**A new species of *Armeria* (Plumbaginaceae) from southern Spain with
molecular and morphometric evidence on its origin**

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Running title: *Armeria* (Plumbaginaceae) from S Spain

Abstract:

The taxonomic status of the populations of *Armeria* from the Horconera massif (Córdoba province), previously misidentified or referred to without an explicit identification, is re-examined on the basis of morphological and molecular data. A multivariate analysis indicates that they can be discriminated from morphologically and geographically close taxa using morphometric characters. According to these results, and taking into account the previous evidence that supports extensive reticulation in the genus, a new species, *A. trianai*, is formally described. Molecular evidence from our previous works, in particular the nuclear ribosomal ITS sequence data, provide the frame for a discussion on the origin of the new entity. It is suggested that *A. trianai* may be the result of introgression of sympatric populations of *A. villosa* subsp. *longiaristata* into a pre-existing taxon, possibly *A. filicaulis* var. *minor* presently occurring in Sierra Tejeda some 50 km apart.

ADDITIONAL KEY WORDS: Multivariate analysis - reticulation – species concept – taxonomy – Córdoba province.

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Introduction

The present paper is part of a research program aiming to clarify the contribution of hybridisation to diversity in the genus *Armeria*. In recent works, we have sampled populations of uncertain taxonomic affinities from the Horconera massif (Córdoba province, Southern Spain) for different molecular markers, without attaching to them an explicit specific label (Fuentes Aguilar, Rosselló & Nieto Feliner, 1999b; Rosselló, Fuentes Aguilar & Nieto Feliner, 1999; Nieto Feliner *et al.* unpubl.). The accumulation of molecular evidence for those populations, referred to as species “a” in previous works, has prompted us to reappraise their taxonomic identity and status.

These populations, originally known from a few specimens, were recorded as *A. maritima* subsp. *alpina* (Willd.) P. Silva (Devesa & Pinto da Silva, 1984; Muñoz & Domínguez, 1985; Devesa, 1987). Such identification was rejected on morphological basis in favor of a plausible hybrid origin, in which *A. villosa* subsp. *longiaristata* (Boiss.) Nieto Fel. would be involved (Nieto Feliner, 1987). Lacking further data, the status of these populations was not explicitly addressed in the account of the genus for *Flora Iberica* (Nieto Feliner, 1990).

More recently, the same entity has been found to be not rare in three mountain peaks within the Horconera massif (Triano, 1998). The largest distance within populations is ca. 4 km, and the area covered is less than 10 km². With the living and herbarium material available thanks to E. Triano, we have been able to sample individuals from those populations for nuclear

ribosomal DNA ITS sequences, chloroplastic sequences (the *trnL-trnF* spacer) and RAPDs (unpubl.).

The objective of this paper is to address the taxonomic identification of these populations in the light of all the available evidence, both morphological and molecular, and also to discuss their possible origin.

On a morphological basis, i.e., using exclusively an identification key that is comprehensive for the Iberian Peninsula (Nieto Feliner, 1990), specimens from these Horconera populations cannot be properly keyed out. Matching the *A. alpina* Willd. group is not possible because of the presence of non-linear leaves (step nr. 11). On the other hand, following the alternative path we get near *A. pubinervis* Boiss. or *A. rothmaleri* Nieto Fel., but without satisfying the characters mentioned in the key (steps nr. 68-70). When not only characters used in the key but all morphological characters considered taxonomically informative are examined, these plants do not fall clearly within any of the taxa recognized in the treatment for the territory (Bernis, 1954; Nieto Feliner, 1990). The study of new material, both living and dry, reveals a consistent combination of characters. This suggests that the Horconera populations deserve taxonomic recognition. However, when proposing formal taxonomic recognition of any entity within *Armeria*, careful attention must be paid to the biological peculiarities of the genus.

These biological peculiarities can be summarised as follows. Internal reproductive barriers are weak (Nieto Feliner, 1997; Nieto Feliner, Izuzquiza & Lansac, 1996) and most populations include diploid obligate outcrossers exhibiting a self-incompatibility system (Baker, 1966). Morphological patterns of variation, detectable doing herbarium work, reveal a complex picture including

great amounts of polymorphism (Bernis, 1954; Nieto Feliner, 1987). Much of such variation is genetic (Lefèbvre, 1971; Philipp, 1974; Woodell & Dale, 1993). Moreover, some morphometric characters, that are reliable markers for introgression because they have clear additive effects, do reflect intermediacy in experimental hybrids (Nieto Feliner, 1997; Nieto Feliner *et al.*, 1996). These features, together with the fact that sympatry among congeners is frequent within the main centre of diversity (the Iberian Peninsula), support reports of hybridisation in the literature (Bernis, 1954; Lefèbvre, 1969; Arrigoni, 1970; Philipp, 1974; Stace, 1975; Nieto Feliner, 1993). Furthermore, the geographical pattern of variation of the molecular ITS regions suggests that hybridisation among sympatric congeners occurs extensively so as to apparently fit the compilospecies model (Fuertes Aguilar *et al.*, 1999b).

Therefore, besides the formal description of the new taxon, a discussion is here provided on its possible origin, taking into account the morphological and molecular evidence.

Material and Methods

In addition to the individual study of relevant characters, a morphometric multivariate approach has been followed to explore phenetic affinities of the new taxon. We have performed analyses on two different data sets. The first has been elaborated on a morphological affinity basis ('morphological matrix'). It includes specimens belonging to the populations from the Horconera massif and to the four species that morphologically resemble them. These are *A. alpina*, *A. cantabrica* Willk. and *A. bigerrensis* (C. Vicioso & Beltrán) Rivas Mart.

subsp. *bigerrensis*, from the *A. alpina* group, and *A. pubinervis* (Appendix 1, Fig. 1). The four species are allopatric with respect to the Horconera populations, the closest one, *A. bigerrensis*, lying ca. 350 km apart. *Armeria alpina* occurs in the Pyrenees, Alps, Carpathians and Balkans. *Armeria cantabrica* is distributed on the Cantabrian range and other northern Spanish massifs. *Armeria pubinervis* occurs in N Spain (Basque country, Navarra) and S France (Pyrénées Atlantiques), but non-typical populations reach the Picos de Europa range, on the eastern end of its distribution. *Armeria bigerrensis* subsp. *bigerrensis* occurs in the Gredos range, in central Spain, and locally in a NW range (Nieto Feliner & Aldasoro, 1995). With this first data set, we tried to see if the plants from the Horconera massif could be discriminated from those, which morphologically appear to be the closest.

The rationale for analysing a second morphometric data matrix stems from the biological characteristics of *Armeria* summarised above. With that background information, sampling only the morphologically similar taxa to look for affinities, without considering the sympatric species, could neglect morphological influence through hybridisation and introgression. To try to account for this potential source of morphological similarity, a second data matrix has been elaborated for morphometric analysis on a spatial proximity basis ('geographical matrix'). Besides the Horconera specimens, this data set includes five taxa: *A. splendens* (Lag. & Rodr.) Webb, *A. villosa* subsp. *longiaristata* and subsp. *bernisi* Nieto Fel., *A. filicaulis* (Boiss.) Boiss. subsp. *filicaulis* and subsp. *nevadensis* Nieto Fel. et al. (Appendix 1). Within subsp. *filicaulis*, we have labelled independently populations from higher altitudes (1200-1700 m) in Sierra Tejeda (Málaga) that exhibit some differing characters

like purple petals and curved short scapes, and were given varietal status (var. *minor* Boissier, 1841-1845).

All measurements have been made on herbarium specimens, which are kept in MA. The total number of herbarium specimens analysed in the morphometric multivariate analysis is 103 (Appendix 1). As explained above, they were separately analysed in two different matrices, the 'morphological matrix' containing 50 specimens and the 'geographical matrix' containing 63 specimens. Twenty characters (Table 1) have been selected for their discriminatory power on the basis of our previous works (Nieto Feliner, 1997; Nieto Feliner *et al.*, 1996). Eleven of them are quantitative continuous, six are ratios between one of those quantitative characters and another not included in the analyses, one is quantitative discrete (number of bracts) and two are qualitative (petal colour, linear leaves). For the eleven continuous characters, values in the data matrix are averages of two or three measurements per specimen. Most of the metric characters were measured with the aid of a Brown & Sharpe Plus digital calliper (model 599-571-3).

The morphometric study was conducted using SPSS 7.5 for Windows. Two different analyses have been carried out on each of the matrices. A principal components analysis (PCA), based on the correlation matrix, was used to examine structural relationships among characters and among species and, accordingly, to reduce the number of original variables to a few representative uncorrelated ones (the PCs).

Because of its property to maximise among-group variation relative to within-group variation, a discriminant analysis (DA) was conducted to test if the Horconera populations could be discriminated efficiently from the rest. Percent of

'correctly' classified specimens was obtained using the rigorous Jackknife method, which places each specimen out when its predicted group membership is going to be calculated.

Taxonomy follows Nieto Feliner (1990) with the addition in Nieto Feliner, Rosselló & Fuertes Aguilar (1998).

Results

Morphometric multivariate analyses

'Morphological matrix'.-- The first three principal components together only explain 55% of the total variance (31.7, 12.1 and 10.9, respectively). The highest factor loadings in the first principal component are those of variables INVODIA, CALXLTH, SPBRLTH, LEAVLTH, and LONBRLTH. Variables SCAPLTH and SH/INV contribute most, with high negative values, to the second principal component, while SPB/LON and LINEAR do so to the third one. The scatterplot of the 50 specimens analysed against the first two principal components does not reveal discrete groups (Fig. 2A). The closest species to the Horconera populations is *A. bigerrensis*, with which there is considerable overlap.

The first two discriminant functions together explain 87% of the variance. The first discriminant function is most highly correlated with LINEAR and SCAPLTH while the second is with INVODIA, INNBRWDTH, LONBRLTH, SPBRLTH, LEAVLTH, CALXLTH, and DIAM. The scatterplot of the specimens against those two functions provides good discrimination for the Horconera populations as well as for *A. bigerrensis* and mostly for *A. pubinervis* (Fig. 2B). Some overlap occurs between *A. alpina* and *cantabrica*. Sixty-two percent of the

cases were correctly classified. But the considerable high number of misclassified specimens only included one from the Horconera massif, which was classified as *A. pubinervis*.

‘Geographical matrix’.--The first three principal components together explain 69% of the total variance (42.6, 16.8 and 9.9, respectively). The first PC is most influenced by variables CALXLTH, INVODIA, DIAM, SPBRLTH, and LINEAR. Variables COLOR and LTH/WDTH contribute most to the second principal component, while SPB/LON does to the third one. The scatterplot of the 63 specimens analysed against the first two principal components, provides a clear ordination of the data despite the fact that the number of groups is higher than in the other matrix (Fig. 2C). The Horconera populations, and *A. villosa* (subsp. *longiaristata* and *bernisi*) form two separate clusters. The remaining specimens are arranged in a loose cloud in which *A. splendens* is adjacent but non-overlapped with the *A. filicaulis* samples.

The discriminant analysis results in 97% of the specimens correctly classified. The first three discriminant functions together explain 86.5% of the variance. The first discriminant function is most highly correlated with CALXLTH, SPBRLTH, TUBELTH, INVODIA, and DIAM while the second is contributed mostly by SCAPLTH and LONBRLTH, and the third is by INNBRWDTH and SPB/LON. We represent the scatterplot of the specimens against the second and third discriminant functions because the first one, although explaining a high percent of the variance, is mostly concerned with the discrimination of *A. villosa* from the rest (Fig. 2D). The scatterplot of the second and third functions provides good discrimination for the Horconera populations as well as for *A. filicaulis*

subsp. *nevadensis*, and the populations of *A. filicaulis* from Sierra Tejada (var. minor). A loose cluster in the middle of the morphospace contains the two subspecies of *A. villosa* and on two opposite ends, *A. splendens* and *A. filicaulis* subsp. *filicaulis*, respectively.

Description of the new species

Based on the comparative morphological study of the specimens from the Horconera massif, and with the support from the morphometric study that has taken into account possible affinities either through common ancestry or through hybridisation, we propose to recognise their taxonomic identity and describe them as a new species:

***Armeria trianai*, Nieto Fel., sp. nov.**

Diagnosis:

Speciei *A. alpina* Willd. (quicum olim commutata) similis; a qua vero, inter alia, basi minus ramificata (planta ideo non caespitosa!), foliis non accurate linearibus (paulo eo amplius vel, ut plurimum, lineari-lanceolatis), paulo tenerioribus, clare sed anguste marginatis, margine ciliatis, albogranulatis (ob salinarum glandularum praesentiam), scapis porro arcuatis, bracteis involucribus stramineis, bracteis spicularibus macula subapicali purpurea nequaquam insignibus differt.

Insuper speciei *A. pubinervi* Boiss. similis, a qua foliis angustioribus (non ita lanceolatis), paulo tenerioribus, albomarginatis (ob salinarum glandularum

praesentiam), scapis porro brevioribus et distincte arcuatis corollaque roseopurpurea differt.

Habitat in montibus calcareis macizo de Horconera dictis, in provincia hispana Córdoba, locis rupestribus, rimosis, inter 1300 et 1500 m sitis.

Holotypus: Spain, Córdoba, Priego, macizo de Horconera, Alhucemas, 30SUG8737, 1350 m, J. Fuertes, B. Gutiérrez, G. Nieto Feliner 3994GN & E. Triano, 25-V-1999, MA 630587. (Fig. 3). Isotypus: MA 630588.

Additional specimens studied: Spain, Córdoba, macizo de Horconera, Pico Bermejo, 30SUG54, bajando al cañalizo de Peñalisa, S. Silvestre *et al.* (SEV 76396, 82315, 82326, SALA 38170). Macizo de Horconera, Tiñosa, 30SUG9038, 1550 m, E. Triano *et al.*, 11-V-1997, MA 631754; Ibidem, E. Triano *et al.*, 15-VI-1998, MA 631755.

The new species is dedicated to E. Triano, who encouraged our re-assessment of the *Armeria* from the Subbaetic massif in Córdoba with his collections and has contributed actively to the floristic study of the area.

Description:

Perennial herb with a very short-branched woody rootstock, the upper parts covered by foliar remains. Scapes 5-15 cm, curved. Leaves 15-40 x (1.2)1.5-4(4.5) mm, monomorphic, concentrated at the end of the rootstock branches, sublinear to linear-lanceolate, (1)-3-veined, obtuse to subacute, with a narrow scarious ciliate margin (cilia ca. 0.1 mm), with white salt crystals scattered on the surface. Involucral sheath 4-9(11) mm. Involucre 13-16 mm in diameter. Involucral bracts 10-13, straw-coloured, the outer shorter than the inner, the

middle and inner awnless. Spikelet bracts clearly visible within the involucre, widely scarious, with a green central portion, without purple subapical spot. Calyx 6.2-7.2 mm long, pubescent on the 10 ribs (hairs 0.3-0.6 mm); lobes 1.2-1.6 mm (including the awn); tube 2-2.8 mm; scarious limb 2.3-3 mm, frequently tawny-coloured, pedicel scar 0.3-0.5 mm. Corolla purplish-pink.

An amendment for the key in Nieto Feliner (1990: 648) to accommodate the new species follows:

- 68. Outer involucral bracts shorter than the median ones..... 67b
- Outer involucral bracts longer than the median ones..... 71
- 67b. Leaves with white salt crystals scattered on the surface; involucral sheath usually <10 mm *A. trianai*
- Leaves without white salt crystals scattered on the surface; involucral sheath usually >10 mm68

Discussion

Morphometric multivariate analyses

The multivariate analysis of the 'morphological matrix' indicates that *A. trianai* shows similarities with some of the taxa in the *A. alpina* group as suggested by the PCA. This also explains the first identification given to the plant (Devesa & Pinto da Silva, 1984). With this result alone, we would need to consider the inclusion of *A. trianai* in the *A. alpina* group. However, PCA typically provides discrimination among species whenever the largest components of the overall variance, the first PC axes, are contributed significantly

by differences among species. On the other hand, when intraspecific variability for some characters is high and these characters are not correlated with those providing among-species discrimination, scatterplots of samples against the first PC axes may not properly depict relationships among the species. That is why a discriminant analysis should be additionally tried to check for discrimination, taking into account both the way specimens are distributed in the scatterplots as well as the percent of correctly classified specimens using a strict procedure as the Jackknife. The discriminant analysis does, in fact, allow good separation not only for *A. trianoi* but also for most of the five groups considered. Overlap between *pubinervis* and *cantabrica* (specimen #35, Appendix 1) in the plot is due to the inclusion of eastern populations of *A. pubinervis* from Picos de Europa. These populations, long recognised as conflicting (Bernis, 1957; Nava, 1988), have been suggested to be the result of introgression from *A. cantabrica* into *A. pubinervis* (Nieto Feliner, 1987).

In addition to the fact that discriminant analysis separates *A. trianoi* from the morphologically similar species, it must be stressed that in the multivariate analysis we are neglecting other important characters. Some of them are difficult to codify, like the degree of branching and condensation of the rootstock. Although these analyses are quite robust to small departures from normality (Marcus, 1990), we have preferred to included only two qualitative characters in order to avoid more serious violation of assumptions. As a consequence, in the PCA and in the DA we are excluding the following characters that separate *A. trianoi* from the *A. alpina* group. The populations from the Horconera massif have a more condensed rootstock, which does not produce the characteristic caespitose habit of the *alpina* group; the leaves are

more tender than in the *alpina* group, lacking the thick shiny epidermis, present a narrow scarious ciliate margin and white crystals accumulating on the surface above the salt glands; the spikelet bracts are more widely scarious and lack the purple spot on the upper third.

Morphometric analysis of the 'geographical matrix' results in a clear discrimination for the *Horconera* populations. The fact that not only DA but also PCA separates them efficiently is due to the coincidence in the most influential variables both for the first PC axis and for the first discriminant function. With these results, we might wonder if it makes sense to analyse this 'geographical matrix', i.e., to compare *A. trianoi* with merely geographically close congeners. On the basis of morphological characters alone, there are clues suggesting kinship between *A. trianoi* and *A. villosa* subsp. *longiaristata* that would justify including the latter in the morphometric study. These clues are the scarious ciliate margin, the arrangement of leaves at the end of the branches, the rootstock, as well as some trends in the involucral bracts shape that are not apparent in every inflorescence. However, when this approach seems to find full justification is when considering the molecular evidence available, summarised below.

Molecular data

Nuclear markers.-- The internal transcribed spacer region of the nuclear ribosomal DNA (ITS) is the most comprehensively sampled marker in *Armeria*. Our previous results (Fuertes Aguilar *et al.*, 1999b), confirmed by unpublished data based on 130 sequences, reveal that variation for this marker shows a remarkable geographical structure for the whole genus. Different species from

the same geographical area have identical or very similar ITS sequences (ribotypes) and those species whose area is large may have different sequences in different areas. This pattern can be explained in terms of gene flow between different species, which we know is possible based on previous evidence, followed by concerted evolution of these multicopy regions (Fuentes Aguilar, Rosselló & Nieto Feliner, 1999a).

Based on such comprehensive sampling, especially for southern Spain, we discovered that the populations from Horconera (stars, Fig. 4, Appendix 2) share their ribotype only with populations of *A. villosa* subsp. *longiaristata* from central Andalusia (Cordoba, Sevilla and Jaen provinces; triangles, Fig. 4, Appendix 2), and the purple-flowered populations of *A. filicaulis* from Sierra Tejeda (var. *minor*; squares, Fig. 4, Appendix 2), as well as one sample of *A. filicaulis* from Sierra de Alfacar (Granada, circle, Fig. 4, Appendix 2). Strikingly, but in accordance with the general geographic pattern detected, other samples of *A. villosa* from other areas within southern Spain present a different sequence. Of the other taxa sampled for morphometrics in this paper, *A. villosa* subsp. *bernisii* shares the sequence both with *A. filicaulis* subsp. *nevadensis* and with *A. splendens*. The ITS sequence of the other species sampled for the multivariate analysis in the 'morphological matrix' is also different from the populations from Horconera (Fuentes Aguilar *et al.*, 1999b). The ITS data thus suggest relationships between *A. trianoi*, the geographically close populations of *A. villosa* subsp. *longiaristata*, and the relatively close purple-flowered populations of *A. filicaulis*.

Our sampling of RAPD markers (unpublished) is more limited and was oriented towards the reassessment of the possible hybrid origin of *A. villosa*

subsp. *carratracensis* in southern Spain (Nieto Feliner *et al.*, 1996; Rosselló *et al.*, 1999; unpubl. data). However, such sampling was wide enough to include material from *A. villosa* subsp. *longiaristata*, as well as subsp. *bernisii*, subsp. *carratracensis* (Bernis) Nieto Fel., *A. colorata* Pau and *A. trianoi*. In a UPGMA phenogram based on a Dice similarity matrix, the samples from *A. trianoi* cluster within a group almost exclusively composed by samples of *A. villosa* subsp. *longiaristata* from central Andalusia. These samples are the same that share the ITS sequence with *A. trianoi*. Therefore, the results from the ITS and from a total DNA but fundamentally nuclear marker like RAPDs, both suggest close relationship between *A. trianoi* and *A. villosa* subsp. *longiaristata* from neighbouring areas.

Chloroplastic markers.-- We have preliminary data (unpubl.) from the *trnL* - *trnF* spacer sequences (Taberlet *et al.*, 1991). The sampling focuses on Andalusian *Armeria* but covers also taxa from other regions, altogether involving a hundred samples. The single haplotype found in several samples of *A. trianoi* is identical to the one detected in *A. villosa* subsp. *longiaristata* from the same area (Cabra, prov. Córdoba, Fig. 4, Appendix 2), and differs from the haplotypes found in *A. filicaulis*.

Origin of Armeria trianoi

In a genus with low reproductive barriers and a region with the highest concentration of morphological diversity, the contribution of hybridisation or introgression in the origin a biological entity should be examined. There is

various evidence (reproductive, ecological, morphometric, molecular, and from experimental hybridisation) supporting not only the hybrid origin of other taxa (Nieto Feliner *et al.*, 1996; Nieto Feliner, 1997) but also the extensive occurrence of reticulation (Fuentes Aguilar *et al.*, 1999 a, b). Accordingly, for *A. trianoi*, we consider two possible scenarios, divergence or reticulation.

For the first scenario (divergence) the main question is whether a search for the sister group of *A. trianoi* would lead us to a taxon other than *A. villosa* subsp. *longiaristata*. As explained above, in the ITS tree *A. trianoi* falls in the same clade as *A. villosa* subsp. *longiaristata* (Fig. 4; Fuentes Aguilar *et al.*, 1999b). But that is a gene tree, affected by molecular mechanisms like biased concerted evolution that homogenises sequences across reproductive groups. Because reproductive groups are different taxa, information on species evolutionary history is being partially erased (Nieto Feliner *et al.* unpubl.). Therefore, we cannot look for the sister group of *A. trianoi* in that gene tree.

Unfortunately, the morphological data in the genus are not suitable for a cladistic analysis. A great portion of the characters that distinguish species are continuous and their ranges overlap largely so that even if some type of gap-coding was applied, the matrix would be very inappropriate. Besides, high levels of intraspecific variability require that a large number of characters be coded as polymorphic or missing. Even in the absence of a reliable species phylogenetic tree, no extant species seem to be more closely related to *A. trianoi* than *A. villosa*. Morphological resemblance with the *A. alpina* group does not seem to support a close relationship. The overall similarity is mainly based on the purple corollas, and other morphometric characters, like the short involucral sheaths, which if considered in the context of the whole genus are very likely due to

convergence. On molecular grounds, *A. trianoi* is not closely related to *A. alpina* either (Fuertes Aguilar *et al.*, 1999b). Besides, as explained above, such overall similarity between *A. alpina* and *A. trianoi* neglects important characters, all of which relate the Horconera populations with *A. villosa* subsp. *longiaristata*. However, the reason why recent common ancestry, without reticulation, does not seem likely to be the true relationship between *A. villosa* subsp. *longiaristata* and *A. trianoi* is that, despite sharing some morphological characters, their overall similarity is moderate. Therefore, if they were true sister species, a significant transformation in some morphological characters in *A. villosa* subsp. *longiaristata* should have occurred to produce *A. trianoi*. These characters in *A. trianoi* departing from *A. villosa* are the short calyces with short lobules relative to the calyx (LOB/CAL), the purplish-pink petals, the white crystals from the salt glands, and the short strongly curved scapes.

From a narrow perspective, i.e., if we just consider that *A. trianoi* shares the ITS sequence with central Andalusian populations of *A. villosa* subsp. *longiaristata*, the molecular evidence does not contradict that *A. trianoi* arose through divergence from central Andalusian populations of the latter. However, when invoking ITS similarity it should be taken into account that part of the nucleotide similarity is due to hybridisation followed by concerted evolution rather than to recent common ancestry (Fuertes Aguilar *et al.*, 1999 a, b; Nieto Feliner *et al.*, unpubl.).

The second scenario is reticulation. Even if various evidence is available for the occurrence of extensive hybridisation within *Armeria*, we lack unequivocal data to explain the origin of *A. trianoi* through reticulation. However, this second scenario explains more efficiently all the existing data.

From the morphological point of view, it is true that the multivariate analysis does not provide support for a hybrid origin, at least in terms of intermediacy (Fig. 2C). *Armeria trianoi* does not appear in an intermediate position to *A. villosa* subsp. *longiaristata* and something else. But intermediacy in the morphospace is not necessarily expected for hybrid taxa, particularly if the hybrid taxon has not arisen directly from a F_1 lineage but has arisen following backcrosses towards one of the parents, i.e. from an introgressed line. Intermediacy occurs only when multigenic characters, that have additive effects, are being evaluated (Rieseberg & Ellstrand, 1993). Even if the characters studied are additive, what suggests hybridity is character-by-character intermediacy not overall intermediacy (multivariate intermediacy cf. Wilson, 1992).

Morphological characters examined on an individual basis, as potential markers for hybridisation, provide evidence that is consistent albeit not conclusive with the reticulation scenario. As stated above, a significant shift in several characters would be needed to explain the origin of *A. trianoi* through divergence from *A. villosa* subsp. *longiaristata* or its ancestors. In inland Andalusia, besides *A. trianoi*, white crystals from the salt glands are exclusively found in *A. filicaulis*. Another of these characters, the purple flowers is unlikely to have arisen through divergence within the *A. villosa* group. All the six subspecies of *A. villosa* bear white flowers, even the ones growing at higher elevations, like subsp. *villosa* and subsp. *bernisii* (Nieto Feliner, 1990). The shift from white to purple flowers in a divergent scenario cannot be excluded. However, the scattered occurrence of pink to purple flowers within other white-flowered groups of *Armeria* is always better explained by hybridisation.

Examples are populations of *A. transmontana* (Samp.) G. H. M. Lawr. in the León province, of *A. pubinervis* in the Pyrenees, and of *A. filicaulis* subsp. *nevadensis*, in Sierra Nevada (Nieto Feliner, 1990; Nieto Feliner *et al.*, 1998).

The argument for invoking the reticulation scenario is also based on the fact that populations gathering those morphological characters that differentiate *A. trianoi* from *A. villosa* subsp. *longiaristata* are present only 50 km apart from the Horconera massif (Fig. 5). These are the populations of *A. filicaulis* described by Boissier as var. *minor*, which besides the purple flowers and salt glands, bear short curved scapes. The quantitative differences in calyx between *A. trianoi* and *A. villosa* subsp. *longiaristata* could also be explained by hybridisation between the latter and *A. filicaulis* var. *minor*.

Our hypothesis is that *A. trianoi* is the result of introgression from *A. villosa* subsp. *longiaristata* into a pre-existing *Armeria* occurring in the altitudinal range of 1300 to 1500 m in the Horconera massif. If we take into account the extant taxa, the simplest explanation would be that *A. filicaulis* var. *minor* was in fact the pre-existing taxon. The morphological data already mentioned and the molecular data (same ITS sequence and very similar banding RAPD pattern for *A. trianoi* as compared to sympatric populations of *A. villosa* subsp. *longiaristata*) both fit such hypothesis (Fuentes Aguilar *et al.*, 1999 a, b; unpubl.)

Although only preliminary chloroplastic evidence is available, if the similarity between *A. trianoi* and *A. villosa* subsp. *longiaristata* for the *trnL* - *trnF* spacer sequences is confirmed by future sampling, a maternal parentage of *A. filicaulis* var. *minor* should be excluded. However, since the ITS sequences already available of *A. filicaulis* var. *minor* are identical to those in *A. trianoi*, the

paternal parentage of the latter is consistent with the available data under the reticulate scenario.

The possibility that the purple-flowered form of *A. filicaulis* (var. *minor*) was the pre-existing taxon also fits the ecological data (Fig. 5). *A. villosa* subsp. *longiaristata* occurs from 800 to 1200 m on a variety of habitats but always on limestone: scrubland, pinewood clearings or understory, rock crevices. *Armeria trianoi* grows on limestone crevices, in summit areas, from 1300 to 1500. *Armeria filicaulis* var. *minor* occurs on limestone outcrops, from crevices to places with some soil, from 1200 to 1700 m. Therefore, the differences in altitudinal range between *A. filicaulis* var. *minor* and *A. villosa longiaristata* may have provided some isolation for the introgressed forms once they were produced.

Armeria bourgaei Boiss. ex Merino was suggested as a possible progenitor for the plant from Horconera based mainly on its coloured petals and altitude range (Nieto Feliner, 1987). However, *A. bourgaei* lacks salt glands in the leaves, and the ITS sequences of four samples from such species are similar to plants inhabiting other Andalusian, more eastern, massifs such as Sierra de Cazorla (Fuentes Aguilar *et al.*, 1999b). We thus think that the above morphological argument relating *A. bourgaei* and *A. trianoi* is not strong enough to displace *A. filicaulis* var. *minor* as the most likely extant candidate for being the above mentioned pre-existing species.

Species concept in Armeria

Features like weak reproductive internal barriers among congeners and a reticulate scenario point to the inadequacy of the biological species concept in *Armeria*, unless we are willing to consider that a genus with ca. 110 morphologically recognisable taxa has to be condensed into a single species. Such radical procedure would only lower the rank of the biological entities we necessarily have to recognise in a taxonomic treatment of the genus. The case has similarities with the genus *Quercus* (Burger, 1975). The ITS evidence supporting the compilospecies model for *Armeria* (Fuentes Aguilar *et al.*, 1999b) adds to the inadequacy of a reproductive criterion to delimit species within this genus.

Aside from a biosystematic approach that would probably consider *Armeria* a kind of syngameon (Grant, 1981) and into a strictly operative taxonomic ground, justification for recognition at the specific level is not devoid of problems either. Morphological patterns of variation involve polymorphism as well as overlapping or sharing of individual characters between sympatric populations that differ in their overall morphologies (Bernis, 1954; Lefebvre, 1971; Philipp, 1974; Woodell & Dale, 1993). However, around one hundred of entities are diagnosable morphologically and ecologically in given areas, although they may tend to fade in others. So, if we agree that these entities need taxonomic recognition, what could be argued is which kind of recognition they deserve in view of their practical problems of delimitation. More specifically, it is a question of how do we treat biological entities originated in a reticulate scenario that are isolated, and maintained, fundamentally by external barriers.

The generation of hybrid races or species relying on external barriers was advocated by Grant (1981) in *Pinus*, *Rhododendron* or *Penstemon*, although it has received little attention in recent years due to the difficulty of documenting it on molecular grounds (Rieseberg, 1997; but see Brochmann, Borgen & Stabbetorp, 2000). To cope with the problem of naming such entities, some practical guidelines were proposed for *Armeria* (Nieto Feliner, 1987). It must be pointed out, however, that any formal taxonomic treatment attempting to reflect reticulate relationships is bound to convey an extra burden of arbitrariness. The main suggestion was that subspecific rank seems appropriate for entities, maintaining clear morphological links with a given species, even if the origin of such entities was introgression from a different taxon. One of the reasons why a hybrid race may have clearly stronger morphological similarities with one of the parents is backcrossing towards it. Thus, subspecific rank was deemed suitable for races originated via introgression that show morphological, ecological and distributional characterisation. On the other hand, and for the same practical reasons, the emphasis for granting specific status was put on a equidistant position of the hybrid entity. This situation typically applies to hybrid taxa that are morphologically intermediate between the two putative parents. However, this rank seems also useful for cases like *A. trianoi*, in which one of the parents is identified but morphologically not indisputably close, and the other parent remains uncertain (Nieto Feliner, 1987; Sardinero & Nieto Feliner, 1998).

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LEGENDS

Figure 1.— Origin of the specimens included in the morphometric multivariate analyses. See appendix for their taxonomic identification.

Figure 2.— Multivariate morphometric analysis of two data matrices in *Armeria*.

The ‘morphological matrix’ includes *A. trianoi*, *A. alpina*, *A. cantabrica*, *A. bigerrensis* subsp. *bigerrensis*, and *A. pubinervis*. The ‘geographical matrix’ includes *A. splendens*, *A. villosa* subsp. *longiaristata*, *A. villosa* subsp. *bernisii*, *A. filicaulis* subsp. *filicaulis*, *A. filicaulis* var. *minor*, *A. filicaulis* subsp. *nevadensis*. A) Principal components analysis of the ‘morphological matrix’. Scatterplot of the specimens against the first two principal components. B) Discriminant analysis of the ‘morphological matrix’. Scatterplot of the specimens against the first two discriminant functions. C) Principal components analysis of the ‘geographical matrix’. Scatterplot of the specimens against the first two principal components. D) Discriminant analysis of the ‘geographical matrix’. Scatterplot of the specimens against the second and third discriminant functions.

Figure 3.— Holotype of *Armeria trianoi*, with details: A) Involucre; B) calyx; C) involucre bract; D) apex of a leaf.

Figure 4.— Scheme of the ITS sequence variation in *Armeria* in Southern Spain. The geographic structure of the ITS tree is revealed by major clades containing sequences from different species occurring in the same area. Main ITS clades and the geographic area where the sequences were

sampled are shown with the same pattern. Only relevant taxa for the present paper are outlined: triangles are *A. villosa* subsp. *longiaristata*, stars are *A. trianai*, squares are *A. filicaulis* var. *minor*, circle is *A. filicaulis* (from unpubl data and Fuertes *et al.*, 1999b).

Figure 5.— Profile of the mountain ranges where *A. trianai* and their putative progenitors *A. villosa* subsp. *longiaristata* and *A. filicaulis* var. *minor* occur. Qualitative morphological characters that support such parentage are outlined. Sector (1) in the pie chart indicates presence (filled) or absence (empty) of salt crystals in the leaves; (2) presence (filled) or absence (empty) of narrow scarious margin; (3) leaves linear-lanceolate to lanceolate (filled), linear (empty); (4) scapes short curved (filled), long straight (empty); (5) petals purplish-pink (filled), white (empty).

Table 1.—Characters used in the morphometric multivariate analysis.

Appendix 1.— List of the specimens included in the morphometric multivariate analyses. All of them are in MA.

Appendix 2.— Origin of the representative specimens sampled for molecular data (nuclear ribosomal ITS and chloroplast spacer *trnL-trnF* sequences) mentioned in the discussion.

TABLE 1

ACRONYM	Carácter description
LEAVLTH	leaf length
LTH/WDTH	ratio leaf length to leaf width
SCAPLTH	scape length
DIAM	diameter of the scape at base
INVODIA	diameter of the involucre
SH/INV	ratio of the involucre diameter to the length of the involucre sheath
BRAC	number of involucre bracts
LONBRLTH	length of longest inner involucre bracts
SHO/LON	ratio of the shortest to the longest involucre bracts
INNBRWDTH	width of inner involucre bracts
AWNLGTH	length of mucro of inner involucre bracts
SPBRLTH	length of spikelet bracts
SPB/LON	ratio of the length of spikelet bracts to the length of inner involucre bracts
CALXLTH	calyx length
LOB/CAL	ratio of calyx lobe length (including awn) to total calyx length
TUBELTH	calyx tube length
TUB/LIM	ratio of calyx tube length to calyx limb length
SCARLTH	length of calyx pedicel scar
COLOR	petal color: white (0), pink (1), purplish (2)
LINEAR	linear leaves (1), non-linear leaves (0)

APPENDIX 1

Armeria trianoi Nieto Fel.

1. Hs, Córdoba, macizo de Horconera, Tiñosa, 30SUG9038, 1550 m, 11-V-1997, E Triano et al.
2. Hs, Córdoba, macizo de Horconera, Tiñosa, 30SUG9038, 1550 m, 15-VI-1998E, E Triano et al.
- 3-10. Hs, Córdoba, macizo de Horconera, Alhucemas, 30SUG8737, 1350 m, 25-V-1999, Nieto Fel. et al., 3992-3996GN.

Armeria alpina Willd.

11. Hs, Huesca, Pyrenees, Benasque, macizo de la Maladeta, Aigualluts 31TCH0728, 8-VII-1997, P Vargas 38PV97.
12. Hs, Huesca, Pyrenees, Posets, 31TBH8925, 3000 m, 21-VII-1987, Nieto Fel. et al. 1722GN (MA 388622).
13. Hs, Huesca, Pyrenees, La Renclusa, 2500 m, 21-VII-1975, G López et al. (MA 388653).
14. Hs, Lleida, Pyrenees, Viella-Migt Aran, collada de Varrados, 31TCH2736, 2040 m, Aedo et al. 2257CA (MA511759).
15. Andorra, Pyrenees, Puerto de Envalira, 31TCH9410, 2600 m, 26-VI-1991, Nieto Fel. et al. 2845 GN (MA 496586).
16. Ga, NW of Briancon, col du Galibier, 2700 m, 13-VII-1982, K Larsen (MA 268285)
17. It, Trento, Campitello di Val di Fassa, Coll Rodella, 2450 m, 46°30'N, 11°35'E, 2-VIII-1997, I Alvarez et al. 1348IA.
18. It, Val di Orco, P.N. Gran Paradiso, 2700 m, 9-VIII-1952, F Sappa & EF Galiano (MA 170082).
19. Au, In monte Schneeberg, VII-1888, K Richter (MA 145825).
20. Bu, Mt. Rila, 2730 m, 23-VII-1952, B Kitanov (MA 180581).

Armeria pubinervis Boiss.

21. Hs, Huesca, Pyrenees, Pico Collarada, 30TYN0834, 2750 m, 31-VII-1985, M Luceño et al. (MA 394861).
22. Hs, Huesca, Pyrenees, Ansó-Fago, 30TXN8153, 1800 m, 5-VIII-1985, JA Alejandro & BF Betoño (MA 337805).
23. Hs, Navarra, Huarte Arakil, Beriain, 30TWN8349, 1350 m, 5-IX-1982, JA Alejandro & BF Betoño (MA 394862).
24. Hs, Navarra, Valle del Roncal, 30TXN85, 2000 m, 2-VII-1987, P Vargas 2472 et al. (MA 394866).
25. Hs, Navarra, puerto de Lizarraga, 1080 m, 28-VII-1968, A Segura Zubizarreta (MA 306066)
26. Hs, Cantabria, Braña Vieja, Tresmares, 30TUN86, 2200 m, 3-VII-1987, E Villanueva et al. 1227EV (MA 394858).
27. Hs, Cantabria, Pesaguero, Peña Bistruey, 30TUN6966, 1950 m, 12-VII-1993, Sánchez Pedraja (MA 530948).
28. Hs, Cantabria, Picos de Europa, Aliva, Pozas de Lloroza, 30TUN57, 1830 m, 13-IX-1988, E Bayón et al. 2130EB (MA 449142).
29. Hs, Cantabria, Picos de Europa, Camaleño, 30TUN5180, 1900 m, 4-VIII-1994, Sánchez Pedraja.
30. Hs, Cantabria, Picos de Europa, el Cable, 30TUN5479, 1850 m, 11-VIII-1984, M Luceño (MA 394864).

Armeria cantabrica Willk.

31. Hs, Álava, Toloño, 30TWN1919, 1200 m, 4-VIII-1982, JA Alejandro (MA 390094).
32. Hs, Navarra, Torralba del Río, Sierra de Kodes, 30TWN5519, 1000 m, 2-VII-1988, JA Alejandro (MA 466999).
33. Hs, Cantabria, Curavacas, 30TUN5582, 2300 m, 11-VII-1978, E Valdes et al. 4228EV (MA 390092).
34. Hs, Cantabria, Potes, puerto de San Glorio, 30TUN5669, 1800 m, 28-VII-1986, JA Alejandro et al. (MA 36404).
35. Hs, Cantabria, Picos de Europa, Peña Vieja, 2-VIII-1973, B Casaseca (MA 377364).
36. Hs, Cantabria, Picos de Europa, Peña Vieja, 4-IX-1944, C Vicioso (MA 390098).
37. Hs, Cantabria, Picos de Europa, Áliva, 11-VII-1981, E Fuertes & P Galán (MA 394935).
38. Hs, Cantabria, Picos de Europa, Fuente De, 30TUN5282, 2300 m, 4-VII-1987, A Izuzquiza et al. 954AI (MA 390114).
39. Hs, Cantabria, Picos de Europa, Fuente De, 30TUN5282, 2300 m, 4-VII-1987, A Izuzquiza et al. 954bAI (MA 390113).

40. Hs, Cantabria, Picos de Europa, Espinama, 30TUN5479, 2200 m, 19-VIII-1976, E Valdés & S Castroviejo 957EV (MA 390100).

Armeria bigerrensis (C. Vicioso & Beltrán) Rivas Mart. subsp. *bigerrensis*

41-50. Hs, Ávila, Sierra de Gredos, Altos del Morezón, 30TUK0758, 2300 m, 22-VI-1986, M Luceño & P Vargas 1289PV.

Armeria filicaulis var. *minor* Boiss.

51-54. Hs, Málaga, Alcaucin, Sierra Tejeda, pr. pico Maroma, 30SVF0384, 1550 m, 26-V-1999, Nieto Fel. et al. 4006GN.

55-56. Hs, Málaga, Alcaucin, Sierra Tejeda, pr. pico Maroma, 30SVF0484, 1600 m, 26-V-1999, Nieto Fel. et al. 4015GN.

57-59. Hs, Málaga, Alcaucin, Sierra Tejeda, pr. pico Maroma, 30SVF0285, 1200 m, 26-V-1999, Nieto Fel. et al. 4020GN.

60. Hs, Málaga, Alcaucin, Sierra Tejeda, pico Maroma, 30SVF0684, 1800 m, 30-V-1999, A Pulido.

Armeria filicaulis subsp. *filicaulis*

61-65. Hs, Málaga, Canillas de Albaida, Sierra Almajara, 30SVF1479, 900 m, 26-V-1999, Nieto Fel. et al. 4025GN.

66-70. Hs, Granada, Albuñuelas. Sierra de las Guájaras, 30SVF3884, 1180 m, 27-V-1999, Nieto Fel. et al. 4041GN.

Armeria filicaulis subsp. *nevadensis* Nieto Fel. et al.

71. Hs, Granada, Güejar-Sierra, Sierra Nevada, Albergue S. Francisco, 30SVG6506, 2200 m, 6-VII-1999, B Gutiérrez BG14 & I. Torá.

72-75. Hs, Granada, Dílar, Sierra Nevada, peñón del Dílar. 30TVG6103, 2460 m, 8-VII-1999, B Gutiérrez BG29 & I. Torá.

Armeria villosa subsp. *bernisii* Nieto Fel.

76. Hs, Málaga, Sedella, Sierra Tejeda, 30SVF0984, 1600 m, 30-v-1999, A Pulido.

77-78. Hs, Granada, La Zubia, Sierra Nevada, 30SVG5404, 1350 m, 28-V-1999, Nieto Fel. et al. 4076GN.

79-80. Hs, Granada, Cáñar, Sierra Nevada, 30SVF6391, 1800 m, 22-VI-1999, Nieto Fel. et al. 4104GN.

81-82. Hs, Granada, Bubión, Sierra Nevada, 30SVF6991, 1950 m, 22-VI-1999, Nieto Fel. et al. 4112GN.

83-84. Hs, Granada, Pórtugos, Sierra Nevada, 30SVF7192, 2230 m, 22-VI-1999, Nieto Fel. et al. 4120GN.

85. Hs, Granada, Bérchules, Sierra Nevada, 30SVF8092, 1830 m, 23-VI-1999, Nieto Fel. et al. 4128GN.

Armeria villosa subsp. *longiaristata* (Boiss.) Nieto Fel.

86-88. Hs, Córdoba, Cabra, la Nava, 30SUG7851, 1000 m, 25-V-1999, Nieto Fel. et al. 4002GN.

89-93. Hs, Granada, Beas de Granada, puerto de la Mora, 30SWG5925, 1300 m, 27-V-1999, Nieto Fel. et al. 4061GN.

Armeria splendens (Lag. & Rodr.) Webb

94-97. Hs, Granada, Monachil, Sierra Nevada, laguna de las Yeguas, 30SVG6601, 2870 m, 7-VII-1999, B Gutiérrez BG23 and I Torá.

98. . Hs, Granada, Capileira, Sierra Nevada, laguna de Aguas Verdes, 30SVG6800, 2990 m, 10-IX-1999, B Gutiérrez BG43 & M Hernández.

99-100. Hs, Granada, Capileira, Sierra Nevada, laguna de Río Seco, 30SVG6900, 3100 m, 10-IX-1999, B Gutiérrez BG45 & M Hernández.

101-103. Hs, Granada, Capileira, Sierra Nevada, laguna de la Caldera, 30SVG7001, 3040 m, 11-IX-1999, B Gutiérrez BG48 & M Hernández.

APPENDIX 2

Armeria trianaei Nieto Fel.

Hs, Córdoba, macizo de Horconera, Alhucemas, 30SUG8737, 1350 m, 25-V-1999, Nieto Fel. et al., 3993 GN.

Armeria filicaulis (Boiss.) Boiss.

Hs, Granada, Beas de Granada, puerto de la Mora, 30SVG5021, 1300 m, 12-VI-1989, Nieto Fel. 2722 GN.

Armeria filicaulis var. *minor* Boiss.

Hs, Málaga, Alcaucin, Sierra Tejeda, pr. pico Maroma, 30SVF0484, 1600 m, 26-V-1999, Nieto Fel. et al. 4017GN.

Hs, Málaga, Alcaucin, Sierra Tejeda, pr. pico Maroma, 30SVF0285, 1200 m, 26-V-1999, Nieto Fel. et al. 4020GN.

Armeria villosa subsp. *longiaristata* (Boiss.) Nieto Fel.

Hs, Córdoba, Cabra, la Nava, 30SUG7851, 1000 m, 25-V-1999, Nieto Fel. et al. 4002GN.

Hs, Sevilla, Estepa, pico Becerrero, 30SUG3527, 850 m, 8-IV-1997, Nieto Fel. & Fuertes, 3853 GN.

Hs, Jaén: Valdepeñas de Jaén, 30SVG3363, 1400 m, 7-II-95, Nieto Fel. & Rosselló, 3679 GN (#5, #7).

Hs, Córdoba: Zuheros, Cueva de los Murciélagos, 30SUG8556, 900 m, 8-IV-97, Nieto Fel. & Fuertes, 3850 GN.

HORTUS REGIUS MATRITENSIS (MA)

Armeria

CORDOBA: Priego, macizo de Horconera, Alhucemas, 30SUG8737, 1350 m, grietas de caliza, G. Nieto Feliner 3994GN, J. Fuertes, B. Gutiérrez & E. Triano, 25-V-1999.