

STUDIES ON TRIBAL SYSTEMATICS
OF AMARYLLIDOIDEAE

1. THE SYSTEMATIC POSITION OF LAPIEDRA LAG.

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Resumen. Se propone una nueva clasificación de las *Amaryllidoideae* mediterráneas, basada en un amplio estudio de la morfología de los bulbos y de los caracteres florales (cuadro 2). Esta clasificación difiere de la de TRAUB (1970) en que se restablece el género *Vagaria* y en que se transfiere el género *Hannonia* de las *Galantheae* a las *Pancreatiae*. La tribu *Galantheae* queda reducida a una subtribu de las *Narcisseae*. Sin embargo, el cambio más importante es el transferir *Lapiedra* de las *Galantheae* a las *Pancreatiae* y el establecimiento de una nueva subtribu: *Lapiedrinae*.

Summary. On the basis of extensive investigations of bulb morphology and a revision of the floral characters, a modified classification of the Mediterranean *Amaryllidoideae* is proposed (table 2). This treatment differs from that of TRAUB (1970) in that the genus *Vagaria* is restored and the genus *Hannonia* transferred from the *Galantheae* to the *Pancreatiae*. The tribe *Galantheae* is reduced to a subtribe of the *Narcisseae*. The most important change, however, is the transfer of *Lapiedra* from the *Galantheae* to the *Pancreatiae* and the establishment of a new subtribe: *Lapiedrinae*.

Zusammenfassung. Auf der Grundlage von umfangreichen Untersuchungen zur Zwiebelmorphologie und einer Überprüfung der floralen Merkmale wird die Gliederung der mediterranen *Amaryllidoideae* verändert (Tabelle 2). Dieses System unterscheidet sich von dem Vorschlag TRAUB (1970) durch folgende Punkte: die Gattung *Vagaria* wird wieder anerkannt; die Gattung *Hannonia* wird von den *Galantheae* zu den *Pancreatiae* überführt; die Tribus der *Galantheae* wird als Subtribus den *Narcisseae* untergeordnet, als wichtigste Änderung wird *Lapiedra* von den *Galantheae* zu den *Pancreatiae* überführt und auf ihr die neue Subtribus *Lapiedrinae* begründet.

INTRODUCTION

In the last half century there have been many systematic changes within the *Liliiflorae*. Many subfamilies have been raised to families or even orders, and therefore the old family names, such as *Liliaceae* and *Amaryllidaceae*, are used with very different circumscriptions: e.g. the *Liliaceae* may include (CRONQUIST, 1968) or exclude the *Amaryllidaceae*; if the *Amaryllidaceae* are excluded, the *Alliaceae* may or may not be included. But at the level of subfamilies there has been little change: The *Allioideae* remain nearly identical, whether they are a subfamily of the *Liliaceae*, the *Amaryllidaceae* or the *Alliaceae*. Also the circumscription of the *Amaryllidoideae* has undergone only minor changes since the last century. It represents a quite natural group, which is best allocated under the subfamily name up to a consolidation of delimitations at the family level. In the following series of papers on tribal systematics of the *Amaryllidoideae*, the position of some misplaced or controversial genera is studied and the limitation of the tribes involved is discussed.

Lapiedra is a monotypic genus created by LAGASCA (1816). The only species, *Lapiedra martinexii* Lag., is endemic to the western Mediterranean region. The geographic distribution in south-eastern Spain and northern Morocco can be approximately circumscribed by a triangle marked by Valencia, Málaga, and Melilla.

During the first half of this century a second species, *Lapiedra chilensis* F. Phil. in R. A. PHILIPPI (1896: 144) from Chile, was recognized within the genus, but in 1963 this South American species was called *Traubia chilensis* (R. A. Phil.) Mold. within the monotypic tribe *Traubieae* (MOLDENKE, 1963, did not realise who the original author of the epithet was). MAHU (1969) stated that this species should be called *Traubia modesta*, based on *Rhodophiala modesta* R. A. Phil., and later RAVENNA (1974) validly published *Traubia modesta* (R. A. Phil.) Rav.

As far as we know, there has never been a doubt about the validity of the genus *Lapiedra*, but the systematic position has been variously changed in the last century. TRAUB & MOLDENKE (1948: 85) state: «The systematic position of *Lapiedra* now appears to be secure among the *Galantheae*, but it must be realized that all of the needed evidence has not been assembled. It is particularly important to determine the chromosome complement before considering the case closed.»

This cytological work has been done by FERNANDES (1950, 1952) who writes in his summary (1952: 67): «From the fact that *Lapiedra Martinexii*

Lag. possesses a Karotype [sic!] similar to that of *Leucojum* L. and *Galanthus* L., the cytological data justify the idea of considering the genus *Lapiedra* as belonging to the tribe *Galantheae* (Pax) Traub and Moldenke, in accordance with the ideas of Pax (1887) and Traub and Moldenke (1947).»

Thus, the case seemed to be closed. But our own investigations on the bulb morphology reveal a new pool of hitherto hidden characters, which have proved to be very useful at the tribal level, and which are not at all in accord with the position of *Lapiedra* among the *Galantheae*.

THE PRESENT TRIBAL SYSTEMATICS OF THE MEDITERRANEAN GENERA OF AMARYLLIDS

According to TRAUB (1970: 81-82) eight genera of Mediterranean *Amaryllidoideae* are recognized which belong to three tribes of two different infrafamilies (Table 1).

Infraclass I *Amaryllidoidinae*

Tribe 13 *Narcisseae* Endl. (1836)

Sternbergia Waldst. & Kit. (1805)

Narcissus L. (1753)

Tapeinanthus Herb. (1837)

Tribe 14 *Galantheae* Salisb. (1866)

Lapiedra Lag. (1816)

Hannonia Br.-Bl. & Maire (1931)

Leucojum L. (1753)

Galanthus L. (1753)

Infraclass II *Pancratioidinae* Traub (1963)

Tribe 20 *Pancratieae* Salisb. (1866)

Pancreatium L. (1753)

Table 1.—Classification of the Mediterranean *Amaryllidoideae* according to TRAUB (1970: 81-82) (*).

In fact, the monotypic *Tapeinanthus* had been already incorporated into *Narcissus* by TRAUB (1969: 46) as *Narcissus humilis* (Cav.) Traub. We can agree with him on this last statement.

On the other hand, when TRAUB (1970: 70) suppressed the genus *Vagaría* by reincorporating *Vagaría parviflora* (Desf.) Herb. into *Pancreatium* in contrast to his previous opinion (TRAUB, 1963), he did not realise that there is another species, *Vagaría ollivieri* Maire, and that MAIRE (1959: 47)

(*) The authorship of SALISBURY is not in accordance with the nomenclatural rules, since he has altered the relative order of the ranks by calling the taxa in question orders as second order subdivisions of the tribe *Liriogamae*.

gives a very interesting note, when discussing the affinities of *Hannonia*: «En raison de ses affinités avec le *V. ollivieri* nous l'avons rangée dans les *Dentiferae*, malgré l'absence totale de paracorolle.»

We cannot but support this view which means that the genus *Vagaria* is to be maintained with two species and that *Hannonia* has to be transferred from the *Galantheae* to the *Pantratieae*.

Thus, in the following discussion the *Narcisseae* comprise the two genera *Narcissus* and *Sternbergia*, the *Galantheae* consist only of *Leucojum* and *Galanthus* and when speaking about the *Pantratieae* we are for the present only referring to *Pantratum* and *Vagaria*. *Hannonia* is left apart as it offers some difficulties, which will be discussed in a later paper, and *Lapiedra* is not yet included as we first have to prove its affinities.

MATERIAL AND METHODS

Thirty-two species belonging to all eight Mediterranean genera of *Amaryllidoideae* were collected in the wild. Several bulbs were immediately analysed scale by scale in the field with a stereomicroscope and/or fixed in FAA. Others were collected for cultivation in a greenhouse, where the periodic development is observed by routine recording. Additional species from garden proveniences are also cultivated. *Lapiedra* is cultivated from 12 localities covering the whole distribution area in Spain and Morocco.

BULB MORPHOLOGY

NARCISSEAE AND GALANTHEAE.

If we exclude the genera *Hannonia* and *Lapiedra* from the *Galantheae*, the remaining four genera of *Narcisseae* and *Galantheae* sensu Traub are very similar in their bulb structure (see fig. 1 A and B):

- a, The prophyll of the renewal bulb has an abnormal position, namely abaxial, whereas the bulblets, which may occur in lower leaf axils, have the normal adaxial position. (In addition to the usual renewal bulb in the axil of the last but one leaf, in some species of *Narcissus* a second one of nearly equal size may occur in the axil of the uppermost vegetative leaf, the half-embracing F_x; its prophyll also has the abaxial position.)
- b, The prophyll shows an amplexicaul insertion (in some individuals of *Sternbergia macrantha* and *St. colchiciflora* the insertion may be more or less open).

- c, Under normal conditions only one shoot generation per growing season is produced (= annual innovation).
- d, The leaf sequence of a flowering bulb begins in each growing season with one or several sheathing cataphylls.
- e, In all four genera a coflorescence is rather frequently present, that is a secondary flower-stalk, or a sympodic system of flower-stalks or only a rudiment of these, which originate in the axil of the uppermost vegetative leaf under the inflorescence.

The characters listed above start from the principle of sympodial bulb-structure. In text-books two types of bulbs are distinguished, monopodial and sympodial ones (TROLL, 1937: 730; EMBERGER, 1960: 321), but in fact only sympodial bulbs exist, as we have shown in a previous paper (MÜLLER-DOBLIES, 1972). In this connection one paper contradicting this interpretation in *Galanthus* (BRUNAUD & TURLIER, 1972) and one supporting it (LEVACHER, 1970) may be mentioned.

As the four genera involved occur in Central Europe, the bulb structure of several species has often been described (the main papers are IRMISCH, 1850, 1860, and BUXBAUM, 1930-31). But an attempt at taxonomic assessment has not been made until now, although the main differences among *Amaryllidaceae* are discussed and figured in two diagrams by PAX (1887: 97) and repeated by PAX & HOFFMANN (1930: 392).

One reason for this gap may be that all four Central European genera show the same bulb structure as they belong in fact to the very same taxon (*Narcisseae* in Table 2).

It is interesting to state that we did not find any character in the bulb structure which separates the *Narcisseae* from the *Galantheae*. There are several characters which are not present in all four genera, but they are represented in three genera, or they are exceptions within one genus, or they even unite the two «wrong» of the four genera. Some examples: the cataphylls at the beginning of a growing season may be placed at the beginning of each shoot generation (*Narcissus*, *Leucojum* p.p., *Galanthus*) or more or less in the middle of it (*Sternbergia*, *Leucojum* p.p. and sometimes *Narcissus*). All the other leaves of the vegetative leaf-sequence can produce normal leaf-blades, but in some species of *Narcissus* and *Leucojum*, the uppermost leaf under the inflorescence is more or less reduced, sometimes to a rudiment of 0,1 mm. In *Narcissus serotinus* and *N. viridiflorus* there are no foliage leaves at all in the normal leaf sequence of a flowering bulb but the function of assimilation has been taken over by the scape of the inflorescence (VOGEL & MÜLLER-DOBLIES, 1975). As to the absence of iterative innova-

tion in *Narcisseae* and *Galantheae*, we must admit that under greenhouse conditions a second shoot generation, consisting of a reduced number of foliage leaves and a terminal inflorescence, can be developed (= subiterative innovation). This is a rare exception, but has been observed in three genera: *Leucojum*, *Narcissus* and *Sternbergia*. A characteristic common to some species of *Galanthus* and *Sternbergia* is the production of an annual bulb, consisting of the leaf bases of only one growing season.

PANCRATIEAE.

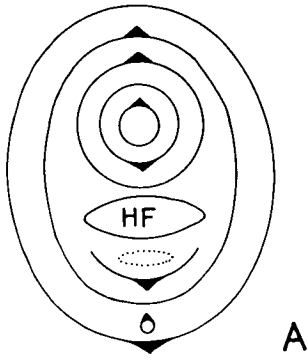
The main characters of bulb morphology of *Pancratium* and *Vagaría* can be summed up in the following list (see fig. 1, C and D):

- a, The prophyll of the renewal bulb has the normal adaxial position of Monocots.
- b, It is a cataphyll clasping less than half the stem.
- c, In one growing season more than one sympodial innovation takes place: iterative innovation (not yet proved for all the species investigated; the number of foliage leaves per shoot-generation varies between three and ten).
- d, There are no sheathing cataphylls in the leaf sequence of a flowering bulb.
- e, In *Pancratium* a cofilorescence is rather uncommon; it was observed once in *Pancratium maritimum* and twice in *P. illyricum*. In *Vagaría ollivieri*, however, its presence is a characteristic feature.

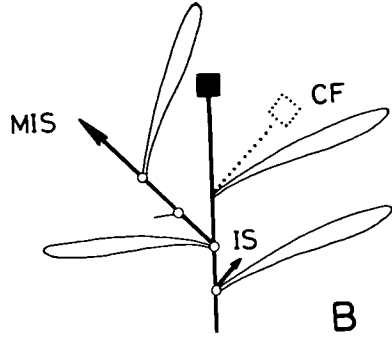
The characters a, b and d of this list are described by IRMISCH (1860) for *Pancratium maritimum*. Our investigations are based on *P. canariense*, *P. foetidum*, *P. illyricum*, *P. maritimum*, *P. trianthum*, *Vagaría ollivieri* and *V. parviflora*.

LAPIEDRA.

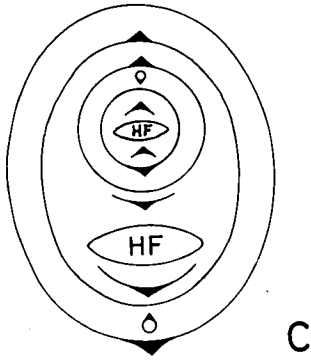
The bulb of *Lapiedra* has a very regular structure. The leaf sequence of a shoot generation begins with an adaxial, less than half-embracing cataphyll and has nearly always three foliage leaves, namely two sheathing ones and the uppermost half clasping the stem. In the axil of the upper sheathing leaf there is the renewal bulb, while the axil of the half-clasping foliage leaf is empty. Not infrequently the inflorescences of two successive shoot generations flower at the same time. More often they flower shortly one after the other. If there are two flower scapes to a bulb, it is also possible that the second one belongs to a bulblet which may develop in the axil of the



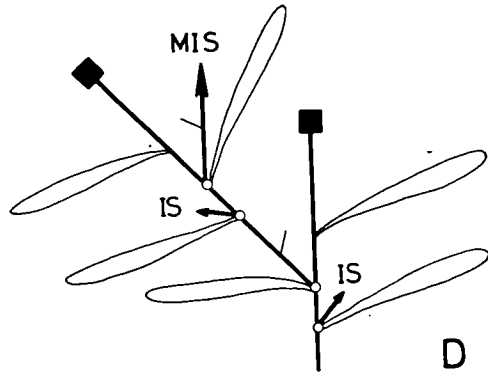
A



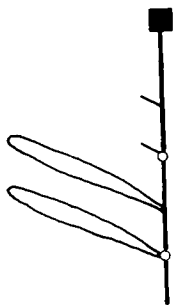
B



C



D



HF = main inflorescence (hierarchiae
inflorescentia principalis = Hauptfloreszenz)

cataphyll with open insertion

cataphyll with amplexicaul insertion

foliage leaf with open insertion

foliage leaf with amplexicaul insertion

Fig. 1.—Innovation conditions in *Narcisseae* (including *Galantheae*, A, B) and *Pantratieae* (C, D). The phenologic relationships between inflorescences, developed leaves and leaf primordia are disregarded. The rather rarely occurring cofillorescence in *Pantratieae* is omitted; fig. C and D thus representing exactly *Lapiedra*. MIS = main innovation shoot (= renewal bulb), IS = innovation shoot (= bulblet), CF = cofillorescence.

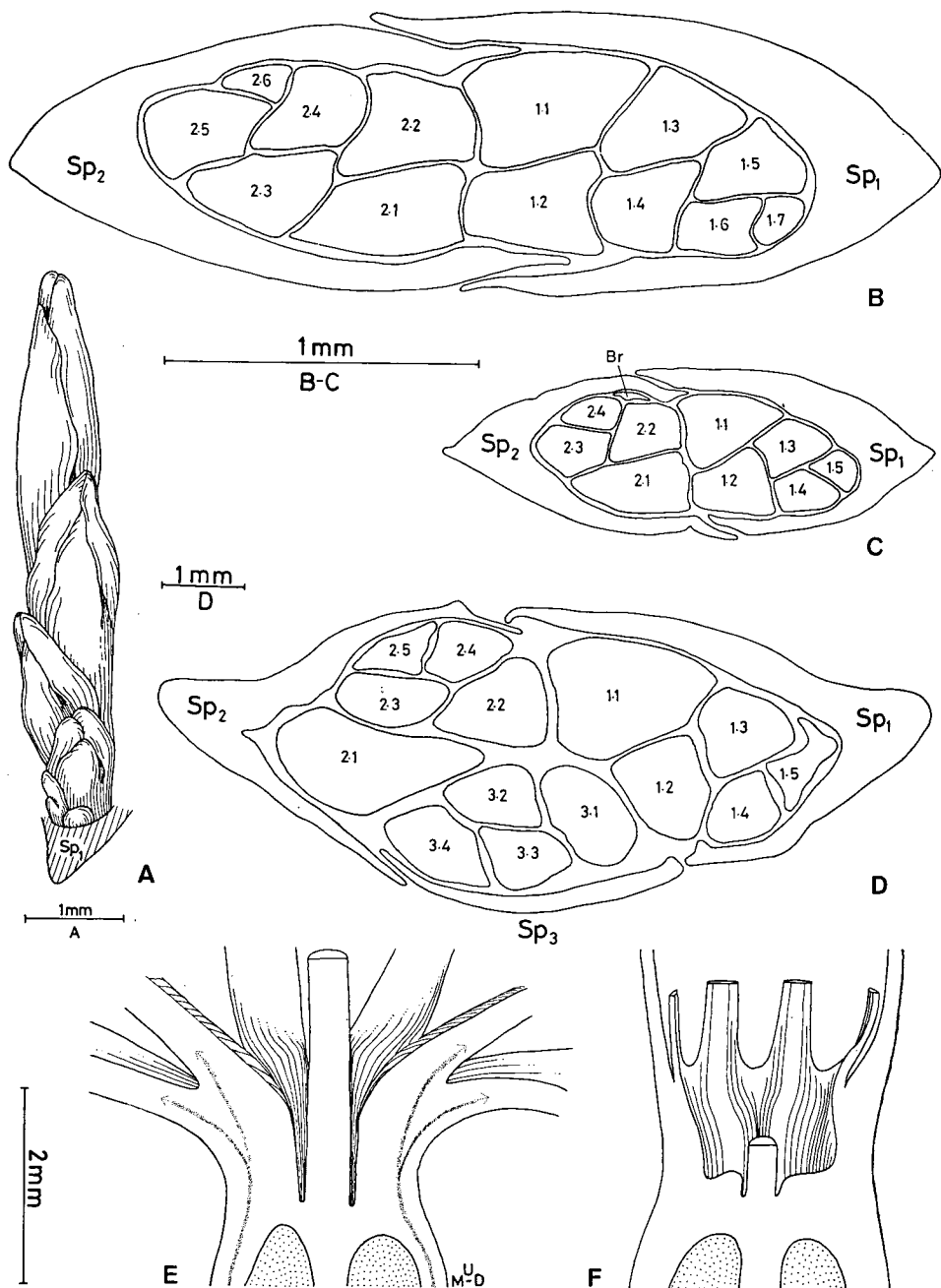


Fig. 2.—*Lapiedra martinezii*. A, scorpioidal cyme in the axil of the removed spathe leaf 1 = Sp₁. B, diagram (cross-section of a bud) of a normal inflorescence with two imbricate spathe leaves. C and D, diagrams of exceptional inflorescences: C contorted aestivation of the two spathe leaves of a very young bud, Br = bract, exceptionally present = prophyll of flower 2.1; D, three spathe leaves and three cincinni. The number of each flower consists of the number of the cincinnus according to its age and behind the point the number of the flower within the cincinnus e.g. 1.1 is the oldest flower of the oldest cyme. E, an open flower cut in half and showing the indistinct tepal tube. F, closed flower (one day after anthesis) cut in half (the tepal tube as well as the very low staminal cup are fairly distinct).

first foliage leaf of each shoot generation. A cophlorescence was never observed.

Thus the bulb structure of *Lapiedra* is in accord with the *Pancreatiae* in all five characters.

REPRODUCTIVE MORPHOLOGY

PREVIOUS REPORTS.

The following floral characters are reported to be of taxonomic importance in Mediterranean *Amaryllidoideae*:

The *Galanthinae* in the original sense of PAX (1887: 105), comprising the three genera *Galanthus*, *Lapiedra*, and *Leucojum*, is the only taxon of *Amaryllidoideae* characterized by the complete absence of a tepal tube (leaving aside the South American *Griffinia gardneriana* (Herb.) Rav., in which the tepal tube is absent or obsolete, according to RAVENNA (1969: 63), and the very short, sometimes almost obsolete, tepal tubes of the South African *Nerine* and *Hessea*).

The absence of a paracorolla is rather widespread among *Amaryllidoideae* but nevertheless of some importance, and characteristic for the *Galanthinae* sensu Pax.

The anthers are medifixed in *Pancratium*, *Vagaría*, *Hannonia*, *Sternbergia* and *Narcissus* p. p., basifixed in *Leucojum*, *Galanthus* and *Narcissus* p. p., and sagittate in *Lapiedra*. The anthers of *Galanthus* and *Leucojum* are usually referred to as parandrous, those of all the other genera are schistandrous.

EVALUATION OF REPRODUCTIVE CHARACTERS FOR THE SYSTEMATIC POSITION OF LAPIEDRA.

In addition to the reproductive characters mentioned above two others of some importance may be mentioned: these are the structure of the partial inflorescence and the elaiosomes of the seeds. Elaiosomes among *Amaryllidoideae* have been reported for *Galanthus* and some species of *Leucojum*, *Narcissus* and *Sternbergia*, that is the *Narcisseae* and *Galantheae*. WERKER & FAHN (1975) mention that the presence of an elaiosome in *Pancratium parviflorum* (*Vagaría parviflora*) was already stated by GALIL in 1952. *Lapiedra* also has a large elaiosome which has been overlooked up till now, so has *Pancratium illyricum*, not until now reported, and perhaps *Vagaría olliiveri*, which is said by MAIRE (1959: 42) to be «strophiolée». Therefore this

character is no obstruction to a transfer of *Lapiedra* from *Galantheae* to *Pancratieae*.

Much the same is true for the partial inflorescences. All the investigated genera of *Amaryllidoideae* with several flowers to an umbel have 2 (rarely more or only one) partial inflorescences of bostrycoid (= helicoid) structure, with the exception of *Clivia* and *Lapiedra*. *Clivia* has several (rarely two) scorpioidal cymes (= cincinni) and *Lapiedra* has two (fig. 2, B-C, exceptionally three, fig. 2, D). Because of this structure, *Lapiedra* is an exception among the *Galantheae* as well as the *Pancratieae*.

In an assessment of the floral characters mentioned in the last chapter, we can state that the insertion of the anther is also not decisive. The sagittate form is an exception among *Amaryllidoideae*, which elsewhere only occurs in *Traubia* from Chile. The beginning of a sagittate base, however, is to be seen in *Leucojum* as well as in *Vagaría* (fig. 3, A-C).

It is true that *Lapiedra* has no distinct staminal cup, but the bases of the filaments are flattened; they touch each other and form a very low connate ring of about 0,15 mm. in height (fig. 3, D-F); this might be interpreted as the ultimate stage of reduction. In any case this type of filament-insertion differs from that in *Galantheae*.

As to the tepal tube of *Lapiedra*, it might also be regarded as reduced. It is in fact indistinct at anthesis (fig. 2, E), which lasts only one day, but by the next day a short tube has become clearly visible (fig. 2, F).

In addition to these rather important characters two minor characters are of interest:

- a, *Leucojum* and *Galanthus* have nodding flowers, but the *Pancratieae* as well as *Lapiedra* have more or less erect flowers.
- b, Among all Mediterranean *Amaryllidaceae* the three genera *Vagaría*, *Hannonia*, and *Lapiedra* are characterised by a green median stripe on the outer side of each tepal segment.

Thus, all the reproductive characters of *Lapiedra* are either of no importance or they tend towards a relationship with the *Pancratieae*. It must be pointed out that in no case is there an obstacle in the floral characters to a transfer of this genus from the *Galantheae* to the *Pancratieae*. But the morphology of the bulb gives a definite indication of relationship between *Lapiedra* and the *Pancratieae*, and that is why we propose to transfer this genus.

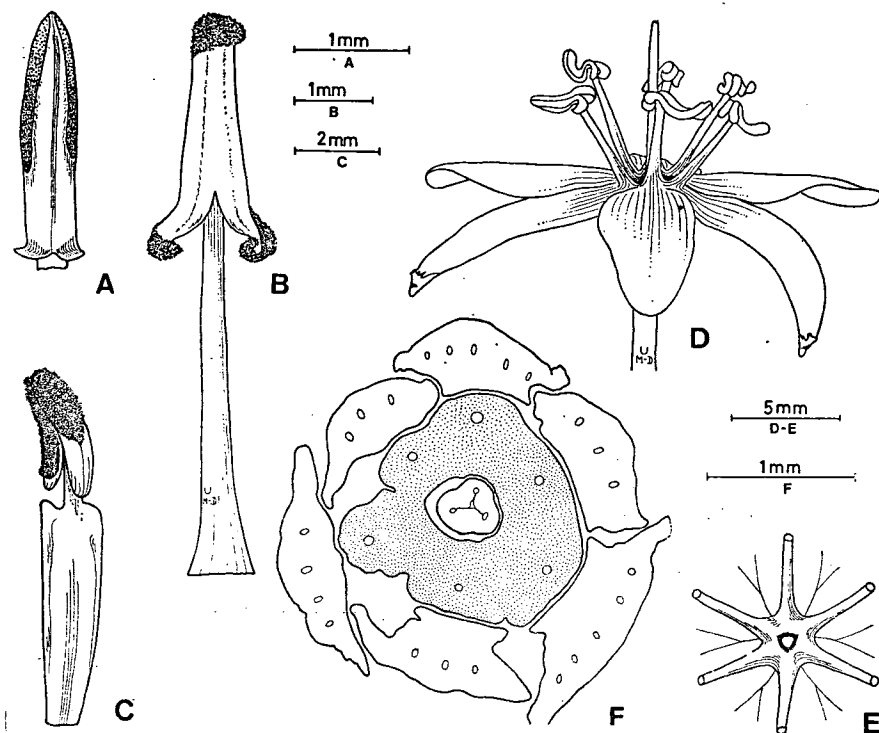


Fig. 3.—A - C, stamens with a more or less sagittate base. A, *Leucojum trichophyllum*; B, *Lapidra martinezii*; C, *Vagarja ollivieri* (filament with two indistinct ventral wings and very variable auricles). D - F, *Lapidra martinezii*; connate insertion of the filaments. D, lateral view of an open flower showing the very low, almost obsolete, staminal cup; E, top view of the connate ring of the filament bases around the style; F, cross-section (somewhat oblique) of a just expanding flower at the level of the connate base of filaments (dotted ring).

Among the *Pancratieae*, *Lapidra* is clearly characterised by the extreme reduction of the tepal tube, the sagittate shape of the anthers, the scorpioidal structure of its cymes, and the lack of nectar. For these reasons we regard it as the only member of the monotypic subtribe:

Lapidrinae D. & U. Müller-Doblies, subtribus nova.

Typus subtribus. *Lapidra* Lagasca, *Gen. Sp. Nov.* 14 (1816).

A *Pancratiinis* perigonii tubo subnullo, nectari deficiente, antheris sagittatis, inflorescentiarum partialium ambarum structura scorpioidea differt.

CLASSIFICATION OF THE MEDITERRANEAN GENERA
OF AMARYLLIDOIDEAE

The previous discussion about the systematic position of *Lapiedra* referred to all eight Mediterranean genera of Amaryllidoideae. Although not yet discussed in detail, the following classification is here proposed (Table 2):

Tribus *Pancratieae* Herb. (1825)

Subtribus *Pancratiinae*

Pancratium L. (1753)

Vagaria Herb. (1837)

Hannonia Br.-Bl. & Maire (1931)

Subtribus *Lapiedrinae* D. & U. Müller-Doblies subtrib. nova

Lapiedra Lag. (1816)

Tribus *Narcisseae* Endl. (1836)

Subtribus *Narcissinae*

Narcissus L. (1753)

Sternbergia Waldst. & Kit. (1805)

Subtribus *Galanthinae* Pax (1887)

Leucojum L. (1753)

Galanthus L. (1753)

Table 2.—Classification of the Mediterranean genera of *Amaryllidoideae* (*).

The necessary transfer of *Hannonia* from the *Galantheae* to the *Pancratieae* was mentioned in the introduction. The results discussed in the chapter on bulb morphology of *Narcisseae* and *Galantheae* point to the fact that there are no differences in bulb morphology between these tribes. With the background of our investigation on the bulbs of 132 species from 36 genera of *Amaryllidaceae*, the *Galantheae* should be reduced to subtribal rank. A more detailed discussion will be offered in further papers on the systematic position of *Sternbergia* and *Hannonia*.

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(*) The author of the tribe *Pancratieae* is different from that in table 1. Since TRAUB (1970: 68, 91) gives the interpretation that the suborder *Amaryllidoideae* of HERBERT is equivalent to infrafamily, the rank marked by a § should be read as tribe and the name *Pancreatiformes* must be changed to *Pancratieae* in accordance with note 2 of article 19 of the I.C.B.N.

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