

Growth-form and taxonomy in *Arenaria* sect. *Plinthine* (Caryophyllaceae)Gonzalo Nieto Feliner¹*Summary*

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A study of the growth-forms in *Arenaria* sect. *Plinthine* is presented, describing and interpreting two different, systematically relevant, patterns that are defined by the position of the innovation buds. The first, apparently the more evolved one, probably constitutes a good synapomorphy for the 7 taxa exhibiting it: innovation buds arise on short, vegetative lateral shoots arising below the starting point of the season's growth of the fertile axis. In the second case innovation buds arise in leaf-axils along the whole length of the season's growth of the flowering shoots, extending to well above the first nodes and up to the base of the inflorescence. Recognition of these two growth-forms helps to solve the old problem of the correct taxonomic placement of the population from Mont Ventoux (S. France), which must be included in *A. aggregata* not *A. erinacea*.

Introduction.

Arenaria sect. *Plinthine* is a clearcut natural group found in the Western Mediterranean region, where it extends from the Maritime Alps (S.E. France, N.W. Italy) to N.E. Algeria, with a maximum diversity in the Iberian Peninsula. Despite of intense recent taxonomic research on this group (for references see López González, 1990: 172), a search for synapomorphies below the sectional level has proved relatively unsuccessful (Nieto Feliner, 1990). A previously neglected character related to growth-form has now been found that appears to be systematically sound and may provide a synapomorphy for about half of the species. This character, also helps solving the old problem of the taxonomic affinity of the population inhabiting the Mont Ventoux (Vaucluse, southern France). Plants from this locality have been recently distributed by the "Société pour l'Échange des Plantes Vasculaires de l'Europe et du bassin méditerranéen" (exs. No. 13970). In a corresponding note, Girard & Lambinon (1991: 62) support the "French floristic tradition" by leaving these plants, at least provisionally, in *A. aggregata* subsp. *erinacea* (Boiss.) Font Quer, a taxon described from Spain.

The circumscription and nomenclature of the taxa here used follows the formal taxonomic treatment by López González (1990).

Growth-form

Within *Arenaria* sect. *Plinthine*, a gross morphological approach might distinguish two different habits of growth: pulvinular with scarcely protruding, few-flowered to one-flowered glomerules, and diffuse with strongly protruding, few-flowered to many-flowered glomerules. However, so simple a distinction does not always indicate true affinity among species since it is severely affected by environmental factors. As a result, both growth forms evidently coexist even within certain

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species, e.g. *A. erina cea* Boiss. and *A. armerina* Bory (Font Quer, 1948; López González & Nieto Feliner, 1986).

The position of the innovation buds (i.e. the buds developing into innovation shoots during the next vegetative phase; cf. Weberling, 1989: 230) with respect to the flowering structures, however, provides a very consistent character, with two different patterns that discriminate two natural groups of species.

Pattern a. - The flowering shoots, at least in their distal half, lack innovation buds; such buds arise predominantly on vegetative shoots which, during the flowering period, are visible as branchlets arising below the season's growth of the fertile axis. At the beginning of the growing season, the terminal buds of innovation shoots formed in the previous season form flowering shoots, while the axillary buds develop into new lateral bud-bearing vegetative shoots (Fig. 1a, 2). These vegetative shoots are uniformly covered with decussate leaves until the end of the fruiting period when their terminal and axillary innovation buds become visible as small green decussate leaflet clusters, contrasting with the spring leaves which are then already dried (Fig. 1a). Because the flowering shoot bears no innovation buds it dies off after fruiting and does not contribute to the "permanent architecture of the plant". It is a differentiated reproductive structure as compared to the second pattern, described below. In some cases the spring leaves of the bud-bearing vegetative shoots are so different morphologically from those of the flowering shoots that one can almost speak of dimorphic leaves, e.g. in *Arenaria querioides* (López González, 1990: 192, fig.53a-c).

Axillary flower buds, arising immediately below the lowest glomerule or flower, should not be mistaken for innovation buds. Such flower buds frequently develop into lateral glomerules or flowers in all the taxa fitting this growth-form, but after the fruiting period they die off. That is why the best time to observe the growth-form is early autumn, when the flowering shoots are dried but still remain on the plant, when the innovation buds have already developed into short overwintering shoots visible as small green decussate leaflet clusters, and when the growth of the current season can still be distinguished from that of previous years (Fig. 1a).

This first growth pattern can be seen in *Arenaria aggregata* (L.) Loisel. subsp. *aggregata* and subsp. *pseudoarmeriastrum* (Rouy) G. López & Nieto Fel., *A. querioides* Pourr. ex Willk., *A. armerina* Bory subsp. *armerina* and subsp. *caesia* (Boiss.) C. Díaz & al., *A. vitoriana* Uribe-Ech. & Alejandre, and *A. oscensis* (Pau) P. Monts. Exceptions to the general pattern have been found only in cases of late blooming, when flowers may appear at the tip of the bud-bearing vegetative shoots described above, probably due to a breakdown of the dormancy normally undergone by the apical buds.

If *Arenaria* sect. *Grandiflorae* McNeill is considered as the sister group of *A.* sect. *Plinthine* (McNeill, 1962: 113; Nieto Feliner, 1990) and if the cyme in that group is accepted as being homologous with a glomerule within *A.* sect. *Plinthine*, then pattern (a) must be considered as derived when compared to the one that follows; in *A.* sect. *Grandiflorae* innovation buds can appear close to the cyme, up to the uppermost leaf-axils.

Pattern b. - Innovation buds occur predominantly in leaf-axils all along the length of the flowering shoots, extending to well above the first nodes of the season's growth and almost up to the terminal glomerule or flower (Fig. 1b). This type of

growth-form lacks well differentiated exclusively reproductive portions; only the flowers and enclosing bracts (glomerules) and, at most, the uppermost nodes die off after fruiting. Most of the season's growth will remain and is integrated into the permanent architecture of the plant. This pattern is particularly efficient for achieving a pulvinular habit, as shown by the specialized, compact cushion-forming *Arenaria alfacarensis* Pamp. (Goyder, 1987), but is not limited to pulvinular species. It is present in *A. tetraquetra* L. subsp. *tetraquetra*, subsp. *amabilis* (Bory) H. Lindb. and

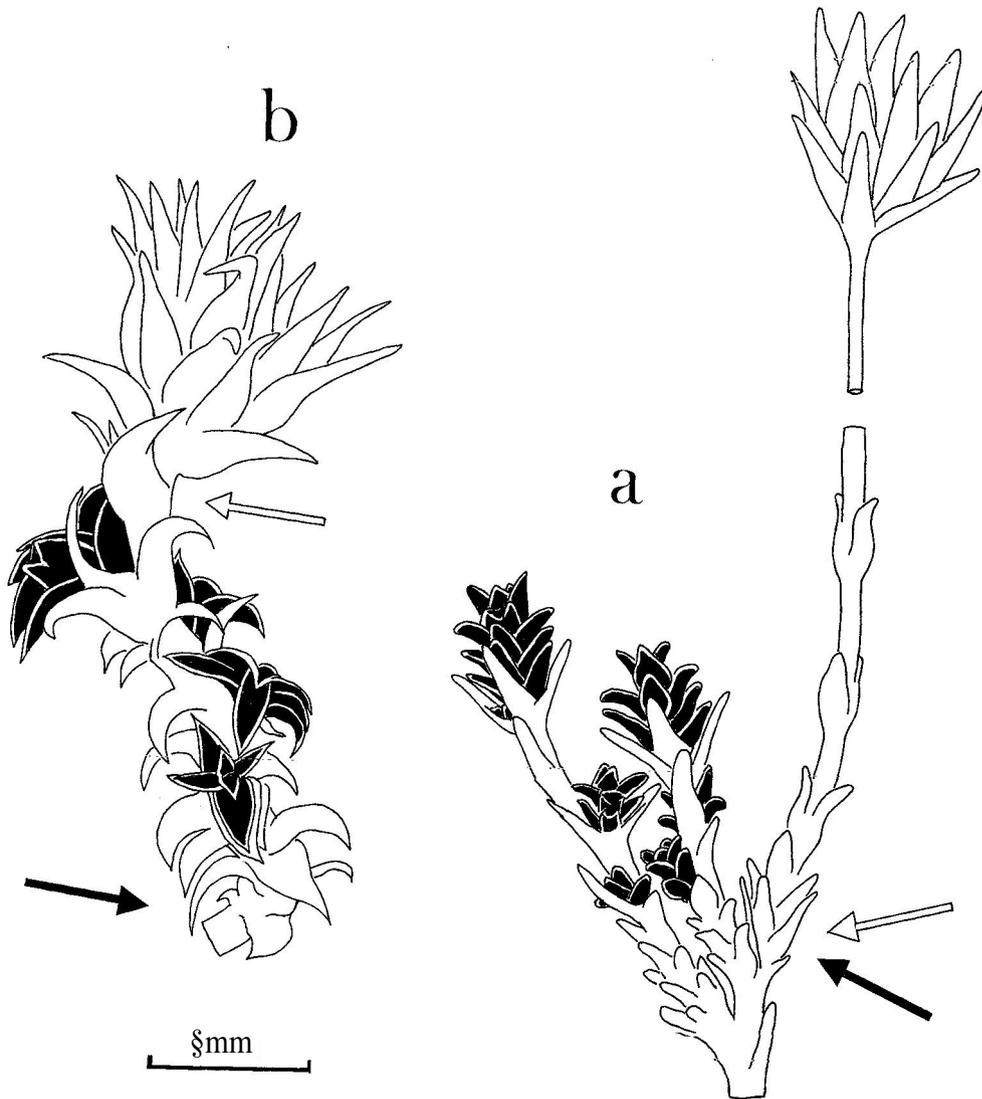


Fig. 1. The two growth patterns recognized in *Arenaria* sect. *Plinthine*; a, *A. armerina*, b, *A. erinacea*; distal portions of branches, in autumn. Short overwintering shoots developed from the innovation buds, the only parts with green tissues in this period, are shown in black. The black arrow indicates the starting point of the current year's growth; the white arrow, the point at which the distal portion of the axis will be shed.

subsp. *murcica* (Font Quer) Favarger & Nieto Fel., *A. tomentosa* Willk., *A. erinacea* Boiss., *A. arcuatociliata* G. López & Nieto Fel., *A. racemosa* Willk., *A. cavanillesiana* (Font Quer & Rivas Goday) Nieto Fel., and *A. javareri* (Nieto Fel.) G. López & Nieto Fel.; *A. aggregata* subsp. *mauritanica* (Batt.) Maire, a poorly known geographically isolated, North-African taxon which has been related to *A. aggregata* (e.g. Greuter & al., 1984), also fits type (b), so that if type (a) is, in fact, a synapomorphy then this taxon cannot be closely related with *A. aggregata* which shows pattern (a). In some taxa not displaying pulvinular habit, particularly in *A. cavanillesiana*, *A. javareri* and *A. aggregata* subsp. *mauritanica*, the middle and upper nodes are quite fragile and disarticulate easily after fruiting, together with the uppermost innovation buds; this results in the dispersion of the entire glomerule(s) containing the seeds, not in vegetative propagation. As a consequence, the lower innovation buds will often be the only ones to overwinter successfully and continue growth, which is thus less efficient than in plants with a pulvinular habit.

The population on Mont Ventoux

The Mont Ventoux population has been referred to *Arenaria erinacea* by French authors (Rouy & Foucaud, 1896: 254; Fournier, 1934-1940: 297), either in the specific or subspecific rank. Chater & Halliday (1964: 119; 1993: 143) consider these plants to be intermediate between *A. aggregata* subsp. *aggregata* and subsp. *erinacea*, whereupon Jalas & Suominen (1983: 15) as well as Greuter & al. (1984: 169)

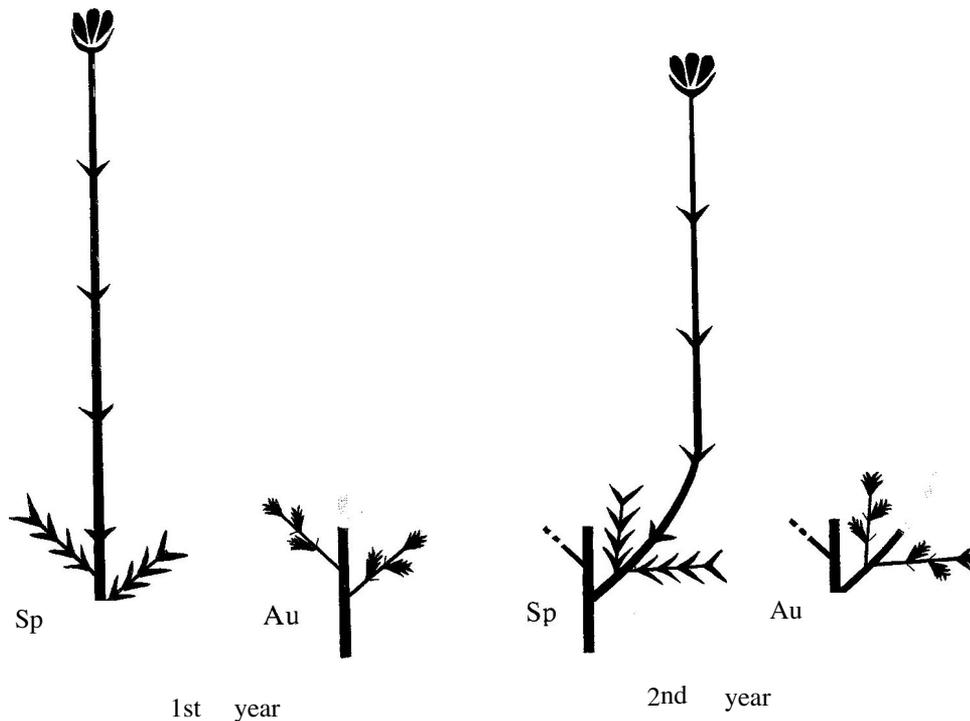


Fig. 2. A two-year schematic sequence in the development of flowering shoots in *Arenaria armerina*; Sp, spring; Au, autumn.

both questioned the occurrence of *A. erinacea* (or *A. aggregata* subsp. *erinacea*) in France. A different opinion was held by Font Quer (1948: 41), followed by López González & Nieto Feliner (1986: 356) and Goyder (1988: 25), who considered such mountain populations as condensed forms of *A. aggregata*; Gontard's (1953: 64-70) discussion, although unclear, also relates the Mont Ventoux plants to *A. aggregata*. Girerd's recent exsiccatum (Girerd & Lambinon, 1991: 62) was available for study along with copious collections made on the same mountain during a joint excursion of the Conservatoire Botanique de Genève and the Real Jardín Botánico de Madrid in 1990.

The growth pattern of the French plants invariably fits type (a), i.e., the innovation buds are consistently placed on short vegetative shoots arising below the starting point of the season's growth of the fertile axis. True, the flowering shoots are shorter than in plants growing at lower altitudes and in less exposed situations, and the glomerules may contain as few as a single flower (but more commonly 3 to 5). Given that Spanish *Arenaria erinacea* consistently exhibits a type (b) growth pattern, the plants from Mont Ventoux, as from all other French localities, cannot be identified with *A. erinacea* or considered as a subspecies of it, but must be included in *A. aggregata*. The fact that more or less pulvinular specimens occur in species of the first group (*A. aggregata*, and also *A. armerina*) adds to the systematic relevance of the character discussed and implies that cushion habit, in this group, arose independently at least twice.

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