largos, las endoaberturas lalongadas. La ornamentación es psilada, a veces microperforada-fosulada. La endexina es gruesa, la base muy delgada o ausente, el infratéctum más o menos granular o con columelas muy cortas ampliamente esparcidas. Se han reconocido cuatro tipos y cuatro subtipos. Los caracteres básicos para la diferenciación en tipos son el número de aberturas, el tamaño y la forma. Los tipos polínicos se corresponden bastante bien con muchos de los géneros segregados de *Antbyllis* y se discute la morfología polínica en relación con la compleja taxonomía del grupo.

Summary. The pollen morphology of 25 taxa has been studied with light and electron microscopy. The pollen is 3, 4, (-5) or 6 (-7)-zonocolporate, circular, elliptical or rectangular in equatorial outline, small to quite large in size, $P \ge 2 - 20-60 \ge 18-60 \mu m$. The colpi are long, the endoapertures lalongate. The ornamentation is psilate, sometimes microperforate-fossulate. The endexine is thick, the foot layer very thin or absent, the infratectum is more or less granular or with very short, widely spaced columellae. Four pollen types and four subtypes are recognised. The primary basis for division into types is aperture number, pollen size and shape. The pollen types correspond well with many of the genera segregated from Anthyllis and pollen morphology is discussed in relation to the very complex taxonomy of the group.

INTRODUCTION

The tribes *Loteae* and *Coronilleae* have always been regarded as being very closely related, and POLHILL (1981) has suggested that there is no practical reason why these should not be amalgamated. However, he cites some evidence,

including a pollen morphological study by FERGUSON & SKVARLA (1981) based on a very small number of pollen samples, that there may be differences to justify a full reappraisal of the tribes and their relationships.

The taxonomy of the genera within the tribes is extremely complicated, authors adopting a variety of approaches, some a broad concept of the genera, while others recognise a large number of segregates. Floristic treatments covering limited geographical areas including, for example, BALL (1968), BALL & CHRTKOVA-ZERTOVA (1968), CULLEN (1968, 1976), MEIKLE (1977) and MUNZ & KECK (1959) have unfortunately not fully addressed the problems of generic limits throughout the entire range of both genera and species. The most obvious problems occur within the genus *Lotus* L. but similar difficulties are present in *Coronilla* L. and *Anthyllis* L. and its related genera.

CULLEN (1968), in his treatment of Anthyllis, adopted a broad circumscription while he retained Cytisopsis Jaub. & Spach, and Hymenocarpos Savi as distinct monotypic genera. MEIKLE (1977) recognised Physanthyllis Boiss. as a distinct genus from Anthyllis. While POLHILL (1981) recognised Cytisopsis and was uncertain of the status of Lyauteya Maire, he suggested both perhaps should be included in Anthyllis. He followed CULLEN (1968), including Cornicina Boiss., Dorycnopsis Boiss. and Physanthyllis in Anthyllis and regarded Hymenocarpos as a monotypic genus. More recently, while reviewing the group for the Med. Checklist, LASSEN (1986, 1987) has shown that Tripodion Medikus is an earlier name for Physanthyllis and recognised three species in Tripodion. He considered the three species of Anthyllis which comprised the segregate genus Cornicina as congeneric with Hymenocarpos, the latter genus now containing four species. LASSEN places Lyauteya in Cytisopsis now with two species and segregates a monotypic Dorycnopsis.

Although there has been considerable work carried out on the macromorphology and micromorphology of genera in the tribe, particularly *Lotus*, as for example vegetative characters and seedlings DORMER (1945, 1946), cytology LARSEN (1955, 1956), GRANT (1965), VIOQUE & PASTOR (1990), and biosystematics ZANDSTRA & GRANT (1968), GRANT & ZANDSTRA (1968), HEYN (1970), very little attention has been paid to pollen morphology. OHASHI (1971) has studied the taxonomy and pollen morphology of a widely interpreted tribe *Coronilleae*. Otherwise the pollen of only a small number of species have been described in regional pollen floras or as part of more general surveys of the family. These include for example HUANG (1968), AYTUG & al. (1971), FAEGRI & IVERSEN (1975), DOMÍNGUEZ & al. (1984) and LECUONA & al. (1987). FERGUSON & SKVARLA (1981) illustrated with scanning and transmission electron microscopy the pollen of *Hymenocarpos* and the exine stratification of one species of *Lotus* (FERGUSON & SKVARLA, 1983).

The most extensive treatment of the pollen of the group is by FERNÁNDEZ (1987) where in a study of the *Fabaceae* for the pollen atlas of western Andalusia some 7 genera and 35 species of *Loteae* and *Coronilleae* are described. Of particular importance to the present investigation are 6 species of *Anthyllis* which are placed in 4 different pollen types: (1) *A. hamosa* with 4 apertures, (2) *A. cornicina* and *A. lotoides* with 6 apertures, (3) *A. podocephala* (polycephala) and *A. vulneraria* with 3 apertures and psilate tectum, and (4) *A. cytisoides* and *A. gerardii* with 3 apertures and fossulate tectum.

The purpose of the present study is first to see if the pollen morphology can provide additional evidence for the delimitation of the genus *Anthyllis* and related genera. Later papers will complete the review of genera in the two tribes and will try to see if the pollen morphology can help to clarify the relationships between the *Loteae* and *Coronilleae* and the affinities of these tribes within the subfamily *Papilionoideae*.

MATERIAL AND METHODS

Pollen material was obtained from the Herbarium, Department of Botany, Faculty of Biology, University of Sevilla (SEV) and the Herbarium, Royal Botanic Gardens, Kew (K), or directly in the field, where it was fixed in glacial acetic acid; voucher specimens are in SEV. Details of specimens examined are given in the Appendix.

The pollen was acetolysed in the standard way (ERDTMAN, 1960). However, the pollen grains often were found to disintegrate when using conventional techniques, especially *Anthyllis tetraphylla*. Much less breakage was found to occur if the proportion of acetic anhydride to sulphuric acid was increased to 18:1.

For light microscopy (LM) slides were prepared by mounting the pollen in glycerol jelly. Twenty measurements of pollen grains (P and E) were made from each specimen. The measurements shown in Table 1 represent the mean and range of all the samples examined of each taxon. Fewer measurements were made of the other characters. Some specimens were studied with scanning electron microscopy (SEM) and transmission electron microscopy (TEM) only and these are indicated in the Appendix. For SEM, pollen was air dried on specimen stubs from 95% ethanol and examined with a Jeol T-100 SEM. For TEM the acetolysed exines were fixed with 2% osmium tetroxide, pre-stained with uranyl acetate and embedded in Epon-araldite (SKVARLA, 1966; SKVARLA & PYLE, 1968). Sections were cut with a diamond knife and post-stained with uranyl acetate and Reynold's lead citrate and examined with a Hitachi H300 TEM.

Types and Taxa	APERT. N ^o	POLAR AXIS	EQUATORIAL AXIS	P/E
Туре I				
Anthyllis cornicina	6	23(25,60)27	22(23,06)26	0,96(1,08)1,17
Anthyllis lotoides	6	21(23,13)26	18(20,06)22	1,00(1,15)1,36
Hymenocarpos circinnatus	(6-)7	23(27,05)34	0,82(1,00)1,13	
Type II				
Anthyllis barba-jovis	4	20(23,22)26	20(23,75)33	0,84(0,97)1,15
Anthyllis hamosa	4(-5)	24(25,85)31	24(28,43)33	0,75(0,86)1,12
Anthyllis henoniana	4	24(27,87)33	20(24,72)28	0,96(1,12)1,28
Anthyllis hermanniae	4	20(23,82)28	20(23,13)27	0,88(1,02)1,18
Anthyllis montana				
subsp. hispanica	4(-5)	28(32,00)34	25(27,26)33	0,96(1,09)1,13
subsp. jacquinii	4	22(26,83)30	21(24,40)26	1,00(1,09)1,20
subsp. montana	4	25(29,26)32	24(26,83)30	0,96(1,09)1,16
Type III				
Anthyllis tetraphylla	3(-4)	48(54,58)60	50856,58)60	0,85(0,96)1,00
Hammatolobium kremerianum	3	33(36,81)41	34(40,12)45	0,79(0,92)1,08
Hammatolobium lotoides	3	30(35,72)40)	30(34,03)37	0,91(1,04)1,18

Type IV

Subtype IVa				
Anthyllis gerardii	3	21(23,62)26	21(22,55)26	0,95(1,04)1,18
Subtype IVb				
Cytisopsis dorycniifolia	3	30(33,25)36	29(30,60)34	1,00(1,08)1,20
Cytisopsis ahmedii	3	27(30,42)32	23(26,38)28	1,07(1,51)1,23
Sybtype IVc				
Anthyllis cherleri	3 .	31(37,86)41	26(31,40)34	1,11(1,20)1,33
Anthyllis polycephala	3	30(32,64)35	26(29,02)32	1,00(1,12)1,25
Anthyllis ramburii	3	24(26,33)28	23(24,26)27	0,96(1,08)1,17
Anthyllis tejedensis	3	30(35,74)42	28(33,49)38	0,96(1,06)1,20
Anthyllis vulneraria				
subsp. maura	3	37(36,60)43	26(33,09)35	1,05(1,19)1,36
subsp. vulneraria	3	31(35,43)40	26(30,95)36	1,02(1,14)1,25
Subtype IVd				
Anthyllis aurea	3	26(29,40)32	26(27,70)30	1,00(1,05)1,19
Anthyllis cytisoides	3	27(29,77)35	20(26,92)32	0,93(1,11)1,50
Anthyllis terniflora	3	24(27,55)32	20(26,11)30	1,00(1,05)1,23

Table I.- Showing taxa examined arranged in pollen types, with aperture number, measurements (µm) of the mean and ranges for the polar (P) and equatorial (E) axes and the shape index P/E.

The nomenclature used throughout the text generally follows TUTIN & al. (1968). The more recent changes proposed by GREUTER & al. (1989) are shown in the list of the specimens examined.

RESULTS

The pollen of *Anthyllis* and related genera is characterised primarily by a usually psilate tectum and an exine stratification with a thick endexine strongly lamellated at the apertures, foot layer absent or very fragmentary, a thin infratectum of short columellae or granular processes which are usually widely spaced and thick, almost complete tectum.

There is variation in size, shape, aperture number, presence of pseudocolpi, and in infratectum. These differences form the basis for the division of the pollen into 4 types with 4 subtypes.

1. Pollen with 6(-7) apertures	Type I
1. With fewer than 6 apertures	2
2. With 4(-5) apertures	Type II
2. With 3 apertures	
3. Infratectum with spaced granules; $P = 30-60 \ \mu m \ \dots \dots$	Type III
3. Infratectum with more or less short columellae or almost absent	;
$P = 21-43 \ \mu m$	Type IV (4)
4. Rectangular in equatorial outline	5
4. Elliptical in equatorial outline	6
5. $P = 21-25 \ \mu m \dots S$	ubtype IVa
5. $P = 27-36 \ \mu m$	ubtype IVb
6. Pseudocolpi present; infratectum almost absentS	ubtype IVc
6. Pseudocolpi absent; infratectum clearly columellate Se	ubtype IVd

TYPE I

Species included: Anthyllis cornicina, A. lotoides and Hymenocarpos circinnatus (Figs. 1-8).

Figs. 1-14. Scale bar on Fig. 14 provides the scale for all micrographs on this plate. Figs. 1-2, Anthyllis cornicina, PhMG, scale bar - 10.5 μ m. 1, outline in equatorial view. 2, outline in polar view. Figs. 3-4, Hymenocarpos circinnatus, PhMG, scale bar = 10.5 μ m. 3, outline in equatorial view showing the fused endoapertures. 4, outline in polar view. Figs. 5-7, Anthyllis lotoides. 5, equatorial view, SEMG, scale bar = 5 μ m. 6, showing detail of aperture and psilate finely perforate tectum, SEMG, scale bar = 1.25 μ m. 7, exine stratification at the apertural area, TEMG, scale bar = 1.5 μ m. Fig. 8, Hymenocarpos circinnatus, exine stratification near the apertural area, TEMG, scale bar = 0.5 μ m. Figs. 9-10, Anthyllis montana, PhMG, scale bar = 10,5 μ m. 9: outline in equatorial view. 10: outline in equatorial view. Figs. 9-12, Anthyllis barba-jovis, SEMG. 11: showing detail of aperture and psilate tectum, scale bar = 2,5 μ m. 12: equatorial view, scale bar = 5,5 μ m. Fig. 13, Anthyllis hamosa, exine stratification in the mesocolpium, TEMG, scale bar = 0,5 μ m.



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Pollen 6 (-7)-zonocolporate, elliptical or rectangular-elliptical in equatorial outline and circular or hexagonal angulaperturate in polar outline; P/E = 0.82-1.36; $P \ge 21-32 \ge 18-34 \ \mu\text{m}$. Endoapertures almost fused or fused (zonorate). Exine 1.5-2 μ m thick at the mesocolpium, thinner at the poles, foot layer absent, infratectum with widely spaced columellae and granules and a thick tectum. Ornamentation psilate, finely perforate.

Hymenocarpos circinnatus shows some small differences from the other two species: it is rectangular-elliptical in equatorial outline, hexagonal in polar outline and has a thicker exine, 2-2.5 μ m.

TYPE II

Species included: Anthyllis barba-jovis, A. hamosa, A. henoniana, A. hermanniae and A. montana subsp. hispanica, subsp. jacquinii and subsp. montana (Figs. 9-14)

Pollen 4(-5)-zonocolporate, more or less elliptical in equatorial outline and quadrangular angulaperturate in polar outline; P/E = 0.75-1.28; P x E = 20-33 x 20-34 μ m. Endoapertures rectangular with or without constriction, or X-shaped, of 3-7 x 6-11 μ m. Exine 1-2.5 μ m thick at the mesocolpium with a thick endexine, thinner at the poles or uniform and lamellate in the apertural area, foot layer very thin, sometimes discontinuous or rarely reduced and a very thick tectum. Ornamentation psilate, finely perforate and fossulate.

A. hamosa shows some small differences from the other species: the foot layer is very reduced and the infratectum has widely spaced columellae.

TYPE III

Species included: Anthyllis tetraphylla, Hammatolobium kremerianum and H. lotoides (Figs. 15-26)

Pollen 3(-4)-zonocolporate (colporoidate), more or less circular in equatorial outline and triangular angulaperturate in polar outline; P/E = 0.79-1.18; P x E = 30-60 x 30-60 μ m. Endoapertures X-shaped or not clearly delimited. Exine

Figs. 15-26.. Scale bar on Fig. 26 provides the scale for all micrographs on this plate. Figs. 15-19, Anthyllis tetraphylla. 15: outline in equatorial view, PhMG, scale bar = 10 μ m. 16: polar view, SEMG, scale bar = 16 μ m. 17: showing exine stratification at the apertural area, TEMG, scale bar = 3,5 μ m. 18: detail of ornamentation in aperture area, SEMG, scale bar = 2,5 μ m. 19: showing exine stratification in the mesocolpium, TEMG, scale bar = 0,7 μ m. Figs. 20-23, 25-26, Hammatolobium lotoides. 20: outline in equatorial view, PhMG, scale bar = 10,5 μ m. 21: showing aperture and aperture membrane, PhMG, scale bar = 10,5 μ m. 22: outline in polar view, PhMG, scale bar = 10,5 μ m. 23: polar view, SEMG, scale bar = 10 μ m. 25: showing exine stratification at the apertural area, TEMG, scale bar = 2,5 μ m. 26: showing exine stratification at the mesocolpium, TEMG, scale bar = 1 μ m. Fig. 24, Hammatolobium kremerianum showing detail of ornamentation at aperture, SEMG, scale bar = 4 μ m.

2-3 μ m thick at the mesocolpium, with a thick endexine, in which two very different layers are differentiated in *A. tetraphylla*, one very thin and with a low electron density and the other thick and electron dense (this may be due to an artifact of staining); in the apertural area the endexine appears lamellated or stratified with a number of layers; foot layer very thin, infratectum with spaced granules and a very thick tectum. Ornamentation psilate, perforate.

A. tetraphylla has bigger pollen grains than the other species: $P \ge E = 48-60 \ge 50-60 \ \mu m$.

TYPE IV.

Subtype IVa

Species included: Anthyllis gerardii (Figs. 27-33)

Pollen 3-zonocolporate, rectangular in equatorial outline and triangular angulaperturate in polar outline; P/E = 0.95-1.18; $P \ge 21-26 \ge 22-25 \ \mu m$. Endoapertures rectangular, of 4-7 $\ge 7-11 \ \mu m$. Exine 1.5-2 μm thick at the mesocolpium, with a thick endexine, more or less lamellated in the apertural area, foot layer absent, short columellae and granules and thick tectum. Ornamentation psilate, perforate and fossulate.

Subtype IVb

Species included: Cytisopsis ahmedii and C. dorycnifolia (Figs. 34-40)

Pollen 3-zonocolporate, more or less rectangular in equatorial outline and subtriangular in polar outline; P/E = 1.00-1.20; P x E = 27-36 x 23-34 μ m. Endoapertures X-shaped, thinning parallel to the colpi, more or less constricted in the median area, of 8-19 x 10-12 μ m. Exine c. 2 μ m thick at the poles; the ectexine is thick and the endexine reduced; endexine thick near the apertures, more or less lamellate in the apertural area, foot layer absent, short columellae and granules and thick tectum. Ornamentation psilate, fossulate.

Figs. 27-40. Scale bar on Fig. 40 provides the scale for all micrographs on this plate. Figs. 27-33, Anthyllis genardii. 27: equatorial view, PhMG, scale bar = 10,5 μ m. 28: equatorial view showing costae, PhMG, scale bar = 10,5 μ m. 29: equatorial view showing endoaperture, PhMG, scale bar = 10,5 μ m. 30: polar view, PhMG, scale bar = 10,5 μ m. 31: equatorial view, SEMG, scale bar = 6 μ m. 32: showing exine stratification at apertural area, TEMG, scale bar = 3,5 μ m. 33: showing exiequatorial view, PhMG, scale bar = 0,7 μ m. Figs. 34-40, Cynsopsis dorycnifolia. 34: equatorial view, PhMG, scale bar = 10,5 μ m. 35: equatorial view showing endoaperture, PhMG, scale bar = 10,5 μ m. 36: polar view, PhMG, scale bar = 0,5 μ m. 37: equatorial view, SEMG, scale bar = 13,5 μ m. 38: showing detail of ornamentation, SEMG, scale bar = 7,5 μ m. 39: showing exine stratification adjacent to apertural area, TEMG, scale bar = 1 μ m. 40: showing exine stratification at mesocolpium, TEMG, scale bar = 0,35 μ m.





Subtype IVc

Species included: Anthyllis cherleri, A. polycephala, A. ramburii, A. tejedensis and A. vulneraria subsp. maura and subsp. vulneraria (Figs. 41-46)

Pollen 3-zonocolporate, elliptical, more or less circular in equatorial outline, and triangular angulaperturate in polar outline; P/E = 0.96-1.36; $P \ge 24-42 \ge 23-38 \ \mu\text{m}$. Endoapertures X-shaped, sometimes rectangular constricted (*A. cherleri*), of 4-10 x 8-14 μ m, with pseudocolpial ridge. Exine 1-2 μ m thick at the mesocolpium, with a thick endexine, foot layer absent, infratectum very reduced, almost absent and a very thick tectum. Ornamentation psilate, finely perforate.

Subtype IVd

Species included: Anthyllis aurea, A. cytisoides and A. terniflora (Figs. 47-52) Pollen 3-zonocolporate, elliptical, more or less circular in equatorial outline and triangular angulaperturate or subcircular in polar outline; P/E = 0.93-1.50; P x E = 24-35 x 20-32 μ m. Endoapertures more or less rectangular and X-shaped, of 5-10 x 5-15 μ m. Exine 1-2.5 μ m thick at the mesocolpium, with a thick endexine, thinner at the poles, foot layer absent, infratectum with spaced columellae at the poles and a thick tectum. Ornamentation psilate, perforate or finely fossulate.

DISCUSSION

Pollen Type I contains Hymenocarpos circinnatum from the eastern Mediterranean and two Iberian species placed by CULLEN (1968) in Anthyllis but segregated by other workers as part of the genus Cornicina. All three species fall within LASSEN'S (1987) recent circumscription of Hymenocarpos. Pollen morphology provides additional support from Lassen's rearrangement based primarily on floral characters. It is noteworthy that pollen morphological characters appear to be correlated with floral morphology and do not reflect the very distinctive fruit morphology of H. circinnatus. These results perhaps parallel the very diverse fruit morphology but relatively little variation in pollen morphology found in Medicago L. (SMALL & al. 1982).

Figs. 41-52. Scale bar on Fig. 51 provides the scale for all micrographs on this plate. Figs. 41-46, Antbyllis vulneraria. 41: equatorial view, PhMG, scale bar = 10,5 μ m. 42: equatorial view showing endoaperture, PhMG, scale bar = 10,5 μ m. 43: polar view, PhMG, scale bar = 10,5 μ m. 44: equatorial view, SEMG, scale bar = 14 μ m. 45: showing detail of ornamentation, SEMG, scale bar = 2,5 μ m. 46: showing exine stratification at apertural area, TEMG, scale bar = 1,5 μ m. Figs. 47-51, Antbylis cytisoides. 47: equatorial view, PhMG, scale bar = 10,5 μ m. 48: polar view, PhMG, scale bar = 9 μ m. 49: equatorial view, SEMG, scale bar = 14 μ m. 50: showing exine stratification at mesocolpium, TEMG, scale bar = 1 μ m. 52: showing exine stratification at poles, TEMG, scale bar = 1 μ m. Fig. 49, Antbyllis terniflora showing detail of exine ornamentation, SEMG, scale bar = 2,5 μ m.

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Pollen Type II with 4(-5) apertures is comprised of species of woody perennials or small shrubs and shows pollen which reflects the macromorphological relationships. However, *Anthyllis hamosa* is also placed in this Type and is the third species of *Anthyllis* segregated into *Cornicina* and now placed by LASSEN (1987) in *Hymenocarpos*. Why *A. hamosa* has different pollen from the species in Type I is not clear but this perhaps reflects the complexity of the macromorphology in the whole group and the very close relationships between the genera.

Anthyllis tetraphylla placed in pollen Type III has rather large pollen grains compared with the rest of the tribe. This species is distinguished from other species in the genus by its two-seeded legume constricted between the seeds, has been segregated as the genus *Physanthyllis*. However, as mentioned above, LASSEN (1986) has shown that *Tripodion* is an earlier name and he placed two other species, *Hammatolobium lotoides* and *Hammatolobium kremerianum*, together with *A. tetraphylla* in the genus *Tripodion*. Although the pollen of these *Hammatolobium* species is smaller in size than *A. tetraphylla* it has a similar psilate tectum and exine stratification. Thus pollen data appears to provide some additional evidence to support Lassen's treatment and POLHILL's (1981) statement that *Hammatolobium* "is seemingly closer to *Anthyllis* and *Lotus* than to *Coronilla*". Our preliminary data on the pollen of *Coronilla* would tend to support this view.

Anthyllis tetraphylla has comparatively larger pollen compared with that of most other species of Loteae examined. It is noteworthy that this species is one of the very few members of the tribe with a base chromosome number of n=8 (GOLDBLATT, 1981; VIOQUE & PASTOR, 1990). The base chromosome number of the tribe is n=6 or 7 (GOLDBLATT, 1981). Hymenocarpos circinnatus so far being the only other taxon with n=8. There is a correlation between chromosome number and pollen grain size in some groups although often the correlation is between pollen size and amount of DNA in the cells (KESSLER & LARSEN, 1969; LAWRENCE, 1986; BENNETT, 1987).

Four subtypes are recognised in Type IV which is characterised by having pollen with three apertures and being small to medium in size. Subtypes IVa and IVb have small rectangular pollen in equatorial outline but differ in size and exine stratification. Subtype IVa is comprised of *Anthyllis gerardii* segregated as the monotypic genus *Dorycnopsis* by GREUTER & al. (1989) and the small pollen differences add support to the distinctness of the species. *Cytisopsis dorycnifolia* and *C. ahmedii* (*Lyauteya ahmedii*) comprise subtype IVb and here also pollen morphology provides supporting evidence for LASSEN (1986) who regards *Lyauteya* and *Cytisopsis* as congeneric. The Anthyllis vulneraria aggregate, together with a number of closely related species from southern Spain, are grouped together in subtype IVc with pollen with distinctive pseudocolpi and a reduced infratectum.

Subtype IVd contains the closely related western Mediterranean shrubby A. cytisoides and A. terniflora together with the perennial Balkan A. aurea. There does not seem to be macromorphological evidence to support the grouping by pollen characters of A. aurea with the other species in the subtype.

Pollen morphology contributes some useful information about the very complex taxonomic relationships between *Anthyllis* and its segregates. In general the results of this study agree quite well with the recent rearrangements and proposals made by LASSEN (1986, 1987) and GREUTER & al. (1989). However, it must be emphasized that some of the differences in pollen morphology, especially those used to separate some of the pollen subtypes, are relatively small and thus perhaps serve to reinforce the problems of clearly defining groups, at least around *Anthyllis*, in the tribes *Loteae* and *Coronilleae*.

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APPENDIX

Specimens examined:

Anthyllis aurea Host. GREECE, Grey-Wilson, 50 (K)

- Anthyllis barba-jovis L. ITALY, Baccari & al., 463 (K); Lester-Garland, s.n. (K)
- Anthyllis cornicina L. (– Cornicina loeflingii Boiss.; Hymenocarpos cornicina (L.) Lassen). SPAIN, Cabezudo (SEV 26828); Bourgeau, 2161 (K) TEM
- Anthyllis cytisoides L. MOROCCO, Wilczetetal, 759 (K) TEM. SPAIN, Aparicio (SEV 53690); Ruíz de Clavijo (SEV 29239); Galiano & al. (SEV 22023)

Anthyllis cherleri Bruger. SWITZERLAND, Sulger Buel (SEV 43936)

- Anthyllis gerardii L. (– Dorycnopsis gerardii (L.) Boiss.). MAURITANIA, Webb, s.n. (K); SPAIN, Rivera (SEV 46530); Rivera (SEV 46524); Galiano & al. (SEV 46124)
- Anthyllis hamosa Desf. (- Cornicina hamosa (Desf.) Boiss.; Hymenocarpos hamosus (Desf.) Lassen). SPAIN, Cabezudo, Silvestre & Valdés (SEV 34997); Rivas & al. (SEV 59118); Rivas, Bellot & Borja, s.n. (K)
- Anthyllis benoniana Batt. SPAIN, López & Valdés Bermejo (SEV 38708); Borja (SEV 1628); Alcaraz (SEV 73028)
- Anthyllis bermanniae L. GREECE, Stamatiadhon (SEV 22770); Polunin (SEV 29059). Cor-SICA, Lambinon & Duvigneaud (SEV 51622)

- Anthyllis lotoides L. (– Cornicina lotoides (L.) Boiss.; Hymenocarpos hispanicus Lassen). SPAIN, Devesa (SEV 32613); Rivera (SEV 46504); Cabezudo, Talavera & Valdés (SEV 22057); Brummitt & Ernst 5819 (K) SEM
- Anthyllis montana L. subsp. hispanica (Degen & Hervier) Cullen. Spain, Segura Zubizarreta (SEV 87490); Caballero, s.n. (K) SEM and TEM
- Anthyllis montana L. subsp. jacquinii (A. Kerner) Hayek. YUGOSLAVIA, Feoli Chiopella & Grostogilini (SEV 51629); Publer, s.n. (K) SEM and TEM
- Anthyllis montana L. subsp. montana. FRANCE, Stork (SEV 28583); Bordère, s.n. (K) TEM
- Anthyllis polycephala Desf. SPAIN, Aparicio (SEV 53694); Aparicio (SEV 53697); Diez, Pastor & Valdés (SEV 67806)
- Anthyllis ramburii Boiss. SPAIN, Hernández (SEV 79364)
- Anthyllis tejedensis Boiss. SPAIN, Asensi & Diez (SEV 108517); Molesworth Allen (SEV 90307)
- Anthyllis terniflora (Lag.) Pau. SPAIN, García, Luque & Valdés (SEV 91104); Rivas (SEV 1633); Ellman & Sandwith, 391 (K); Rivas Goday, s.n. (K)
- Anthyllis tetraphylla L. (– Physanthyllis tetraphylla (L.) Boiss., Tripodium tetraphyllum (L.) Fourr.). MOROCCO, Trethewy, 277 (K) TEM. SPAIN, Diez & Ortiz (SEV 123012)
- Anthyllis vulneraria L. subsp. maura (G. Beck) Lindb. PORTUGAL, Silva, Fontes & Silvo (SEV 3216); Benito Rainba (SEV 3212)
- Anthyllis vulneraria L. subsp. vulneraria. ENGLAND, Wyatt, 014 (K) TEM. SPAIN, Aparicio & Cabezudo (SEV 57304); Rivera (SEV 46512); Romanos (SEV 22664)
- Cytisopsis ahmedii (Batt. & Pitard) Lassen (- Lyauteya ahmedii (Batt. & Pitard) Lassen). MOROCCO, Pitard, 3273 (K)
- Cytisopsis dorycnifolia Jaub. & Spach (- C. pseudocytisus (Boiss.) Fertig). LEBANON, Maitland, 144 (K). Syria, Samuelsson, 3976 (K) TEM
- Hammatolobium kremerianum (Cosson) Lassen (- Tripodion kremerianum (Cosson) C. Muller; Ludovicia kremeriana Cosson). ALGERIA, Bourgeau, s.n. (K). MOROCCO, Faure, s.n. (K)
- Hammatolobium lotoides Fenzl (- H. graecum Boiss.; Tripodion graecum (Boiss.) Lassen). GREECE, Pichler, s.n. (K); Halácsy, s.n. (K). TURKEY, Albury & al., ACW 660 (K) TEM
- Hymenocarpos circinnatus (L.) Savi. CRETE, Reverchon, 46 (K.). GREECE, Lewis, 584 (K); Brummitt, 6525 (K); Brummitt, 6340 (K)

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