

Geography-related sub-generic diversity within the Mediterranean trapdoor spider genus *Nemesia* (Araneae, Mygalomorphae, Nemesiidae)

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Abstract: Three different male and female super-specific types are distinguished according to variations in the morphology of the bulb and spermathecae within the genus *Nemesia* Audouin, 1826. Plotting the distributions of these sexual types on a map of the Mediterranean indicates the existence of geography-related sub-generic diversity in which the *Nemesia* fauna of the eastern Mediterranean differs markedly from that of the western Mediterranean. While the eastern Mediterranean *Nemesia* fauna is highly homogeneous, the fauna of the western Mediterranean is very diverse. The eastern and western *Nemesia* faunae appear to overlap in the central Mediterranean. Efforts to relate the specific bulb types to the particular types of spermathecae described here were only partly successful.

Key words: biodiversity, biogeography, distribution, model taxon, taxonomy

The trapdoor spider genus *Nemesia* Audouin, 1826 is currently considered to be a potentially valuable model system for studies in evolutionary biology (DECAE 2010, Arnedo pers. comm.). The fact that *Nemesia* exhibits high species diversity in the geographically confined region of the Mediterranean offers exceptional opportunities for studies on local variation and speciation. Moreover, the common occurrence of *Nemesia* throughout the region, both on islands and continents, in a range of different habitats (from sandy shores to alpine heights and from semi-deserts to humid forests), its supposedly sedentary habits, its poor capacity for dispersal and its probably ancient origin, reveals the genus as a coherent sample of evolving lineages that offer highly prospective opportunities for virtually all lines of biological research. Unfortunately, this potential for biological research into *Nemesia* is hampered by a lack of basic knowledge. The taxonomy of *Nemesia* is poorly resolved and partly confused, the real species diversity cannot even be estimated and there is no good insight into the internal organization of the genus in terms of the possible existence of sub-generic groups. A basic problem is that classical spider taxonomy is exclusively focused on morphological variation in preserved specimens, and that such variation is very difficult to observe in *Nemesia*. Study of the taxonomically most

informative morphological structures – male and female sexual organs and the spinnerets – has become common practice only very recently, which means that the whole taxonomical framework of the genus urgently needs revision. A productive first step might be to try recognizing *Nemesia* species groups based on the variation of the bulb and the spermathecae types, and matching the sexes. The recognition of evolutionary older sub-generic groups within *Nemesia* would have particular significance if it could be linked to the geographical dynamics of the Mediterranean; a region with a history of major geographical shifts (AGER 1980) and dramatic geophysical events such as the Messinian salinity crisis (KRIJGSMAN et al. 1999) and the formation of glacial refugia during the Pleistocene (MÉDAIL & DIADEMA 2009). This paper is a first attempt to discover such geography-related sub-generic diversity within *Nemesia*.

Material and Methods

This study is based on variations in the morphology of both male and female sexual organs (i.e. bulbs and spermathecae). Because no objective criteria exist for classifying different types of spider bulbs and spermathecae, the classifications used here are necessarily arbitrary and provisional. The classifications adopted are, however, based on experience resulting from detailed observations of well over one thousand *Nemesia* specimens and as such might function as practical tools for discovering broad scale patterns in *Nemesia* sub-generic diversity. A Ceti-Medo.2 stereomicroscope with camera lucida equipment was

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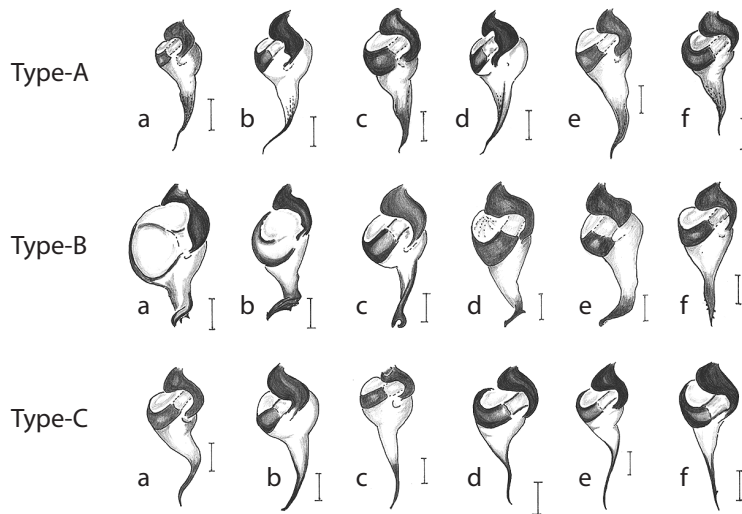


Fig. 1: Classification of three different types of bulbs found within *Nemesia* (18 examples). Top row: Type-A bulbs with distinct longitudinal ribs on the proximal embolus. Middle row: Type-B bulbs, proximally somewhat enlarged bulbs with conspicuous ornamentation or modifications of the embolus tip. Bottom row: Type-C, relatively simple pyriform bulbs, embolus tips pointed, smooth or furnished with tiny denticles, but without ribs or conspicuous modifications. All drawings are taken in ventral view on the right hand bulb. Aa = *N. pannonica*, Ab = *N. spec.* from Sardinia, Ac = *N. spec.* from Puglia, Ad = *N. daedali*, Ae = *N. kahmanni*, Af = *N. spec.* from Molise, Ba = *N. uncinata*, Bb = *N. valenciae*, Bc = *N. carminans*, Bd = *N. spec.* from Murcia, Be = *N. spec.* from Saida, Bf = *N. spec.* from Bejaia, Ca = *N. spec.* from Emilia-Romagna, Cb = *N. manderstjerneae*, Cc = *N. spec.* from Andalucia, Cd = *N. bristowei*, Ce = *N. badia*, Cf = *N. bacelarae*. Species indicated as "*N. spec.*" are not yet formally named. Scale lines = 0.25mm.

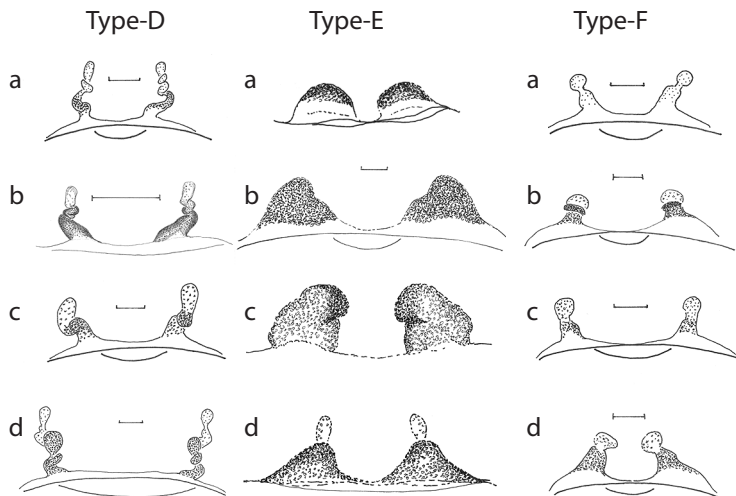


Fig. 2: Classification of three different types of spermathecae found within *Nemesia* (12 examples). Left column: Type-D spermathecae tube shaped, tripartite, central part twisted and/or folded. Middle column: Type-E spermathecae grossly enlarged, one or two partite spermathecae without twisted parts. Right column: Type F spermathecae, tube shaped two or three partite without twists or folds. All drawings are taken in ventral view. Da = *N. spec.* from Peloponnesus, Db = *N. meridionalis*, Dc = *N. manderstjerneae*, De = *N. spec.* from Toscana, Ea = *N. uncinata*, Eb = *N. spec.* SW Portugal, Ec = *N. santeulalia*, Ed = *N. caementaria*, Fa = *N. arboricola*, Fb = *N. athiasi*, Fc = *N. macrocephala*, Fd = *N. ungoliant*. Species indicated as "*N. spec.*" are not yet formally named. Scale lines = 0.25mm.

used for examining and drawing bulbs and spermathecae submerged in 70 % ethanol. Bulbs were drawn from the organ on the right hand side of the spider in ventral view. Spermathecae were prepared for study by dissection and removing the coverage of greasy tissue mechanically with sharpened needles. This method leaves the spermathecae in situ with minimal damage to the spider specimens. Drawings were done in pencil and Artline pens for graphical design. Registration of species identity, geographical origin of each specimen and classification of sexual types were compiled in a Microsoft Excel sheet.

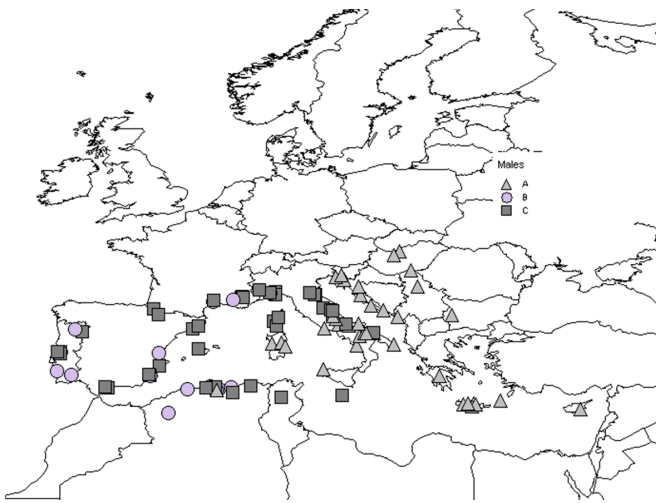
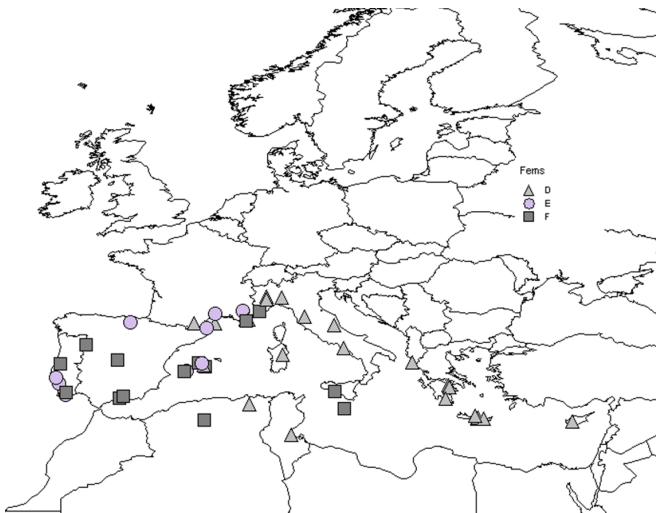
Six different 'sexual types', three male-types (Fig. 1) and three female-types (Fig. 2), could be distinguished. A sample of 107 ♂♂ and 47 ♀♀, collected at localities widely spread throughout the Mediterranean Region was classified according to these sexual types. The results were plotted on a map of the Mediterranean using DIVA-GIS (HIJMANS et al. 2005). In an effort to match male and female sexual types, ten established species – for which both sexes were represented in the sample – were compared (Tab. 1) and set in a geographical context.

Results

Plotting 107 male records, classified according to three different bulb-types (Fig. 1), on a map shows a distinct difference between the eastern and western Mediterranean (Fig. 3). Type-A bulbs (i.e. longitudinal ribs on the proximal embolus) are the only bulb-type present in the eastern Mediterranean. In the western Mediterranean

Tab. 1: Match of male and female sexual types in ten established *Nemesia* species present in a sample of 107 ♂♂ and 45 ♀♀. Ordered alphabetically on male types.

Species	Distribution	Male-type	Female-type
<i>Nemesia caranhaci</i> Decae, 1995	Crete	A	D
<i>Nemesia meridionalis</i> (Costa, 1835)	S Italy	A	D
<i>Nemesia caementaria</i> (Latreille, 1799)	S France	B	E
<i>Nemesia uncinata</i> Bacelar, 1933	S Portugal	B	E
<i>Nemesia athiasi</i> Franganillo, 1920	W Iberian	B	F
<i>Nemesia manderstjernae</i> L. Koch, 1871	SE France	C	D
<i>Nemesia dubia</i> O. P.-Cambridge, 1874	Pyrenees	C	D
<i>Nemesia bacelarae</i> Decae, Cardoso & Selden, 2007	Portugal	C	E
<i>Nemesia ungoliant</i> Decae, Cardoso & Selden, 2007	Portugal	C	F
<i>Nemesia macrocephala</i> Ausserer, 1871	Sicily-Malta	C	F

**Fig. 3:** Geographical distribution of three here distinguished bulb-types found in a sample of 107 male *Nemesia* spiders. Triangle = Type-A, circles = Type-B, squares = Type-C.**Fig. 4:** Geographical distribution of three here distinguished spermathecae-types found in a sample of 47 female *Nemesia* spiders. Triangle = Type-D, circles = Type-E, squares = Type-F.

bulb-types B and C predominate and only in the central Mediterranean do all bulb-types overlap. Plotting 47 female records, classified according to three different spermathecae-types (Fig. 2), produces a highly similar distribution of sexual types (Fig. 4). D-type spermathecae (tube-shaped with central twists or sharp folds) exclusively populate the eastern Mediterranean, while in the western Mediterranean E and F type spermathecae dominate. As in males, the central Mediterranean is a zone of overlap for all three female sexual-types (Fig. 4).

Relating sexual types of males and females (Tab. 1) indicates that Type-D spermathecae match with either Type-A (*N. caranhaci* & *N. meridionalis*) in the eastern Mediterranean, or with Type-C bulbs (*N. dubia* & *N. manderstjernae*) in the north-western Mediterranean. Type-E spermathecae match with Type-B bulbs (*N. caementaria* & *N. uncinata*) or with Type-C bulbs (*N. bacelarae*). Type-F spermathecae match either with Type-C (*N. ungoliant* & *N. macrocephala*,) or with Type-B (*N. athiasi*).

Discussion

Perhaps the most obvious conclusion to be drawn from this study is that the *Nemesia* fauna in the eastern Mediterranean differs strongly from that in the western Mediterranean. While the eastern fauna appears to be highly homogeneous – all *Nemesia* species occurring east of approximately 14.5° E have Type-A bulbs and Type-D spermathecae – the fauna of the western Mediterranean is highly diverse (Figs. 3 & 4). All designated male and

female sexual types are found in the western Mediterranean, although Type-A males and Type-D females have not yet been found on the Iberian mainland. In the central Mediterranean the eastern and western *Nemesia* faunas overlap. It is not clear from the data if this zone of overlap indicates east-west dispersal of *Nemesia* species or a vicariance pattern related to historical shifts in the local geography (AGER 1980, DECAE 2010). This study does not reveal any locally restricted species groups in the western Mediterranean, although the two different bulb types found in combination with Type-D spermathecae (Tab. 1) might indicate the existence of a local species group in the north-western parts of the region. The combination Type-C/Type-D (*N. dubia* & *N. manderstjerna*) has thus far only been found in an area roughly running from northern Italy to the central Pyrenees. The intuitive expectations that enlarged bulbs (i.e.

Type-B) should match with enlarged spermathecae (Type-E) and that simple bulbs (Type-C) should match with simple spermathecae (Type-F) are only partly corroborated. Two species, both from the western parts of the Iberian Peninsula (*N. bacelarae* & *N. athiasi* see Tab. 1) contradict these expectations. The study sample contains few clearly conspecific males and females. Most specimens included are either representatives of unnamed and undescribed species or single males or females of described species. As such the sample is more or less representative for the current general state of *Nemesia* taxonomy. The *Nemesia* list in the World Spider Catalog (PLATNICK 2012), shows that about half of all species are known by one sex only and about one third of all names listed must be regarded as incertae sedis (personal opinion). This study of sub-generic diversity therefore not only shows the probable existence of geographical patterns



Fig. 5: Geographical distribution of ten established *Nemesia* species. Matching bulb types with types of spermathecae. *N. caranhaci* & *N. meridionalis* (Type-A/Type-D), *N. manderstjerna* & *N. dubia* (Type-C/Type-D), *N. unguilant* & *N. macrocephala* (Type-C/Type-F), *N. caementaria* & *N. uncinata* (Type-B/Type-E), *N. bacelarae* (Type-C/Type-E), *N. athiasi* (Type-B/Type-F).

in *Nemesia* diversity, it also shows that an improved taxonomy is urgently needed as a prerequisite for exploiting the great potential of *Nemesia* as a biological model taxon as indicated in the Introduction.

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