Seed morphology of Iberian species of the genus *Aconitum* L.

JULIÀ MOLERO & M. ANTONIETA PUIG

Resum

MOLERO, J. & M. A. PUIG (1990). Morfologia de les granes de les espècies ibèriques del gènere *Aconitum* L. Collect. Bot. (Barcelona) 19: 111-127

Es presenta un estudi morfològico-biomètric de les granes dels tàxons del gènere *Aconitum* L. presents a la Península Ibèrica. Es tracten aspectes que fan referència a: 1) disposició de les granes al fol·licle, 2) definició de paràmetres (forma general i ornamentació de l'episperma), 3) biometria i 4) descripció de les granes dels representants ibèrics. Els microcaràcters relacionats fonamentalment amb el relleu epispèrmic, forma i ornamentació de la base d'inserció (hílum i cél·lules umbil·licals), són els que es mostren més útils per discriminar els tàxons i els que proporcionen més informació filogenètica.

Els resultats que s'exposen coincideixen, en línies generals, amb els d'altres autors (SEITZ, 1969; CAPPELETTI & POLDINI, 1984). Es presenten, tanmateix, discrepàncies importants pel que fa a la morfologia seminal, en especial de l'ornamentació de l'episperma, en les espècies *A. anthora, A. napellus* s.l., *A. burnatii* i *A. vulparia* subsp. *ranunculifolium*. Es presenta, sovint, polimorfisme seminal en les diferentes poblacions, aïllades geogràficament, d'una mateixa espècie o subspècie, tant en el context ibèric com d'Europa central i meridional. Es conclou que aquest polimorfisme és una manifestació més de la plasticitat fenotípica del gènere, particularment intensa en les espècies colonitzadores d'àmplia valència ecològica (*A. napellus,* s.l.; *A. vulparia,* s.l.), possiblement conseqüència de la deriva genètica de les poblacions.

Mots claus: *Aconitum, Ranunculaceae,* Granes, Micromorfologia, Taxonomia, Evolució.

Abstract

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A biometric-morphological study of the seeds of the taxons of the genus *Aconitum* L. occurring in the Iberian peninsula is given. The following features are treated: 1) arrangement of the seeds on the follicle, 2) definition of the parameters (general shape and ornamentation of the episperm), 3) biometry, and 4) description of the seeds of the Iberian taxa. Microcharacteristics related to the seed coat, shape and ornamentation of the insertion base (hilum and surrounding cells) have been found most useful in differentia-

J. MOLERO & M. A. PUIG: Laboratori de Botànica. Facultat de Farmàcia. Universitat de Barcelona. Avgda. Diagonal s/n, 08028 Barcelona.

ting the taxa; furthermore, they may provide more phylogenetic information than other features.

The results given agree generally with those reported by other authors (SEITZ, 1969; CAPPELETTI & POLDINI, 1984) but some important discrepancies have been noted with reference to seminal morphology, particularly episperm ornamentation in the species *A. anthora, A. napellus* s.l., *A. burnatii* and *A. vulparia* subsp. *ranunculifolium.* Seminal polymorphism is frequently observed in different geographically isolated colonies of the same species or subspecies, both in the Iberian Peninsula and in Central and Southern Europe. We conclude that polymorphism is further evidence of the phenotypical flexibility of this genus, probably owing to genetic drift in the populations. This flexibility is particulary important in colonizing species of wide ecological valence (*A. napellus,* s.l.; *A. vulparia* s.l.).

Keywords: *Aconitum, Ranunculaceae,* Seeds, Micromorphology, Taxonomy, Evolution.

ANTECEDENTS

DE CANDOLE (1818) used carpological characteristics to distinguish between the sections of the genus *Aconitum.* REICHENBACH's (1819) monograph on the genus *Aconitum* includes a short decription of the seeds of each species. GAYER (1909) describes the general characteristics of the seeds for each section and uses this characteristic with great moderation as one of several factors to be taken into account. It was not until the publication of the studies by GOTZ (1967), SEITZ (1969) and SKALICKY (1982), that the morphological characteristics of seeds came to be considered as distinguishing factors. Regarding other genera akin to *Aconitum,* reference should be made to studies of the genus *Delphinium* by HUTH (1895), PAWLOWSKY (1963) and specially MALYUTIN (1973, 1987) which conifrm the importance of seed morphology as a prime taxonomic and evolutionary characteristic. More recently, CAPPELETTI & POLDONI (1984) undertook research into the morphological variability of the seeds of the European species of the genus *Aconitum,* reaching conclusions of a taxonomic and evolutionary nature. On the subject of the internal anatomy and structure of the episperm, the works of LONAY deserve mention (1907).

In the present study, we carry out a carpological review of recognized taxa in the Iberian Peninsula (MOLERO & BLANCHÉ, 1986), referring to external and biometrical aspects of the morphology, and we compare our findings with the evolutionary hypothesis established by CAPPELETTI & POLDINI *(l. c.).*

MATERIAL AND METHODS

Most of the seeds were gathered directly in the field from mature follicles. In a few cases samples were taken from herbarium sheets. It should be pointed out that in this study the term population is used to describe seeds obtained from one or more individuals living together in identical ecological conditions, in a precise geographical area which never exceeds approximately 100 square meters. In the case of herbarium sheets, it refers to seeds obtained from different follicles from the individual(s) contained in the sheet.

In order to check the biometric studies, a Zeiss mod. DRC binocular stereoscope was used to examine a random sample of fifty seeds taken from mature follicles of various individuals in a given population; in herbarium sheets, between 20 and 25 seeds were studied. Statistical analysis was performed on 30 populations, though qualitative observations were made on a larger number of samples.

The samples were washed in ethylic alcohol (96°), mounted on metal slides using colloidal silver; they were metallized using a Diode Sputtering Polaron-5000 metallizer at 16 mA, 1,3 Kv

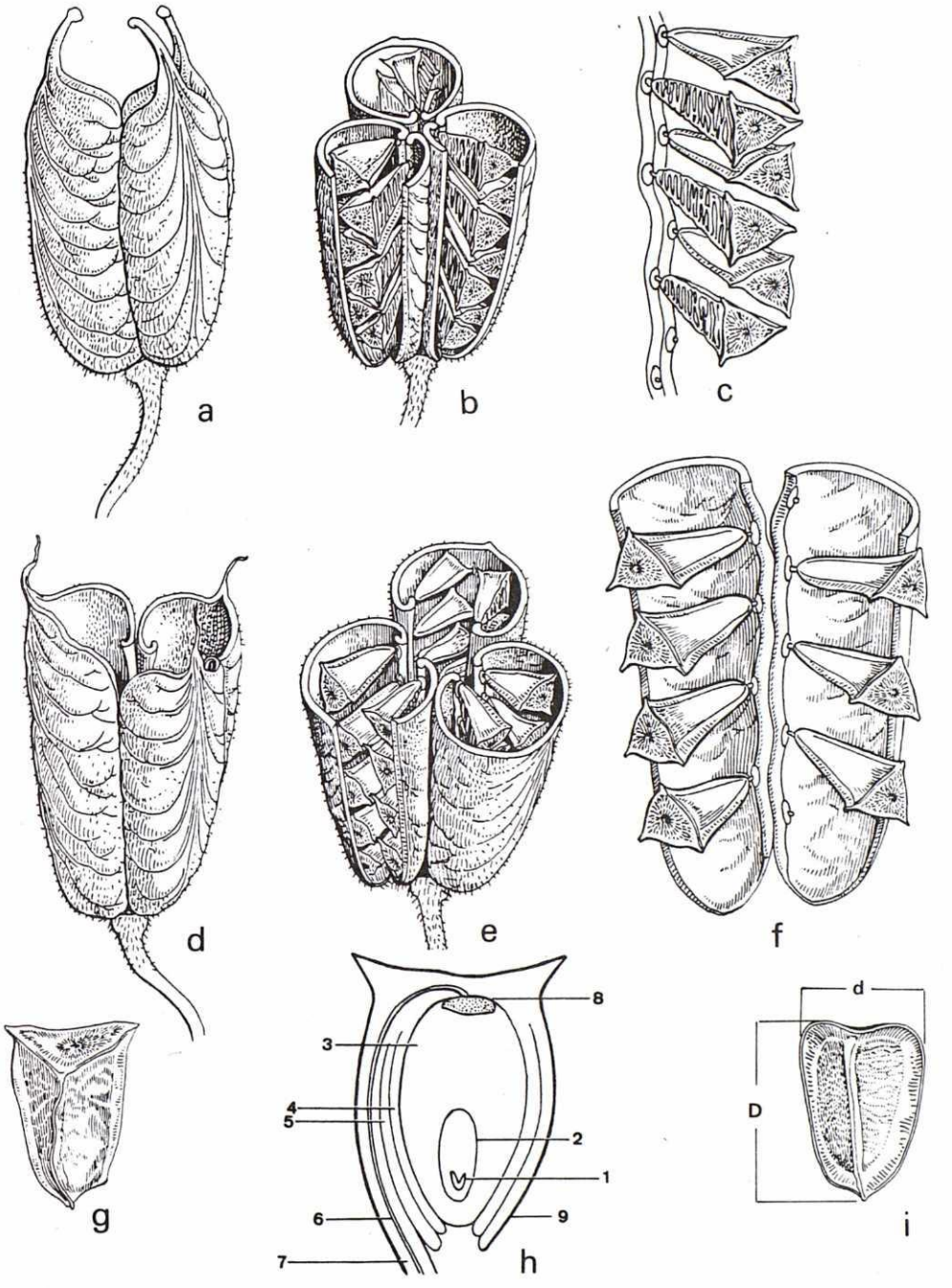

Fig. 1.— Polyfollicle and seed of *Aconitum:* a, b, d, e) general view of the polyfollicle and cross and longitudinal sections; c, f) detail of the alternate arrangement of the seeds in the follicle and insertion in the placenta; g) general view of the seed *(A. anthora);* h) young seed: 1 - embryo, 2 - embryo sac, 3 - nucellus, 4 - inner integument, 5 - outer integument, 6 - conducting bundles, 7 - funicle, 8 - chalaza, 9 - outer episperm; i) axes measured: D - maximum length, d - maximum widht.

for four minutes and then observed under a STEREOSCAN mod. S.4. scanning electron microscope.

Information about the place of origin of the material studied will be found in the appendix.

The instruments used in this research belong to the Electron Microscopy Service of the University of Barcelona.

RESULTS

1. Overall seed structure and arrangement in the follicle

The fruit of species belonging to the genus *Aconitum* are polyfollicles consisting of 1(3-5) follicles which are free when mature though always joined at the base (Fig. 1: a, b, d, e). Placentation is of the ventral-submarginal type. The number of seeds per follicle is variable, ranging from (6) 8-12.

The seed (Fig. 1: g, i) is usually subpyramidal in shape with a triangular cross section. At the edges are more or less well developed longitudinal wings, though in some cases these may be absent (Sect. *Anthora,* Sect. *Aconitum* Subsect. *Napellus,* Sect. *Lycoctonum,* p.p.). In more advanced forms, there may be an evolution towards subconical seeds (Fig. 5, i') with a subcircular cross section, a longitudinal wing (which can be reduced to a mere ridge), equipped with well developed transverse wings (Sect. *Aconitum* Subsect. *Cammarum,* Sect. *Lycoctonum* p.p.).

The internal structure is typical of the fertilized anatropous ovule from which it comes (Fig. 1, h).

Seeds are inserted into the follicle through the zone close to the micropyle (Fig. 1, c, f), through which the funicle penetrates. They are arranged alternately, parallel to the middle plane of the follicle as defined by the central and dorsal sutures. Two of the seed faces, known as the internal or adaxial faces, are in contact with each other, while the third, termed the external or abaxial face, is in contact with the wall of the follicle and is generally characterized by its rough or lamellated appearance. The internal or adaxial longitudinal wing is defined by the intersection of the adaxial faces while the external or abaxial longitudinal wings, which are sometimes absent, are defined by the intersection of the abaxial and adaxial faces.

In view of the way the funicle is inserted into the placenta, the shape of the seed must be defined as subpyramidal and not as obpyramidal (as appears at first sight), contrary to the opinion of MAIRE (1964) upheld erroneously by MOLERO & BLANCHÉ (l.c.). The seed is inserted into the placenta through the apex of the pyramid. Examination of the internal structure (Fig. 1, h) reveals a phloem-like woody bundle (funicle) which goes through the zone of the micropyle (the apex of the pyramid) and along the inside of the internal longitudinal wing before connecting with the base or hilum zone. It runs through the spongy tissue (the first stratum of the episperm) of the intercellular space.

2. Terminology and definition of parameters

Axes. The axes established (Fig. 1, i) are: maximum longitudinal diameter (D) and maximum transverse diameter (d).

Longitudinal wings. Epispermic expansions from the hilum zone to the apex of the pyramid, defined by the intersection of the three largest faces of the pyramid. On the basis of this parameter, three types of seeds can be distinguished:

a) Seeds with three equally developed longitudinal wings (Fig. 2, a).

b) Seeds with three longitudinal wings, the adaxial wing being more developed (Fig. 2, h; Fig. 3, s; Fig. 4, u, b', c').

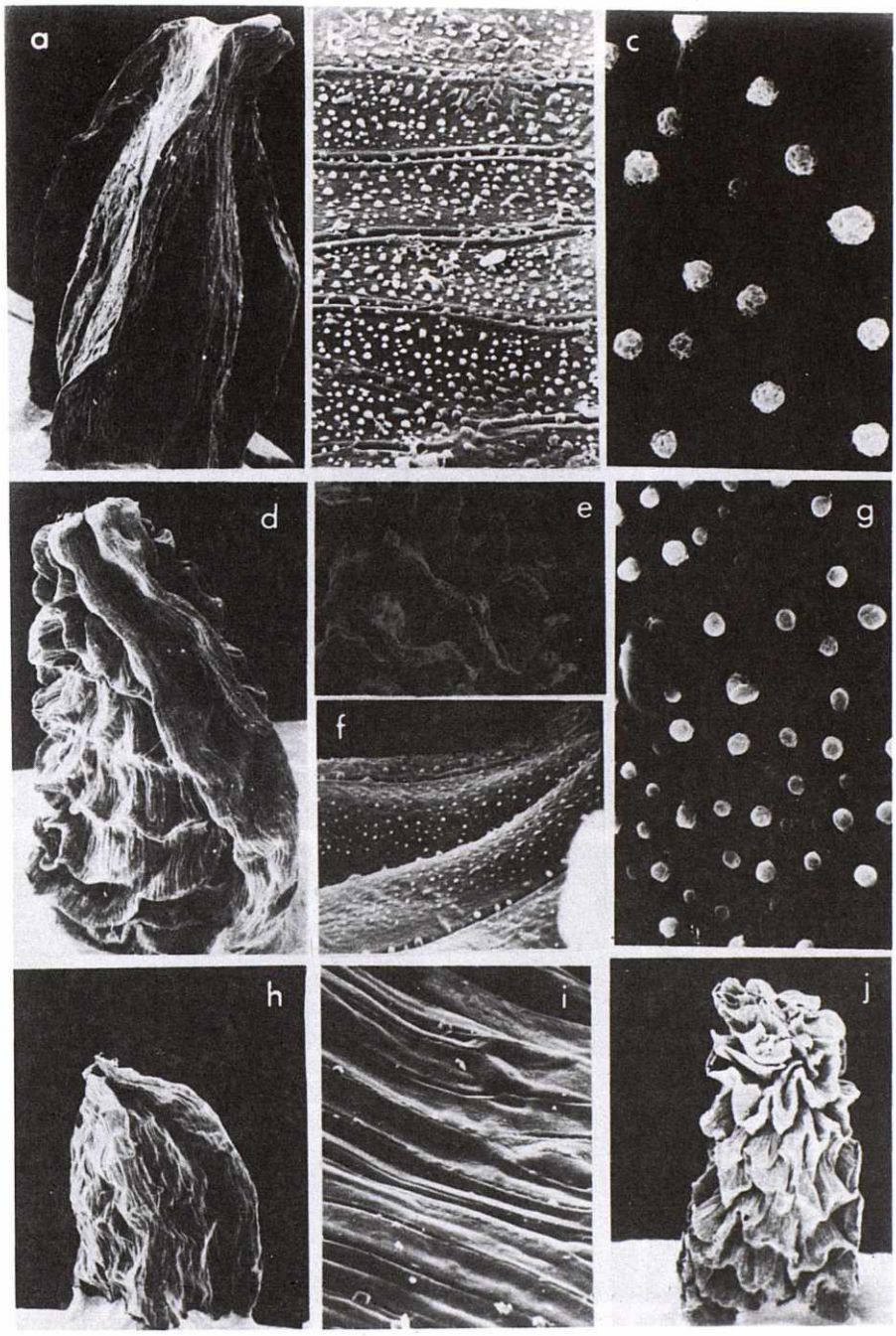

Fig. 2.— *Aconitum anthora* (Bassegoda, BCF): a) general view (x 14); b) detail of the cells of the episperm (x 360); c) detail of the papillas (x 3000). *Aconitum vulparia* subsp. *neapolitanum* (Montejo de la Sierra, BCF): d) general view (x 18); e) detail of the transverse lamellas on the abaxial face (x 14); f) detail of the rectangular cells of the lamellas (x 409); g) detail of the papillas (x 3000). *Aconitum vulparia* subsp. *ranunculifolium* (Setcases, BCF): h) general view (x 9); i) cells of the episperm of the abaxial face (x 190). *Aconitum vulparia* subsp. *neapolitanum* (l.s.): j) abaxial view (x 16).

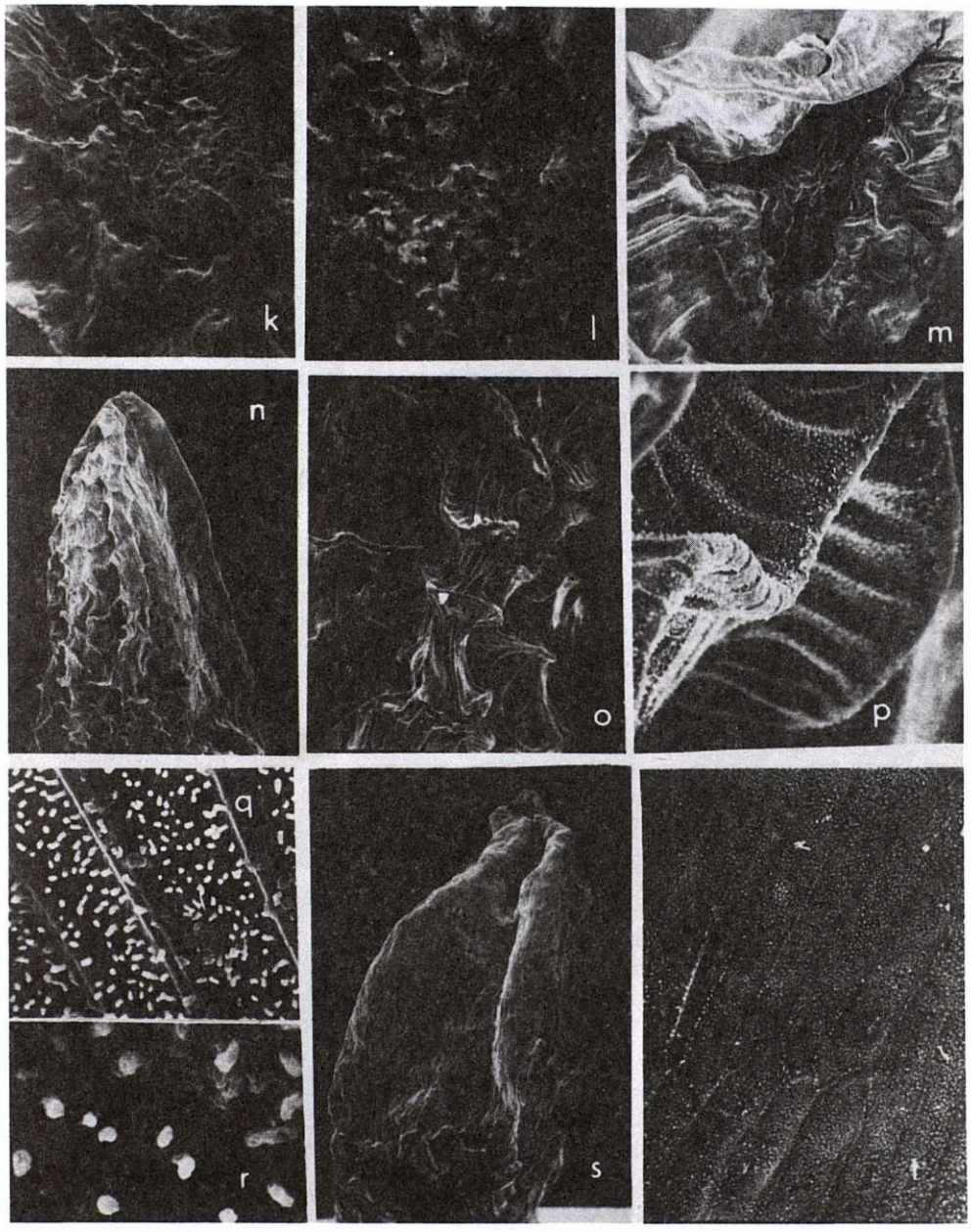

Fig. 3.– *Aconitum anthora* (l.c.): k) detail of the hilum area (x 42). *Aconitum vulparia* subsp. *neapolitanum* (l.c.): l) detail of the insertion area (x 23). *Aconitum burnatii* (Hoya de la Mora, BCF); m) detail of the hilum area (x 23); n) side view (x 8); o) detail of the lamellas on the abaxial face (x 24); p) detail of the transverse cells and ornamentation of the lamellas (x 150); q-r) density and shape of the papillas (q x 500, r x 1620). *Aconitum burnatii* (Oroel, BCF): s) general view (x 10); t) detail of the cells of the episperm on the abaxial face (x 10).

c) Seeds with a single longitudinal wing, the developed adaxial wing (Fig. 2, d; Fig. 3, n; Fig. 5, f', i').

Transverse wings. Transverse expansions of the episperm found on the lateral faces of the seed. According to their degree of development the following types can be distinguished:
a) smooth faces without transverse expansions;
b) faces with:
– rough transverse expansions of the episperm ranging from 0.005 to 0,01 mm (Fig. 2, h, l; Fig. 3, o, p).

– folded transverse expansions of the episperm ranging from 0.02 to 0.05 mm (Fig. 2, d, e; Fig. 3, n, o; Fig. 5, g).
– lamellated transverse expansions of the episperm exceeding 0.05 mm (Fig. 2, j; Fig. 3, p; Fig. 5, i', j').

Shape of the cells of the episperm and ornamentation. We classify these as rectangular (Fig. 2, t, i; Fig. 3, p) and rectangular chiselled at the apex (Fig. 3, t); they can be smooth (Fig. 2, i) or ornamented by rough, spherical (Fig. 2, c, g; Fig. 4, e'; Fig. 5, k') or stick-like papillas (Fig. 3, q, r; Fig. 4, v, w, y). Their density can be high, medium or low.

Hilum zone and ornamentation. The hilum zone is located on the more or less concave base of the pyramid. We distinguish between lateral surfaces (the walls) which can be more or less sloping, and a base zone. According to the shape, we refer to:
a) *a funnel-shaped hilum* possessing long, almost vertical walls that are clearly distinct from the base surface, which is small (Fig. 4, 7);
b) *a deep crateriform hilum* which has shorter, more sloping walls than type a, and a relatively larger base surface (Fig. 3, m);
c) *a wide crateriform hilum* which has very long sloping walls practically joined to the base (Fig. 5, f'; Fig. 3, k, l).

The type of cells which form the base of the hilum have been classified as: crested, somewhat wrinkled-undulate and irregularly overlapping lamellated. The last are generally found in wide crateriform hilums.

3. Biometry

Table 1 shows the degrees of variation of D and d for each of the taxa under study. The histograms of D and d (Fig. 6), and the graph representing the relationship between D and d (Fig. 7) are based on these figures.

Study of the histogram reveals that there is no direct relationship between the values of D and d within the same taxon; the same lengths do not always correspond to the same widths. The seeds of section *Napellus* can be differentiated by their larger diameter from those of section *Anthora* and *Lycoctonum*. No distinction can be made between these sections on the basis of the measurements of d. The parameters D and d are not sufficient in themselves to distinguish between all the taxa.

Graph D/d clearly sets section *Napellus* apart from sections *Anthora* and *Lycoctonum*. Within section *Napellus,* it distinguished between *A. napellus* subsp. *vulgare* var. *compactum* and the remaining taxa in the section whose measurements partly overlap. The highest value within this overlapping group corresponds to *A. burnatti* and the lowest to *A. napellus* subsp. *vulgare* var. *splendens*. In terms of size, *A. variegatum* subsp. *pyrenaicum,* which belongs to subsection *Cammarum,* belongs to the group made up of *A. napellus* s.l. together with the species *A. napellus* subsp. *vulgare* var. *splendens* and *A. napellus* subsp. *castellanum*. In section *Anthora* and *Lycoctonum,* the measurements of almost all the taxa overlap, with the exception of *A. vulparia* subsp. *ranunculifolium*.

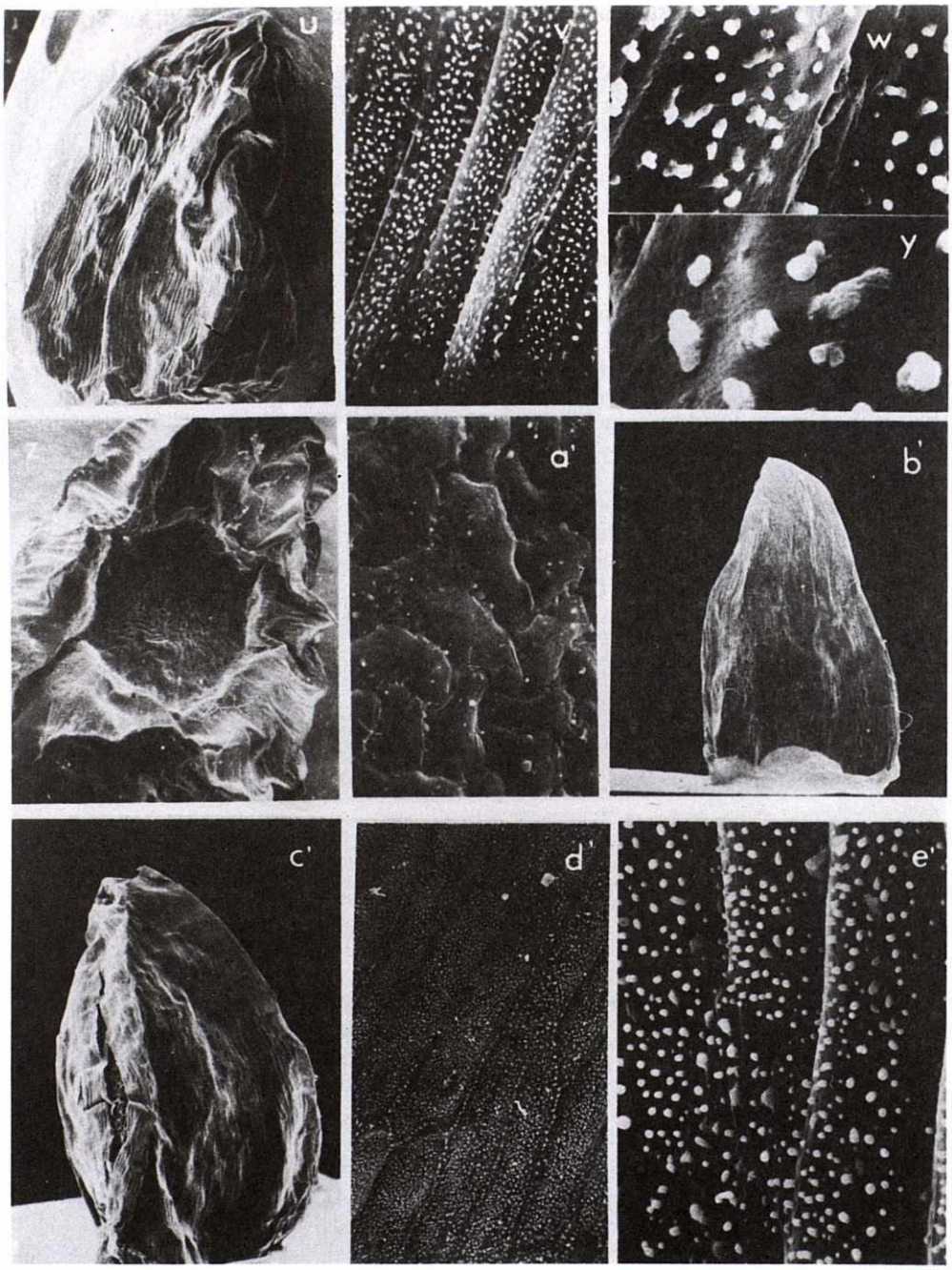

Fig. 4.– *Aconitum napellus* subsp. *castellanum* (Laguna del Marquesado, BCF): u) general view (x 7); v) cells of the episperm at the centre of the adaxial face (x 200); w-y) arrangement, shape and density of the papillas (w x 190, y x 800); z-a') detail of the hilum area and shape of the cells (z x 20, a' x 190). *Aconitum napellus* subsp. *vulgare* var. *compactum* (Setcases, BCF): b') general view (x 10). *Aconitum napellus* subsp. *lusitanicum* (León, Vegamián, BCF); c') general view (x 10); d') cells of the episperm at the centre of the adaxial face (x 100); e') detail of the papillas (x 500).

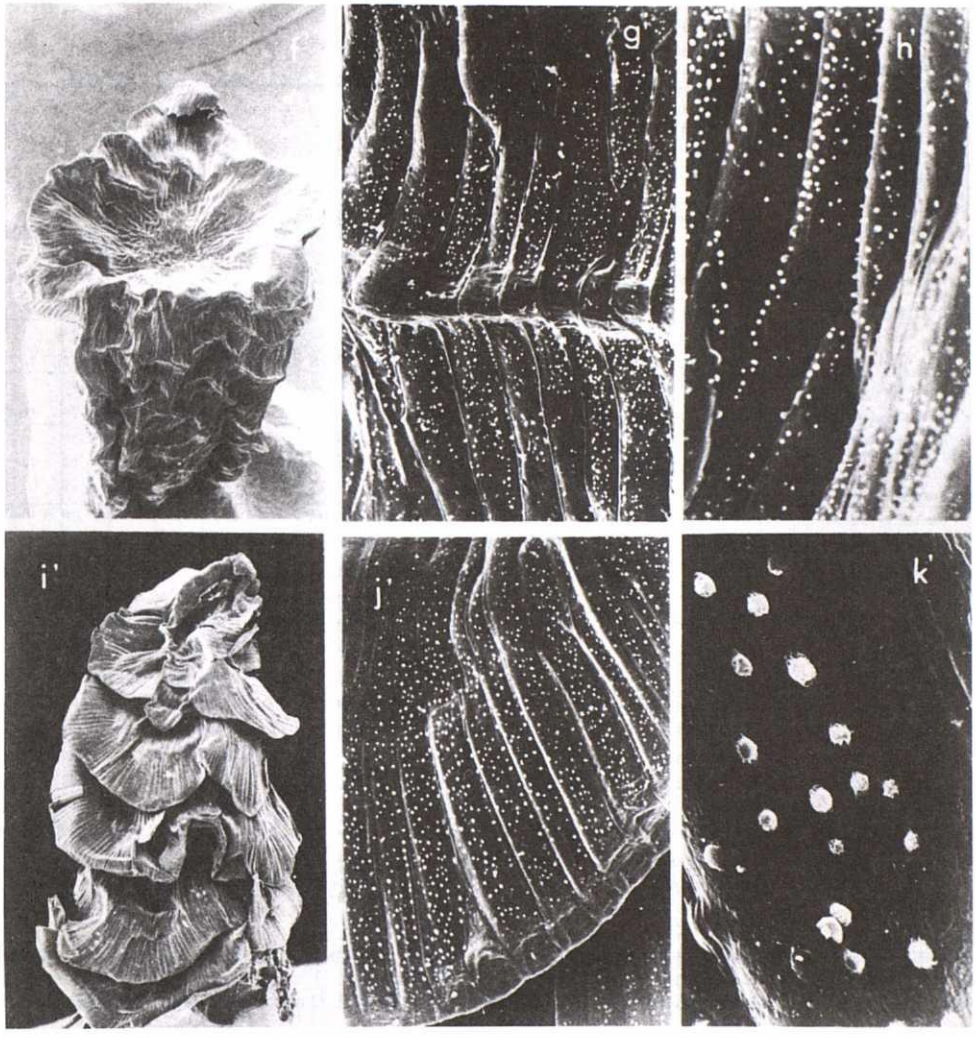

Fig. 5.– *Aconitum napellus* subsp. *vulgare* (Kuartango, Herb. J.A. Alejandre): f') view of the hilum zone (x 11); g') transverse expansion of the contact zones of the cells of the episperm, showing the base of the lamellas (x 150); h') detail of the ornamentation (x 255). *Aconitum variegatum* subsp. *pyrenaicum* (San Sebastian, Herb. J.A. Alejandre): i') general view (x 20); j') detail of the lamellas on which the cells of the episperm and the terminal edge are visible (x 170); k') details of the papillas of the episperm (x 670).

4. Morphological description of the seeds

A. napellus subs. *vulgare*

Measurements (2.5)4.3(6) × (1.5)2.3(3) mm. Subpyramidal shape with concave faces; subtriangular cross section. Three well defined longitudinal wings, the adaxial being more developed (aproximately 1 mm wide), and the abaxials measuring 0.4-0.5 mm. Smooth or striate adaxial faces, abaxial faces smooth or with crosswise roughness or even folds (Fig. 5, g'). Rectangular cells an the faces. Glossy black to dark-brown episperm with medium density papillas wich are rough spherical (Fig. 5, h'). Wide crateriform hilum, with wrinkled, undulate cells (Fig. 5, f').

Taxon	Pobl.	Localitat	D	$\bar{D} \pm Es$	$\bar{D}$	d	$\bar{d} \pm Es$	$\bar{d}$
A. napellus vulgare	P1	Vi: Valdegovia	3,25-4,50	3,89±0,11		1,75-2,75	2,35±0,07	
A. napellus vulgare	P2	O: Lago de Enol	4,00-6,00	4,48±0,14		1,50-2,75	2,41±0,11	
A. napellus vulgare	P3	*Le: Puebla de Lillo	3,75-5,25	4,57±0,10	4,28	1,50-2,75	2,16±0,10	2,21
A. napellus vulgare	P4	Pa: Areños	2,50-5,00	4,00±0,18		1,50-3,00	2,18±0,12	
A. napellus vulgare	P5	*Hu: Bujaruelo	3,50-4,50	4,12±0,18		1,50-2,50	1,96±0,82	
A. nap. vulg. compactum	P6	Gi: Nuria	3,50-5,50	4,68±0,10		1,75-2,75	2,27±0,07	
A. nap. vulg. compactum	P7	B: Pedraforca	3,75-5,00	4,45±0,14	4,57	1,75-2,50	2,13±0,13	2,20
A. nap. vulg. splendens	P8	*Cerdagne: Font-Romeu	3,00-4,00	4,02±0,20	4,02	1,50-2,50	1,96±0,12	1,96
A. nap. lusitanicum	P9	Le: Vegamian	3,50-4,75	4,09±0,09		1,50-2,50	1,93±0,06	
A. nap. lusitanicum	P10	*Portugal: San Martinho d' Angueira	4,00-5,50	4,72±0,15	4,40	1,75-3,00	2,40±0,13	2,16
A. nap. castelanum	P11	Sa: Las Honfrias	3,00-4,50	3,80±0,11		1,50-2,75	1,94±0,09	
A. nap. castelanum	P12	Cu: Laguna del Marquesado	3,75-5,00	4,44±0,12	4,11	1,50-3,00	2,24±0,09	2,09
A. burnatii	P13	Gr: Srra. Nevada	3,25-4,50	4,04±0,11		1,50-2,75	2,16±0,10	
A. burnatii	P14	Gr: Srra. Nevada	3,50-5,25	4,46±0,13	4,34	1,50-2,75	2,02±0,09	2,31
A. burnatii	P15	*Hu: Oroel	3,75-5,25	4,52±0,14		2,25-3,00	2,75±0,08	
A. varieg. pyrenaicum	P16	SS: Zaldibia	3,50-4,50	4,21±0,10		1,50-3,50	1,90±0,10	
A. variega. pyrenaicum	P17	*Hu: Ibon de Estanes	3,75-4,75	4,10±0,04	4,16	1,75-3,00	2,08±0,04	1,99
A. anthora	P18	Andorra	3,75-2,50	3,30±0,08		2,25-1,50	1,80±0,06	
A. anthora	P19	Gi: Vall de Ribes	3,50-4,50	3,94±0,08		1,50-2,50	1,96±0,01	
A. anthora	P20	Gi: Bessegoda	3,00-4,50	4,07±0,12	3,77	1,50-2,75	1,97±0,09	1,95
A. anthora	P21	*Hu: Pineta	3,00-4,50	3,80±0,10		1,75-2,50	2,08±0,10	
A. vulp. neapolitanum	P22	Andorra	3,00-4,50	3,69±0,08		1,50-2,25	1,94±0,05	
A. vulp. neapolitanum	P23	*Gi: Les Bulloses(La Cerdanya)	3,50-4,50	4,09±0,08		1,50-2,00	1,78±0,05	
A. vulp. neapolitanum	P24	M: Montejo de la Sierra	3,00-4,50	3,60±0,10		1,25-2,00	1,85±0,06	
A. vulp. neapolitanum	P25	A: Lagran	2,75-4,50	3,70±0,25	3,67	1,25-3,00	2,31±0,18	2,05
A. vulp. neapolitanum	P26	*Hu: Jaca	3,00-4,00	3,72±0,13		2,00-2,50	2,20±0,10	
A. vulp. neapolitanum	P27	O: Lago de la Ercina	2,75-4,00	3,14±0,16		1,50-2,50	1,90±0,11	
A. vulp. neapolitanum	P28	*Gu: Aldeanueva de Atienza	3,25-4,00	3,81±0,14		1,75-3,00	2,29±0,13	
A. vulp. neapolitanum	P29	Cu: Tragacete	3,00-4,25	3,61±0,15		1,75-2,50	2,16±0,10	
A. vulp. ranunculifolium	P30	Gi: Vallter	3,00-4,00	3,55±0,07	3,55	1,50-2,50	1,80±0,06	1,80

Table 1.– Biometry of the seeds of the taxa belonging to the genus *Aconitum* under study. P 1-30: number of populations studied; the locations marked with an asterisk *, come from a herbarium sheet. D: interval of variation for the maximum diameter (length); d: interval of variation for the minimum diameter (width); $\bar{D}$ and $\bar{d}$: averages; Se: standard error.

A. napellus subsp. *vulgare* var. *compactum*

Measurements (3.5)4.6(5.5) × (1.7)2.2(2.7) mm. Shape, (Fig. 4, b'), cross section and longitudinal wings, as for preceding taxon. Smooth adaxial faces, abaxial face with slight crosswise roughness. Dark-brown to light-brown episperm. Wide crateriform hilum with wrinkled, undulate cells.

A. napellus subsp. *vulgare* var. *splendens*

Measurements (3.5)4.4(5.5) × (1.5)2.2(3) mm. Shape, cross section, longitudinal wings, adaxial and abaxial faces, as for *A. napellus* subsp. *vulgare* var. *compactum*. Brown episperm. Wide crateriform hilum with wrinkled, undulated cells.

A. napellus subsp. *lusitanicum*

Measurements (3.5)4.4(5.5) × (1.5)2.2(3) mm. Subpyramidal shape with concave faces; triangular cross section. Three well defined longitudinal wings, the adaxial being more

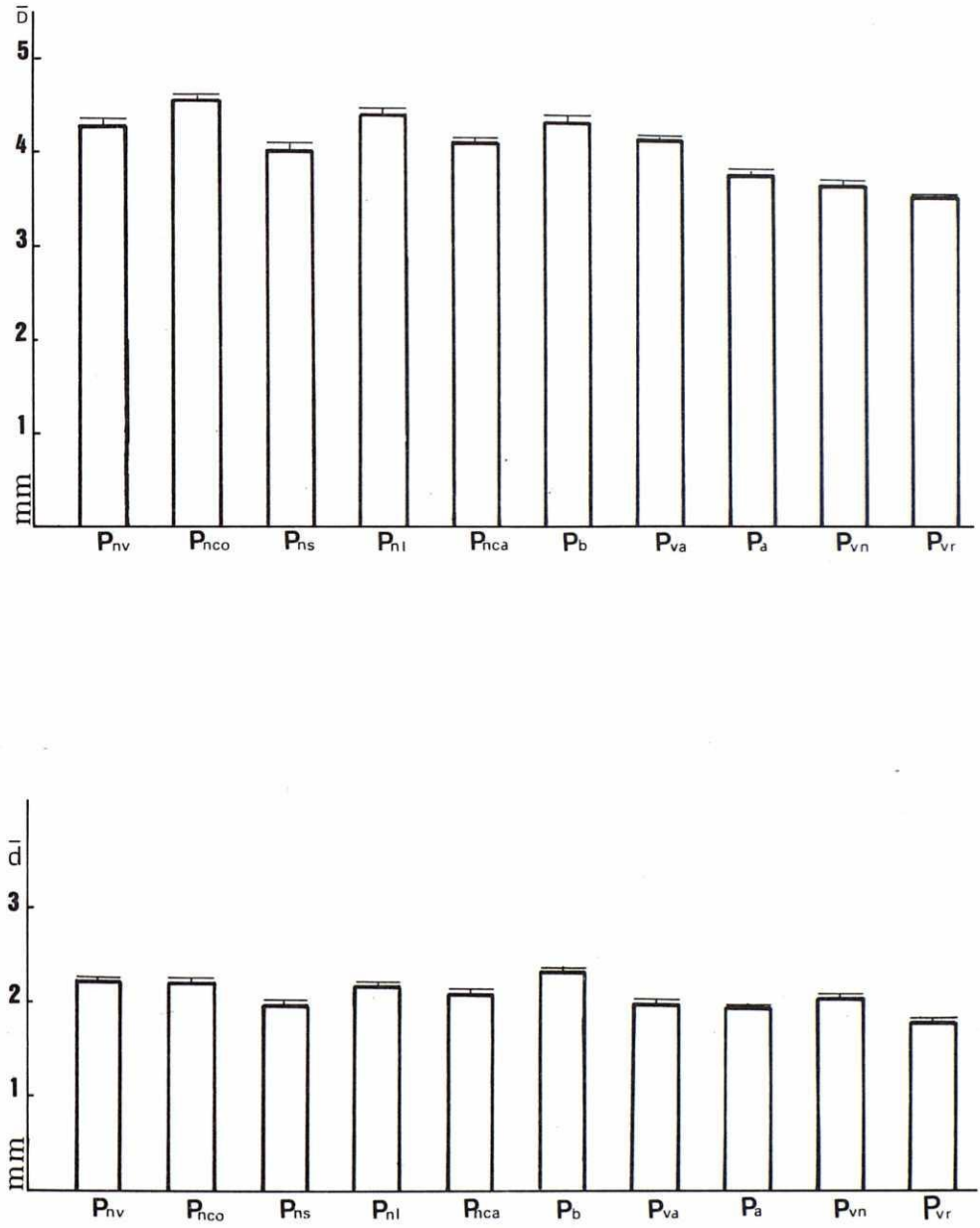

Fig. 6.– Histogram representing the lenght ($\overline{D}$) and width ($\overline{d}$) of the seeds of the taxa studied (see Appendix on materials studied).

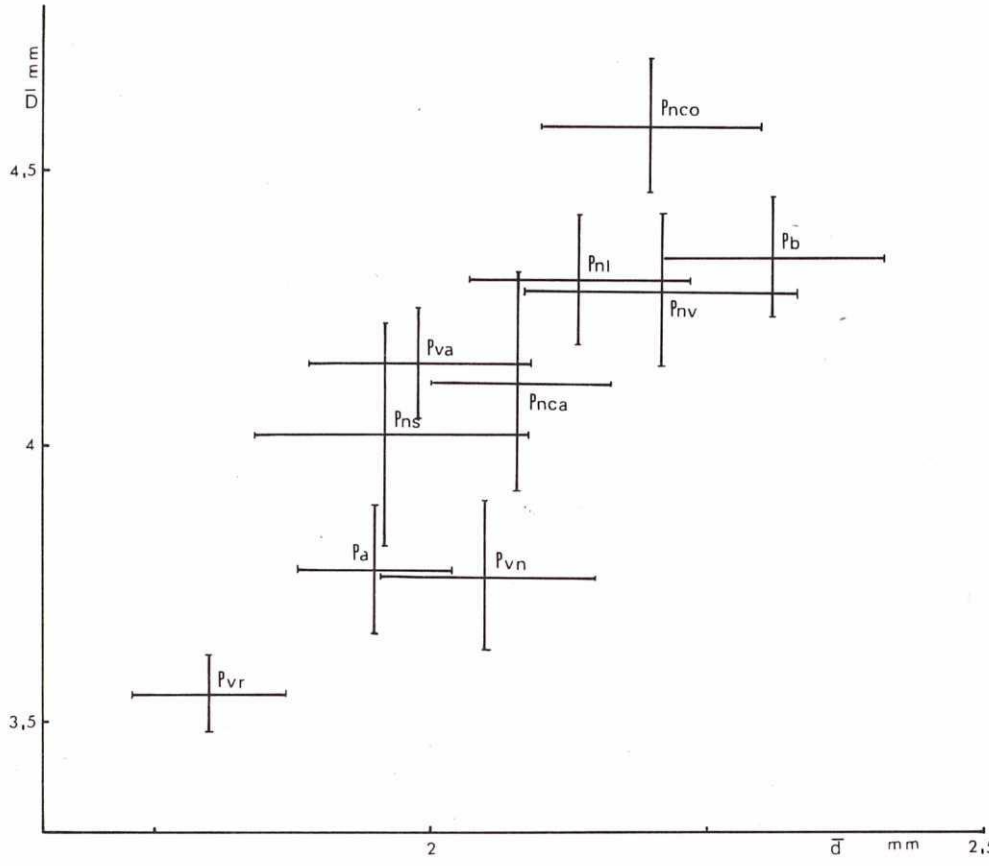

Fig. 7.– Relationship between the length ($\overline{D} \pm Se$) and widht ($\overline{d} \pm Se$) of the seeds of the taxa studied.

developed (approximately 1 mm wide) (Fig. 4, c'), the abaxials 0.4-0.5 mm. Smooth adaxial faces, crosswise roughness on the abaxial, and rectangular cells, tapered at the apex (Fig. 4, d'). The episperm with high density papillas stick-like, is a shiny dark brown colour (Fig. 4, e'). Wide, crateriform hilum with wrinkled, undulate cells.

A. napellus subsp. *castellanum*

The two populations of this taxon studied present dimorphism.

1. Population in Cuenca (Laguna del Marquesado)

Measurements (3.8)4.4(5(× (1.5)2.2(3) mm. Subpyramidal shape with concave faces (Fig. 4, u) and subtriangular cross section. Three well defined longitudinal wings, the adaxial being more developed (approximately 1 mm, in widht) and the abaxials measuring 0.4-0.5 mm. Smooth adaxial faces. Abaxial face smooth or with slight crosswise roughness. Rectangular cells on the faces (Fig. 4, v). Episperm black to brown with high density papillas, wich are rough, spherical to stick-shaped (Fig. 4, w, y). Funnel-shaped hilum with wrinkled, undulate polygonal cells (Fig. 4, z, a').

2. Population in Salamanca (Las Honfrias)

Measurements (3)3.8(4.5) × (1.5)1.9(2.8) mm. Though no differences in shape, section and longitudinal wings were found, we observed that the adaxial faces were smooth or with crosswise roughness while the abaxial face had folds arranged in 5-6 horizontal or slanting alternate, non-helicoidal rows. Black to brown episperm. Deep, crateriform hilum with wrinkled, undulate cells.

A. burnatti

As in the above taxon, dimorphism was found.

1. Populations in Granada (Sierra Nevada): Barranco de Valor, Hoya de la Mora.

Measurements: (3.3)4.2(4.9) × (1.5)2.1(2.8) mm. Subpyramidal shape with concave faces (Fig. 3, n); triangular cross section. Three longitudinal wings, the adaxial being more developed than the other two. Adaxial faces smooth or with crosswise roughness, the abaxial face can present crosswise roughness or folds (Fig. 3, o, p). Rectangular cells on faces (Fig. 3, q, p). Episperm is with medium-dense stick-shaped papillas, shiny reddish-brown to brown (Fig. 3, r). Deep, crateriform hilum with wrinkled, undulate cells (Fig. 3, m).

2. Population in Huesca (Oroel).

Measurements: (3.7)4.5(5.2) × (2.2)2.7(3) mm. Shape (Fig. 3, s), section and longitudinal wings as in previous population. Smooth adaxial faces, the abaxial face smooth or with very slight crosswise roughness. Faces with rectangular cells tapered at the apex (Fig. 3, t). Light brown episperm with a high density of papillas. Hilum as in the previous population.

A. variegatum subsp. *pyrenaicum*

Measurements: (3.6)4.2(4.6) × (1.6)2(3.2) mm. Shape ranges from subpyramidal to subconical (Fig. 5, i) and cross section from subtriangular to subcircular. A single longitudinal wing, the adaxial, which measures 0.6-1 mm and is sometimes reduced to a simple ridge. Folds on the adaxial faces spreading towards the abaxial face, giving rise to translucid lamellas (Fig. 5, j') arranged obliquely from one end of the face to the other forming (5)-6-8 rows. The lamellas are made up of rectangular cells. Shiny black episperm with rough spherical low-density papillas (Fig. 5, k'). Deep crateriform hilum with wrinkled-undulate cells.

A. anthora

Measurements: (3)3.8(4.5) × (1.5)2(2.7) mm. Subpyramidal shape with slightly concave faces (Fig. 2, a); triangular cross section with distinct awns at the corners. Three equally developed longitudinal wings. Smooth adaxial and abaxial faces with rectangular cells (Fig. 2, b, in reclining posture, not erect). Shiny black episperm on which high-density rough, spherical papillas can be seen (Fig. 2, c). Deep, crateriform hilum with rough, crested cells (Fig. 3, k).

A. vulparia subsp. *neapolitanum*

Dimorphism is present, as in the previous species, the differences being related to shape, since the measurements are very similar (2.7)3.7(4.5) × (1.2)2(3) mm. Two types of seeds can be distinguished:

1. Populations in Guadalajara (Aldeanueva de Atienza); Huesca (Jaca); Oviedo (Lago de la Ercina); Madrid (Montejo de la Sierra).

Shape ranging from subpyramidal with convex faces to subconical (Fig. 2, d); subtriangular to subcircular cross section. Single longitudinal wing, usually dorbly ridged. Adaxial faces with crosswise roughness, abaxial face folded, sometimes with 6-7 (8) rows of non-translucid lamellas arranged obliquely and irregularly (Fig. 2, e). Faces with rectangular cells (Fig. 2, f). Black to brown episperm with medium-high density papillas irregularly arranged wich are rough spherical (Fig. 2, g). Widely crateriform hilum with irregularly overlapping lamellas (Fig. 3, l).

2. Populations in Cuenca (Tragacete); Andorra (Canillo); Cerdanya (Font Romeu).

Subpyramidal shape with concave faces; triangular cross section. Three longitudinal wings, the adaxial being approximately 1 mm wide, the abaxials less developed. Smooth adaxial faces, the abaxial face with crosswise roughness; presence of rectangular cells. Episperm as in type 1 population. Wide crateriform hilum, without clearly differentiated lamellas.

A. vulparia subsp. *ranunculifolium*

Measurements (3)3.5(4) × (1.5)1.8(2.5) mm. Subpyramidal shape with concave faces (very rarely, spheroidal sector truncate at the distal end); subtriangular cross section. Three longitudinal wings, the adaxial (Fig. 2, h) being much more developed than the other two. Adaxial faces smooth but the abaxial bears slight crosswise roughness. Presence of rectangular cells. Shiny black to brown episperm either devoid of papillas or with only a few isolated papillas (Fig. 2, i). Illdefined crateriform hilum zone with cells presenting crests or folds.

DISCUSSION

1. In the genus *Aconitum,* as in *Delphinium* and *Consolida* (MALYUTIN, 1973, 1987), characteristics related to seed morphology have proved useful in differentiating taxonomically between sections, subsections and most (if not all) species (GAYER, l.c.; SEITZ, l.c.). Moreover, they provide very useful information on which to base evolutionary hypotheses. This is especially true of studies covering a geographical area sufficiently large to permit the occurrence of diverse forms on account of the presence of natural groups of different origins. By studying the whole of Europe, CAPPELETTI & POLDINI (1984) were able to reach more general conclusions regarding evolution, in addition to strictly taxonomic ones. Since our research covers a smaller geographical area, the results are less farreaching.

2. Broadly speaking, the findings of our study of the Iberian representatives agree with those of other European authors (SEITZ, l.c.; CAPPELETI & POLDINI, l.c., etc.). In some cases, however, quite important discrepancies arise, and these call for comment.

SKALICKY (1982) described the seeds of Polish populations of *A. anthora* as subpyramidal and lacking longitudinal wings, a finding that does not coincide with Iberian or central European populations, which consistently have three well developed wings. Moreover, CAPPELETTI & POLDINI (l.c.), referring to populations of the same species in the Alps, report the presence of tuberculate protuberances on the faces of the seeds which are the origin in an evolutionary sense of the folds and transverse lamellas, which in other closely related taxa are caused by the need to adapt to new environments. We have observed these protuberances to be lacking in Iberian populations. Also missing are the slightly umbonate square cells around the hilum which, in Iberian populations, are irregular and crested. Thus in this species seed morphology seems to vary in accordance with geographical origin. Confirmation of these differences is required before any type of speculation can be undertaken.

The seeds of the group *A. napellus* show considerable variation. Not all populations correspond to the pattern characteristic of the species; three unequal longitudinal wings, the adaxial one being wider than the two abaxials. Though subsp. *vulgare* usually conforms to the rule, in other taxa (subsp. *lusitanicum,* subsp. *castellanum*) the wings are reduced to simple angular ridges. Moreover, in subsp. *lusitanicum,* the transverse folds on the abaxial face are less developed than in species from the rest of Europe. Furthermore, Pyrenean populations (Peña Oroel) of *A. burnatti* lack the characteristic fold and lamellas on the abaxial face which are consistently found in populations in the Sierra Nevada and the Alps.

In the group *A. vulparia,* variation is even greater. As in the case of subsp. *neapolitanum (A. lamarkii),* the description of the European taxon is virtually identical to that of type 1 of the Iberian populations, though in the latter at least one longitudinal wing is always found (in other

European populations all three wings may be missing). Regarding subsp. *ranunculifolium,* the descripton given by the Italian authors does not differ from the typical subspecies [1], whereas the populations studied from the eastern Pyrenees (type 2), present substantial differences: the seeds are smaller, clearly pyramidal, and angular at the insertion of the faces; they do not possess longitudinal or transverse wings of any type, and have smooth faces, which lack the spheroidal papillas that are found in subsp. *neapolitanum.* The existence of such sharp contrasts make it possible to defend subspecific status as the most appropriate for subsp. *ranunculifolium.* It needs to be checked however whether populations of this taxon from the Alps present the same or a similar type of seed.

3. Detailed study of the Iberian representatives of the genus *Aconitum* does not contradict the evolutionary hypothesis established by CAPPELETTI & POLDINI. It does however raise certain questions.

The Italian authors suggest that, where seeds are concerned, the direction of the evolutionary process within the genus is revealed by the more functional morphological changes they undergo in order to adapt to distribution in a variety of contrasting habitats. *A. anthora,* a taxon that for many reasons is considered primitive, lives in open, xerothermic mountain locations with scarce vegetation. Being large and subpyramidal, with smooth faces and three broad longitudinal wings, the seeds can easily be scattered by the wind. On the other hand, in taxa like *A. vulparia* subsp. *neaolitanum,* and even more so in *A. variegatum* subsp. *pyrenaicum,* which live in nemoricolous, mesophilous-hygrophyte locations, where there are few gusts of wind to scatter the seeds, the latter take on more aerodynamic, subconical shapes. The longitudinal wings disappear almost completely, and are replaced by transvere wings, or lamellas inserted spirally, which increase the surface area and make the seeds lighter, thus improving floatability and facilitating dispersion. On account of its ecological requirements, the complex *A. napellus-burnatii* occupies an intermediate position. It has subpyramidal seeds, longitudinal wings are either rare or wholly absent, and sometimes presents transverse folds or lamellas on one or all three faces. The evolutionary trend is characterized by gradual reduction of the longitudinal wings (which are characteristic of the older taxa) and parallel development of transverse wings (present in those taxa that are considered more highly evolved). The development of the transverse wings may respond to two causes: oppression of the epidermic cells of the seeds in the follicle or the outwards expansion of these cells.

The behaviour of the Iberian taxa does not entirely fit this hypothesis. The wide variation of seed shapes (both original and derived) that coexist within the same taxon makes it difficult to account for certain intermediate mechanisms, though the overall trend is confirmed. Especially eloquent is the case of the group *A. vulparia* already mentioned. The type of seed found in subsp. *ranunculifolium* could be justified as a secondary adaptation to anemochore dispersion at altitude (the populations live at between 1500 and 2000 m). However, highly typical forms of *A. variegatum* subsp. *pyrenaicum,* which colonized megaphorbic communities of the Montane-Subalpine levels of the Pyrenees, produce quite typical seeds, similar to those of the central European lowlands.

Trends within the *A. napellus* group are not clearer, as illustrated by the case of *A. burnatii* referred to above.

4. In short it is our opinion that the polymorphism detected in the seeds of the genus *Aconitum* is a further sign of the phenotypic plasticity of this genus, which rarely develops totally stable characteristics. The majority of taxa belonging to the genus, specially those from certain groups (*A. napellus* s.l., and *A. vulparia,* s.l.) must be defined by a set of more or less

(1) We are unaware that taxonomic criterion was used in identifying the materials attributed by CAPPELLETTI & POLDINI (1984) to subsp. *ranunculifolium.* If they followed the opinion of WARNCKE (l.c.), then it is merely a synonym for subsp. *neapolitanum.* The criterion we used for the Iberian populations is identical with that of TAMURA & LAUENER (1979).

variable characteristics rather than by one or two "good" constant characteristics. This is probably a consequence of the genetic drift of the populations, which are often isolated in mountainous spots. The often variable colonizing ecology of these more plastic groups conditions the appearance of small, distinctive features on the seeds, possibly as a result of modifications to adapt seed dispersion to new habitats.

APPENDIX OF MATERIALS STUDIED

After the name of each taxon, at the level of species or lower categories, the abbreviation used in Graphs 6 and 7 is given in parentheses.

Sect. **Aconitum** Subsect. **Napellus** (DC.) Gáyer

Aconitum napellus L. subsp. **vulgare** Rouy & Fouc. (Pnv)

P1: Vizcaya, Valdegovia, 13-X-1985, *B. Fdez. de Betoño & J. A. Alejandre* (Herb. Alejandre); P2: Asturias, *supra* Covadonga, Lago Enol, 1650 m, 23-VIII-1986, *J. Molero* (BCF); P3: León, Puebla de Lillo, 4-X-1986, *F. Llamas* (BCF); P4: Palencia, stream close to Areños, 15-VIII-1986, *C. Blanché & R. Ferrer* (BCF); P5: Huesca, Bujaruelo, 1580-1650 m, *P. Montserrat* (JACA 1230).

Aconitum napellus L. subsp. **vulgare** Rouy & Fouc. var. **compactum** Reinchenb. (Pnco)

P6: Girona, Núria, close to the shrine, 1850 m, 10-IX-1985, *J. Molero* (BCF); P7: Pedraforca, 2100 m, 22-IX-1985, *J. Simón* (BCF).

Aconitum napellus L. subsp. **vulgare** Rouy & Fouc. var. **splendens** (Font-Quer) O. Bolòs & J. Vigo. (Pns)

P8: Cerdagne, Targasonne (Font Romeu), 1800 m, 5/14-IX-1925, *Fr. Sennen. G.*

Aconitum napellus L. subsp. **lusitanicum** Rouy. (Pnl)

P9: León, Vegamian, 25-X-1984, *J. Molero* (BCF); P10: S. Martinho d'Angueira 1923, *A.A. Taboarda* (COI 17/514).

Aconitum napellus subsp. **castellanum** J. Molero & C. Blanché (Pnca)

P11: Salamanca, *loco dicto* Las Honfrias, 30-IX-1986, *C. Benedí & J. Molero* (BCF); P12: Cuenca, Laguna del Marquesado, in hydromorphous environments, 1500 m, 12-X-1986, *J. Molero* (BCF).

Aconitum burnatii Gáyer (Pb)

P13: Granada, Hoya de la Mora, Srra. Nevada, 12-X-1986, *J. Molero Mesa* (BCF); P14: Granada, Srra. Nevada, Barranco de Valor, 26-X-1983, *J. Molero Mesa* (BCF); P15: Huesca, Oroel, below Faixa Paco, Umbría de la Cruz, 1500 m, 29-VIII-1982, *P. Montserrat & L. Villar* (JACA 4806).

Sect. **Aconitum** Subsect. **Cammarum** (DC.) Rapaics,

Aconitum variegatum L. subsp. **pyrenaicum** Vivant & Delay. (Pva)

P16: San Sebastian, Zaldibia, 5–X-1986, *B. Fdz. de Betoño & J. A. Alejandre* (Herb. Alejandre); P17: Huesca, Paso de Escate, Ibón de Estanes, 1700 m, 10-XI-1986, *C. Calvo* (JACA).

Sect. **Anthora** DC.

Aconitum anthora L. (Pa)

P18: Andorra, Canillo, 1800 m, 14-X-195, *J. Seoane & M. Suarez* (BCF); P19: Girona, Vall de Ribes, above Planoles towards Coma de Batet 1700 m, 19-X-1986, *J. Molero & A. Rovira* (BCF); P20: Girona, peak of mount Bassegoda, 1400 m, 5-X-1985, *J. Molero* (BCF); P21: Huesca, Valle de Pineta, 1400 m, 12-IX-1974, *P. Montserrat* (JACA 6300).

Sect. **Vulparia** DC.

Aconitum vulparia Reichenb. subsp. **neapolitanum** (Ten.) Muñoz Garmendia (Pvn)

P22: Andorra, above Encamp, towards Ordino, shady spot beside a stream, 1600 m, 20-VIII-1985, *J. Molero & A. Rovira* (BCF); P23: Girona, La Cerdanya, towards Les Bulloses, 6-XI-1986, *J. Simón* (BCF); P 24: Madrid, Montejo de la Sierra, 14-IX-1985, *J. Molero* (BCF); P25: Alava, Lagrán, sunny spot on the Paso de la Cruz, 150 m, 17-VIII-1973, *P. Montserrat & L. Villar* (JACA 4501); P26: Huesca, east of Oroel, 1400 m, in a sparsely wooded fir forest, 27-VIII-1969, *P. Montserrat* (JACA 6028); P27: Asturias, above Covadonga, Lago de Ercina, 1800 m, 16-VIII-1986, *C. Blanché & R. Ferrer* (BCF); P28: Guadalajara, Aldeanueva de Atienza, la Dehesa, 3-VI-1974, *S. Silvestre* (SEV 1941); P29: Cuenca, Tragacete, shady rocks at the source of the Júcar, 15-VIII-1975, *G. López* (MAF 95838).

Aconitum vulparia Reichenb. subsp. **ranunculifolium** (Reinchenb.) Laínz (Pvr)

P30: Girona, Vallter (Setcases), 1700 m, 15-IX-1986, *J. Molero & J. Vigo* (BCF).

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