Neilreichia **13–14**: 305–323 (2022/2023)

What is a species in *Veronica*? Reflections on the occasion of Manfred A. Fischer's 80th birthday

Dirk C. Albach

Institute of Biology and Environmental Sciences, Carl von Ossietzky University of Oldenburg,
Carl-von-Ossietzky-Str. 9–11, 26111 Oldenburg, Germany; e-mail: dirk.albach@uni-oldenburg.de

Abstract: The species is the central category of organizing the diversity of life. Yet, many different species concepts, such as the morphological, biological, ecological, and phylogenetic concepts, have been used by biologists, preventing clear comparability. Based on the history of species description in the genus *Veronica*, I demonstrate that the biosystematics approach by Manfred A. Fischer from the 1960s onwards has started to renew our understanding of what a species is in this genus. Detailed investigations of morphology, ecology, reproductive barriers, and, later, genetic cohesion and testing of species limits have continued from his earliest analyses of the *V. hederifolia*-complex. We now recognize 455 species in the genus *Veronica* but still only few species have been rigorously analyzed, leaving certainly a lot of work for future systematists working on this beautiful genus.

Key words: biosystematics; history; phylogeny; polyploidy; species concept

Zusammenfassung: **Was ist eine Art in *Veronica*? Reflexionen anläßlich des 80. Geburtstages von Manfred A. Fischer**
Die Art ist die zentrale Kategorie für die Organisation der Vielfalt des Lebens. Dennoch wurden von Biologen viele verschiedene Artkonzepte wie das morphologische, biologische, ökologische und phylogenetische Konzept verwendet, was eine klare Vergleichbarkeit von Arten verhindert. Anhand der Geschichte der Artbeschreibung in der Gattung *Veronica* zeige ich, dass der biosystematische Ansatz von Manfred A. Fischer seit den 1960er-Jahren dazu führte, dass sich unser Verständnis, was eine Art in dieser Gattung ist, komplett erneuerte. Detaillierte Untersuchungen der Morphologie, der Ökologie, der Fortpflanzungsbarrieren und – später – der genetischen Kohäsion sowie die Prüfung der Artgrenzen wurden seit seinen ersten Analysen des *V. hederifolia*-Komplexes fortgesetzt. Heute sind 455 Arten in der Gattung *Veronica* bekannt, aber nur wenige wurden gründlich analysiert, so dass es für künftige Systematiker, die sich mit dieser schönen Gattung befassen, sicherlich noch viel zu tun gibt.

Introduction

> '… why, if species have descended from other species by insensibly fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion instead of species being, as we see them, well defined?' (Darwin 1859: 171)

Categorizing the diversity of life from microbial life to large mammals and trees has intrigued mankind for millennia. The central category in this respect is the species. However, defining what a species is, has evaded scientists ever since. Even Darwin (1859; cited above) was puzzled and did not find a solution to the problem. In his time, morphology was the only means to describe species, although large crossing programmes in

DOI: https://doi.org/10.5281/zenodo.10120141

plants were conducted by Linné, Kölreuter and Gärtner in the 18th and early 19th centuries (Kingsbury 2009). Only in the middle of the 20th century, crossing barriers between species became part of species concepts, notably by the ornithologist Mayr (1942). Since plants are known to hybridize promiscuously, his biological species concept, however, was not widely used in plants (Hörandl 2022), despite the fact that reproductively isolated lineages are more common in plants than in animals (Rieseberg 2006). The second half of the 20th century saw a rise in new data analyzed to describe species and new types of analyses to reveal relationships between them, leading to emphasis on either ecology (Van Valen 1976) or phylogeny (de Queiroz & Donoghue 1988) in species concepts. Especially the latter, with increasing amounts of genetic data, has shifted the focus of species definition to the genetic level and species delimitation methods based on genetic data have been suggested to be a more objective way to delimit a species (e. g., Yang & Rannala 2010, Toprak & al. 2016, Hausdorf & Hennig 2020). Nevertheless, a common definition of species is still not in sight with some emphasizing criteria that distinguish evolutionary lineages from other such lineages, while others emphasize criteria that strengthen cohesion within species (Wells & al. 2022). Yet others stress that these species concepts only discuss what distinguishes species, not what a species is. These latter concepts, starting with Simpson (1961) and Wiley (1978) and leading to the general lineage concept (de Queiroz 1999), still have the problem of how these lineages are identified. Wiley (1978), for example, explicitly excluded the necessity of morphological and ecological distinction and allowed gene flow between species as long as species identity is maintained. Consequently, species are identified by different scientists using different criteria, and species are often not comparable even among plants.

To compare species richness across clades or regions, comparable units need to be based on common criteria. Further, these criteria need to be testable, and species, therefore, are hypotheses that are falsifiable in the sense of Popper (Fitzhugh 2009). Based on this idea, species are identified by discontinuities among populations. These discontinuities can be found in different aspects of a species as discussed in previous concepts. These dimensions of a species can be defined as phenotype, ecology, cross-compatibility, and genetic cohesion, although it can be debated whether these dimensions are really independent and whether there are not more than four. With respect to phenotype, finding discontinuities resembles the classical morphological/phenetic species concept. However, the phenotype includes also characters such as phytochemistry and chromosome number, and the methods have diversified and become more sophisticated (e. g., Zapata & Jiménez 2012). Discontinuities in ecology have been emphasized in the ecological species concept (Van Valen 1976). The exact ecological characters to distinguish species can vary in scale. They can be broad-scale climatological characters, such as those used by WorldClim (Fick & Hijmans 2017) for ecological niche modelling, and methods to detect significantly different niches have been developed (Warren & al. 2008). These ecological discontinuities can also be on a smaller geographic scale and would need to be detected, for instance, in a phytosociological manner (e. g., Bjorå & al. 2008). Furthermore, these ecological characters can also encompass biological interactions, e. g., different food resources or different symbiotic partners (Těšitelová & al. 2013). Discontinuities in cross-compatibility are detected classically by crossing programmes (Ramsey & al. 2003) and constitute the biological species. However, nowadays cross-compatibilities may also be inferred by genetic analyses to detect the cross-species and genome-wide extent of hybridization and introgression. Such approaches blur the analyses of discontinuities in cross-compatibility and genetic cohesion.

The phylogenetic dimension has been heavily disputed. There has been a long debate about whether a species should be a monophyletic group (Cracraft 1987, de Queiroz & Donoghue 1988, Baum 1992) or is often paraphyletic (Rieseberg & Brouillet 1994, Avise & Wollenberg 1997) or necessarily polyphyletic at the beginning (Rosenberg 2003). It is now clear that this is a debate on the time of speciation relative to the divergence of two lineages. Lineages are usually polyphyletic at divergence and become reciprocally monophyletic after a time of transition in which one lineage is monophyletic but the other paraphyletic (Rosenberg 2003). In most models of speciation, such as budding speciation, one would consider that the first lineage is monophyletic at the onset of speciation (Avise & Wollenberg 1997, Coyne & Orr 2004). However, it is not clear when phenotypic and ecological discontinuities as well as reproductive barriers evolve relative to the monophyly of a lineage. Likely, it will remain to some extent subjective at what point along this line of evolving discontinuities diverging lineages should be called two different species.

Such questions have rarely been investigated in detail for a species, and the dating of such discontinuities is likely to remain impossible for most species, which is why species remain hypotheses to be investigated in ever more detail in the future. More sophisticated methods of analysis allow elucidating more and more aspects of the species limits. Here, I do not just refer to genomic data and analyses of the pangenome of a species alone (Bobay 2020 for prokaryotes but transferable to eukaryotes) but also to metabarcoding of the microbiome of a plant and to species-specific differences in the microbiome (Geisen & al. 2021). Apart from these, ongoing studies to understand the phenotype, ecological niches, and reproductive barriers in more and more detail will help to understand species limits. The inability to analyze all individuals and all characters of a species recently lead Wells & al. (2021) to consider species as heuristics, tested against new data again and again. Consequently, establishing an inventory of life will remain a never-ending task and any database an approximation of real life. Nevertheless, such an approximation remains important for other fields of research, depending on the assignment of individuals to species.

History of species in *Veronica*

Here, I discuss species delimitation in the genus *Veronica* to present the current state of knowledge and the influence of Manfred A. Fischer on it. The genus *Veronica* is a member of the family Plantaginaceae, formerly Scrophulariaceae (Olmstead & Reeves

1995, ALBACH & al. 2005) and comprises 455 species (based on my own unpublished list) that occur worldwide from the tropics to the deserts and the Arctic and from sea-level to 5500 metres a.s.l. in the Himalayas. Of these 455 species, 39% are named after a morphological feature, 25% commemorate people (but just 4 out of these 113 species are named after women), 19% are named after a locality, 9% in relation to some other species and 8% after their habitat. They can be as small as 2 cm or as tall as 7 m, are short-lived and reproducing within 4–6 weeks or are long-lived alpine perennials. The earliest mention of the name *Veronica* is, according to my literature search, by MATTIOLI (1568) as an important medicinal plant. However, species of the genus *Veronica* were already mentioned in the "New Kreuterbuch" of FUCHS (1543), in which he described a male ("Erenbreiß mennle") and a female *Veronica* ("Erenbreiß weible"), the first being *V. officinalis*, the second likely belonging to a completely different genus. Other species (identifiable as *V. agrestis, V. beccabunga*, *V. hederifolia*, *V. chamaedrys*, *V. teucrium*) are described at different places in his book. DODOENS (1578) also described both species and the second as having yellow flowers supporting the notion that it is not a *Veronica* in our sense. This is further supported by his description of species of *Dianthus* as Veronica altilis. Thus, the circumscription of the genus was not based on obvious morphological characters until subsequent authors did so. Among these, GERARD (1597) is notable in this respect since he still recognized female and male *Veronica* but referred to "Elatine" for the female *Veronica* and "Paules Betonie" for the male *Veronica*, under which he recognized six species, which can be identified mostly as today's *Veronica* species (*V. officinalis*, *V. serpyllifolia*, *V. longifolia* and three unidentifiable species). Other species we nowadays recognize as *Veronica* were described under the name "Anagallis". BAUHIN (1623) provided a major step in this respect, listing eight species under *Veronica*, all except one clearly referable to species recognized today. Additionally, he acknowledged the similarity of these to nine species that we nowadays consider members of *Veronica*, but were then given the names Chamaedrys, Anagallis and Alsine, all described following his *Veronica* in the narrow sense.

Linné described 26 species of *Veronica* in "Species Plantarum" (LINNÉ 1753), of which 20 are still recognized today. Species were continuously described, with peaks in the mid-19th century (Fig. 1), especially due to intensified investigation of Southwest Asian floras, the centre of diversity of the genus, by BOISSIER (1844, 1879) and others. By 1900, 229 of the 455 species accepted today have been described, entirely based on morphological comparisons. By that time, the first phylogenetic tree for species of *Veronica* was published (JUEL 1891). Starting in 1906, Ernst Lehmann (LEHMANN 1906) and his students investigated systematically the genus considering in more detail chorology, ecology and, after the first report of chromosome numbers in the genus by HEITZ (1926), the number of chromosomes (e. g., HUBER 1927, GRAZE 1933). Nevertheless, their species concept was still largely a morphological/phenetic species concept, though investigating in more detail intraspecific variation.

LEHMANN (1914) was also the first to conduct systematic crossing studies among species of *Veronica* in order to detect species limits. Crossing programmes to evaluate

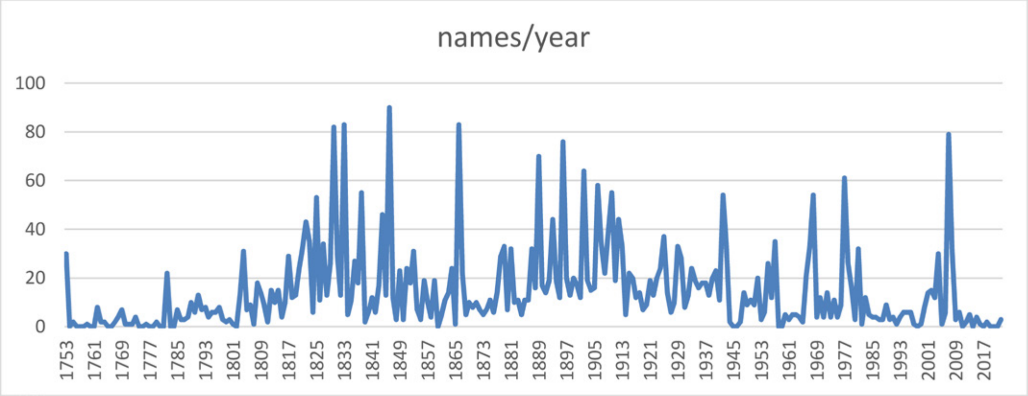

Fig. 1: Timeline for the description of the 455 species of *Veronica* recognized today. — **Abb. 1:** Anzahl der Beschreibungen von *Veronica*-Arten über die Jahre (dargestellt sind die 455 heute akzeptierten Arten).

reproductive barriers between species are labour intensive. Consequently, there are few such projects in *Veronica*. Linné (1787) was the first to report crossings in *Veronica* but his hybrid combinations (*V. spuria* = *V. maritima* × *Verbena officinalis*; *V. hybrida* = *V. spicata* × *V. officinalis*; *Campanula hederacea* = *C. aliqua* × *V. hederifolia*) are implausible. Gärtner (1849) reported unsuccessful hybridization of *V. agrestis* with *V. nummulariaefolia* (? *V. serpyllifolia*) and concluded that hybridization in the genus is rare. Lehmann and his students (Graze 1933, Beatus 1935, Schlenker 1935, Zündorf 1939, Schmitz 1946) continued these studies, which helped support species limits but rarely changed previous considerations. Since then, to the best of my knowledge, our study on *V. spicata* and *V. longifolia* is the only other crossing experiment published with the aim of testing species limits (Buono & al. 2021). These studies have in common that cross-fertility between species in garden environments is high and polyploidy serves as the major reproductive barrier in controlled crosses of *Veronica* species. Therefore, these studies from the first half of the 20th century seem to have discouraged others from pursuing such studies. Thus, the biological species concept has had only minimal impact on species delimitation in *Veronica*.

The second half of the 20th century saw major contributions to our knowledge of species diversity in the genus through large flora projects with descriptions of new species (Borissova 1955, Fischer 1978, 1981, 1982, 1991, Mouterde & Fischer 1984). These projects provided the basis for in-depth analyses of species groups, especially by Manfred A. Fischer (Fig. 2; e.g., Fischer 1970a, 1972, 1987) and publication of new species (Fischer 1977a, b, 1984). Despite mostly based on morphology, in many of these species descriptions, chromosome numbers played an important role for decisions on species limits (cytotaxonomy sensu Fischer 1967, 1970a, b or karyosystematics sensu Öztürk & Fischer 1982), strongly influenced by Friedrich Ehrendorfer (Fischer 1997). In these studies, karyological analyses were considered to provide insights into species boundaries and phylogenetic relationships that were not possible by morphology alone (FISCHER 1967). Fischer's study on *V. hederifolia* serves as an example and is the most rigorous of his analyses. Using information on ploidy level in this group of diploid (*V. triloba*), tetraploid (*V. sublobata*) and hexaploid (*V. hederifolia*) species (Fig. 3), Fischer detected non- or just partially overlapping characters to distinguish plants of different ploidy levels. Here, the length of the leaf lamina, the length of the deepest indentation of the leaf margin, the length of the longest pedicel in fruit, the average sepal length, and the mean pollen diameter were measured. FISCHER (1967) assigned the index

Fig. 2: Manfred A. Fischer in the field, collecting *Veronica scardica* in the serpentine area near Redlschlag (Burgenland, Austria). Photo: Josef Weinzettl, 20 May 2017. — Manfred A. Fischer im Gelände, beim Sammeln von *Veronica scardica* im Serpentingebiet von Redlschlag (Burgenland, Österreich). Foto: Josef Weinzettl, 20. Mai 2017.

1.0 to the character values measured in the diploid, 2.0 to those in the hexaploids and 3.0 to those in the tetraploids. Multiplication of the index with a character-specific value of diagnosability provided a "Sippenindex" in analogy to the hybrid index of Anderson (1953): 1–1.5 for *V. triloba*, 1.5–2.0 for *V. hederifolia*, 2.5–3.0 for *V. sublobata*. This index allowed assignment of plants of unknown ploidy to one of the three species. Thus, the three species sensu Fischer (1967), including the newly published *V. sublobata*, are essentially phenetically determined species. Ploidy was used as an absolute diagnostic character ("absolutes Differentialmerkmal") with which the morphological diagnostic

Fig. 3: *Veronica hederifolia* (left) and *V. sublobata* (right) can be identified based on various characters of the flower and the flower stalk with the decisive character being ploidy; they can be commonly found growing next to each other as in these plants from northern Germany. Photo: Dirk Albach. — **Abb. 3:** *Veronica hederifolia* (links) und *V. sublobata* (rechts) können anhand verschiedener Blüten- und Blütenstielmerkmale unterschieden werden, das ausschlaggebende Merkmal ist aber die Ploidiestufe; die beiden Arten kommen oft nebeneinander vor, wie bei diesen norddeutschen Pflanzen. Foto: Dirk Albach.

characters with their characteristic combination could be tested. The analysis of habitat and chorology in Fischer (1967) demonstrated the influence of an ecological species concept, while the discussion of chromosome numbers and the report of a lack of observed hybrids indicated the influence of the biological species concept. Thus, we don't have a typical morphological/phenetic species concept but rather a biosystematic species concept (although Fischer never called it that).

However, ploidy as the absolute diagnostic character of Fischer (1967) may not always be such an absolute character. In an analysis of *Veronica cymbalaria*, Fischer (1975) was able to separate the diploid (*V. panormitana*, *V. trichadena*) from the tetraploid and hexaploid plants (Fig. 4) but considered the latter two ploidy levels as both belonging to *V. cymbalaria* due to the lack of morphological and chorological separation. Multiple origins of tetraploids, as in *V. chamaedrys* (Bardy & al. 2010), *V. cymbalaria* (Albach 2007) or *V. spicata* and *V. longifolia* (Buono & al. 2021), have since cast more doubt on the absoluteness of ploidy as diagnostic character.

It is noteworthy in this respect that chemotaxonomy did not have such a function as a differential character as in many other genera. While phytochemistry has contrib-

Fig. 4: *Veronica cymbalaria* (left) and *V. panormitana* (right) can be best differentiated by ploidy but also by some morphological characters such as flower size; they can grow sympatrically as these here near Antalya in southern Turkey. Photo: Dirk Albach. — **Abb. 4:** *Veronica cymbalaria* (links) und *V. panormitana* (rechts) können am eindeutigsten anhand der Ploidiestufe, aber auch mittels einiger morphologischer Merkmale wie der Blütengröße unterschieden werden; die beiden Arten können zusammen vorkommen wie etwa hier nahe Antalya in der südlichen Türkei. Foto: Dirk Albach.

uted to the knowledge of the genus since the first phytochemical analysis (SWIATEK & DRUZYNSKI 1968a, b) and was an important first indication that the infrageneric structure of the time was artificial (GRAYER-BARKMEIJER 1973), it has been always used for higher-level grouping of species (e. g., TASKOVA & al. 2004, 2012) rather than species delimitation, with the exception of studies by MITCHELL & al. (2001).

Veronica in the era of molecular systematics

By this time, the use of DNA sequences in the genus had already started with the analyses of WAGSTAFF & GARNOCK-JONES (1998) and ALBACH & CHASE (2001), which provided a more reliable kind of data to infer relationships in the genus above the species level and made it possible to test relationships among species and populations independently. Consequently, the concept of the genus and its subgenera has become essentially a phylogenetic concept with some supporting evidence from morphology, biogeography, karyology and phytochemistry (ALBACH & al. 2004). Nevertheless, even the 14 species that have been described since 2000 are mostly based on a morphological/phenetic species concept. And even those species that were established based on phylogenetic evidence in a DNA-based phylogenetic analysis were previously recognized at lower ranks and therefore not their recognition but only their rank is based on genetic divergence (DOOSTMOHAMMADI & al. 2022), with the possible exception of *V. dalmatica* (PADILLA-GARCÍA & al. 2018). Thus, the question remains whether the morphological/phenetic species concept is sufficient, with other kind of data mostly aiding in deciding on the taxonomic rank.

The species delimitation for the *Veronica hederifolia*-complex by FISCHER (1967) was much debated and not always confirmed (NORDENSTAM & NILSSON 1969, DE JONGH & KERN 1971). Even FISCHER (1975) admitted that the phenotypic limits are blurred in southern regions. However, the species delimitation withstood the test of time and DNA, which confirmed the three species in Central Europe as three independent genetic clades, despite evidence for some hybridization and possible further independent lineages in southeastern Europe and Turkey (HERRMANN 2021). Further sampling of individuals from this region and as yet understudied morphological data combined with information on ploidy and DNA sequence data will be necessary to evaluate species limits in this region. Thus, DNA sequence data serve as an “absolute diagnostic character” much like ploidy served as such for FISCHER (e. g., 1967, 1970b) and provides a more detailed resolution of relationships.

A further example for this is the study by BARDY & al. (2010) on *Veronica chamaedrys*. FISCHER (1970b, 1973) had separated the diploid plants as *V. vindobonensis* based on a combination of diagnostic morphological characters, distribution area and ploidy. However, the more detailed analyses of BARDY & al. (2010) revealed that the distributions overlap more than previously thought and that morphological character states are continuous. Further, the DNA-based analyses demonstrated that the tetraploids evolved independently from various groups of diploids several times. Thus, DNA again serves as an absolute character but at finer resolution than ploidy levels, which can be a homoplasious character.

In essence, the biosystematic species concept of Fischer has simply been updated and expanded by Albach (e.g., Albach 2007, Doostmohammadi & al. 2022) by using DNA-characters and phylogenetic information to assess species rank, similar to how Fischer used ploidy information (Fischer 1967). In fact, the biosystematic species concept of Fischer does not differ considerably from the unified species concept of De Queiroz (2005, 2007) with species being "separately evolving metapopulation lineage segments" (De Queiroz 2007) with morphology, karyology, and DNA-based phylogenetic information as diagnostic properties. What has hitherto not been assessed rigorously in *Veronica* is the analysis of the timing of the emergence of species-defining properties. Did morphological differences evolve before, simultaneously or after reciprocal monophyly? In some cases, such as *V. wormskjoldii*, it is apparent that the species have not gained monophyly with respect to their budding species (Albach & al. 2006) despite morphological diagnosability. In *V. cymbalaria* differences in ploidy and thus probably reproductive isolation have not yet lead to morphological diagnosability or monophyly of either cytotype (Albach 2007), therefore both cytotypes are recognized as a single species.

However, as pointed out by Wells & al. (2021), the unified species concept of De Queiroz (2007) provides a framework for what a species is but it does not provide an operational framework for when the species status has been attained. An instructive example in *Veronica* has been provided by the study of Bardy & al. (2010) mentioned above. Morphologically, only *V. krumovii* has been found to be distinct, but evidence from phylogenetic analyses demonstrates that it is a hybrid between the northeastern and the southern lineages. The southern lineage, corresponding to *V. chamaedryoides*, is monophyletic, although reciprocal monophyly has not been tested rigorously. Morphologically, the distinction is not clear and the morphospaces are partially overlapping. Therefore, Bardy & al. (2010) decided to recognize this taxon as a subspecies.

I admit that the rank of subspecies is ambiguous and deserves a definition similar to the term species. It functions as a placeholder for situations in which there is disagreement as to whether the taxa are sufficiently different to be recognized as species. Subspecies, following, slightly modified, Stuessy (2009), are geographically separable units that are genetically and morphologically partially distinct but distinction is insufficient to allow recognition in the absence of geographical information. Additionally, morphological similarity has to be based on inheritance rather than convergent ecological adaptation. This ambiguity in differentiation makes subspecies prime targets for further investigation on species status with further data and increased sampling.

The ambiguity of the subspecies is exemplified by the case of *Veronica tenuifolia*. Martínez Ortega & al. (2004) recognized three subspecies in this species because they lack clear morphological characters to distinguish them at species rank. However, these authors recognized the genetic cohesion of each of the three taxa, absence of gene flow between them, as well as their phytogeographical separation, suggesting that they may deserve species rank. Thus, it is not surprising that the study by Hausdorf &

HENNIG (2020) using the genetic data of MARTÍNEZ ORTEGA & al. (2004) alone came to the conclusion that the three taxa should be recognized at the species level. They argued that the genetic distance between the three taxa is larger than expected based on genetic versus geographical distance regression within taxa. Thus, the three taxa do not behave like one large continuous species. In contrast to MARTÍNEZ ORTEGA & al. (2004), HAUSDORF & HENNIG (2020) did not consider morphological differences, following a genetic cohesion-type species concept. Relying on genetic data alone, however, should not be enough for the recognition of species since separating genetic sister-groups not differentiated by morphology is frustrating for field botanists and other biologists. Thus, in these cases, the subspecies rank seems more appropriate to point out strong intraspecific structuring while emphasizing the lack of morphological differentiation.

It remains to be seen how to handle groups in which DNA sequence data suggest more than one lineage but morphology (and ploidy) does not separate these lineages. Certainly, paraphyletic species are common (RIESEBERG & BROUILLET 1994) and *Veronica wormskjoldii* (ALBACH & al. 2006) is an example from the genus *Veronica*. Here, the two geographically restricted species, *V. cusickii* and *V. copelandii*, have possibly evolved phenotypically and attained monophyly due to genetic drift faster than the presumed ancestor *V. wormskjoldii*. For the two lineages of *V. wormskjoldii* subsp. *nutans*, it will be clear in a few thousand years whether they evolve monophyly with respect to *V. cusickii* and *V. copelandii* or whether they evolve morphological discontinuities that will allow separating them at the species rank.

However, there may also be cases in which convergence may blur species boundaries and phylogenetic data have been instrumental to elucidate such patterns. One example is dense, interwoven indumentum. This has, based on DNA sequence data, separately evolved in *Veronica bombycina* and *V. bolkardaghensis*, which were considered conspecific but have recently been separated based on DNA sequence data (DOOSTMOHAMMADI & al. 2022). However, this step has not (yet) been taken for *V. incana*, which also appears to consist of at least two separate lineages (Nehrke & Albach, in prep.; Fig. 5). A second character revealed to be homoplastic is the pinnatifid leaf. Previously considered to be conspecific based on the similarly pinnatifid leaves, *V. dalmatica* was separated from *V. austriaca* subsp. *jacquinii* initially based on phylogenetic evidence, and this was corroborated by other morphological characters, different ploidy levels and distinct distribution areas (PADILLA-GARCÍA & al. 2018). Separating *V. multifida* into multiple species seems a further necessity based on the apparently convergent evolution of pinnatifid leaves, but this requires in-depth morphological and further phylogenetic analyses (DOOSTMOHAMMADI & al. 2022). Convergence may also extend to ecological characters, but this is rarely studied systematically with only few species distribution models available for species of *Veronica* (SOUSA-SILVA & al. 2014, BUONO & al. 2021, LÓPEZ-GONZÁLEZ & al. 2021, OMAR & ELGAMAL 2021).

Finally, there is the issue of hybrid species. The debate about the frequency of hybridization in *Veronica* started with LINNÉ (1787) and GÄRTNER (1849) and continued with HÄRLE (1932) and FISCHER (1974), among others. DNA data and phylogenetic analyses have helped address the issue. A number of studies have now demonstrated hybrid origins of species such as *V.* ×*gundisalvi* (López-González & al. 2021), *V.* ×*sessiliflora* (Fig. 6), *V.* ×*schmakovii* and *V.* ×*altaica* (Khan & al., submitted). Overall, however, few of the hybrids proposed on the basis of morphology have been analyzed. Based on the available information, homoploid hybridization seems to occur within subgenera and is largely evolutionarily inconsequential with hybrids mostly remaining locally with their parents.

Polyploid speciation may be a different issue in *Veronica*. Albach & al. (2008) estimated ca. 15%–20% of all speciation events to be due to polyploidy. This may have been an overestimation since it is possible that some now purely polyploid species were

Fig. 5: *Veronica incana* has been shown by DNA comparison to include two separate genetic lineages with this population from central Ukraine being the true *V. incana*. Photo: Dirk Albach. — **Abb. 5:** *Veronica incana* umfasst zwei klar getrennte genetische Linien, wobei die hier gezeigte Population aus der zentralen Ukraine zur echten *V. incana* gehört. Foto: Dirk Albach.

derived via autopolyploid origin and their ancestor is now extinct or has not yet been found. Autopolyploidy seems to be predominant in *Veronica* subsect. *Pentasepalae* (Padilla-García & al. 2018) and in general. Soltis & al. (2007) asked for recognition of autopolyploid lineages. However, autopolyploid lineages in *Veronica* are rarely differentiated morphologically and ecologically to an extent that it is possible to identify these plants without analyzing chromosome numbers or genome size. In many cases, these autopolyploid lineages originated multiple times independently (e. g., Bardy & al. 2010, Buono & al. 2021) and are still considered conspecific. Exceptions are *V. sennenii* and *V. angustifolia*, which are autopolyploid derivatives of *V. satureiifolia* (Padilla-García & al. 2018).

Fig. 6: *Veronica porphyriana* (left) and *V. pinnata* (right) are the parents of *V. ×sessiliflora* (middle), growing side by side in the Altai Mountains. Photo: Dirk Albach. — **Abb. 6:** *Veronica porphyriana* (links) und *V. pinnata* (rechts) sind die Eltern von *V. ×sessiliflora* (Mitte), nebeneinander wachsend im Altai-Gebirge. Foto: Dirk Albach.

On the other hand, a few cases of allopolyploidy have been confirmed using DNA markers, e.g., *Veronica cymbalaria* (= *V. panormitana* × *V. trichadena*; Albach 2007) with two origins of the tetraploid level and multiple origins of the hexaploid level. A taxonomically difficult problem is the allopolyploid origin of *V. wormskjoldii* subsp. *wormskjoldii* from *V. alpina* and *V. wormskjoldii* subsp. *nutans* (Albach & al. 2006). A morphological separation of polyploid from diploid *V. wormskjoldii* is not possible and even the distinction from diploid *V. alpina* is difficult. The clearest example of an allopolyploid origin in *Veronica* so far is *V. persica*, a tetraploid derivative of *V. polita* and *V. ceratocarpa* (Albach, unpub.), a pattern that was already suggested by Fischer (1987). Allopolyploids in *V.* subsect. *Pentasepalae* have not yet been recognized at the species level since these are mostly aberrant individuals or single populations (Padilla-García & al. 2018). Thus, based on these few examples, allopolyploidy seems to occur only between closely related species, so close that they can be considered in the grey zone between auto- and allopolyploidy.

So where do we stand in terms of comparability of species in *Veronica*? A few groups such as *V.* subsect. *Pentasepalae* have been studied intensively (Andrés-Sánchez & al. 2008, Rojas-Andrés & al. 2015, Rojas-Andrés & al. 2016, Padilla-García & al. 2018). The European to Siberian members of *V.* subg. *Pseudolysimachium* have also been well studied (Bardy & al. 2011; Khan & al., submitted, Albach, Nehrke, Daubert, Höpke, unpub.). In many groups we only scratched the surface with phylogenetic analyses, such as *V.* sect. *Canae* (Buhk & al. 2015). In others, such as *V.* sect. *Beccabunga*, phylogenetic analyses have so far raised more new questions than helped to delimit natural species (Ellmouni & al. 2017). Finally, there are groups such as *V.* sect. *Acinifolia* and *V.* sect. *Subracemosae* (*V. biloba* and relatives) with almost no information on phylogenetic relationships so far, but in which chromosome counts suggest multiple cytotypes within what we consider a single species today (Albach & al. 2008). Thus, there is an urgent need to study and understand species diversity in order to protect the significant units of evolution and to preserve these wonderful species for future generations.

Acknowledgements

I thank Manfred A. Fischer for the many discussions on various groups of *Veronica* and their diagnosability, their relationships and their evolution.

References

Albach D. C. (2007): Amplified fragment length polymorphisms and sequence data in the phylogenetic analysis of polyploids: multiple origins of *Veronica cymbalaria* (Plantaginaceae). – New Phytol. **176**: 481–498. https://doi.org/10.1111/j.1469-8137.2007.02172.x

Albach D. C. & Chase M. W. (2001): Paraphyly of *Veronica* (Veroniceae; Scrophulariaceae): Evidence from the internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA. – J. Pl. Res. **114**: 9–18. https://doi.org/10.1007/PL00013971

Albach D. C., Martínez Ortega M. M., Fischer M. A. & Chase M. W. (2004): A new classification of the tribe Veroniceae – Problems and a possible solution. – Taxon **53**: 429–452. https://doi.org/10.3417/2006094

Albach D. C., Meudt H. M. & Oxelman B. (2005): Piecing together the "new" Plantaginaceae. – Amer. J. Bot. **92**: 297–315. https://doi.org/10.3732/ajb.92.2.297

Albach D. C., Schönswetter P. & Tribsch A. (2006): Comparative phylogeography of the *Veronica alpina* complex in Europe and North America. – Molec. Ecol. **15**: 3269–3286. https://doi.org/10.1111/j.1365-294X.2006.02980.x

Albach D. C., Martínez-Ortega M. M., Delgado Sanchez L., Weiss-Schneeweiss H., Özgökce F. & Fischer M. A. (2008): Chromosome numbers in Veroniceae: Review and several new counts. – Ann. Missouri Bot. Gard. **95**: 543–566. https://doi.org/10.3417/2006094

Anderson E. (1953): Introgressive hybridization. – Biol. Rev. (Cambridge) **28**: 280–307. https://doi.org/10.1111/j.1469-185X.1953.tb01379.x

Andrés-Sánchez S., Rico E., Herrero A., Santos-Vicente M. & Martínez Ortega M. M. (2008): Combining traditional morphometrics and molecular markers in cryptic taxa: Towards an updated integrative taxonomic treatment for *Veronica* subgenus *Pentasepalae* (Plantaginaceae sensu APG II) in the western Mediterranean. – Bot. J. Linn. Soc. **159**: 68–87. https://doi.org/10.1111/j.1095-8339.2008.00917.x

Avise J. C. & Wollenberg K. (1997): Phylogenetics and the origin of species. – Proc. Natl. Acad. Sci. U.S.A. **94**: 7748–7755. https://doi.org/10.1073/pnas.94.15.7748

Bardy K. E., Albach D. C., Schneeweiss G. M., Fischer M. A. & Schönswetter P. (2010): Disentangling phylogeography, polyploid evolution and taxonomy of a woodland herb (*Veronica chamaedrys* group, Plantaginaceae s. l.) in southeastern Europe. – Molec. Phylogen. Evol. **57**: 771–786. https://doi.org/10.1016/j.ympev.2010.06.025

Bardy K. E., Schönswetter P., Schneeweiss G. M., Fischer M. A. & Albach D. C. (2011): Extensive gene flow blurs species boundaries among *Veronica barrelieri*, *V. orchidea* and *V. spicata* (Plantaginaceae) in southeastern Europe. – Taxon **60**: 108–121. https://doi.org/10.1002/tax.601010

Bauhin C. (1623): Pinax theatri botanici. – Basel: Joannis Regis. https://doi.org/10.5962/bhl.title.712

Baum D. (1992): Phylogenetic species concepts. – Trends Ecol. Evol. **7**: 1–2. https://doi.org/10.1016/0169-5347(92)90187-G

Beatus R. (1935): Genetische und zytologische Untersuchungen in der *Veronica*-Gruppe *Fruticulosae* der Sektion *Veronicastrum*. – Flora **130**: 153–175. https://doi.org/10.1016/S0367-1615(17)31858-X

Bjorå C. S., Hemp A., Hoell G. & Nordal I. (2008): A taxonomic and ecological analysis of two forest *Chlorophytum* taxa (Anthericaceae) on Mount Kilimanjaro, Tanzania. – Pl. Syst. Evol. **274**: 243–253. https://doi.org/10.1007/s00606-008-0032-0

Bobay L.-M. (2020): The prokaryotic species concept and challenges. – In Tettelin H. & Medini D. (Eds.): The Pangenome: pp. 21–49. – Cham: Springer. https://doi.org/10.1007/978-3-030-38281-0_2

Boissier E. (1844): Diagnoses plantarum orientalium novarum **1(4)**. – Leipzig: B. Hermann.

Boissier E. (1879): Flora orientalis **4**. – Geneve & Basel: H. Georg. https://doi.org/10.5962/bhl.title.20323

Borissova A. G. (1955): *Veronica*. – In Shishkin B. K. & Bobrov E. G. (Eds.): Flora URSS **22**: 329–500 – Moskva & Leningrad: Izdatel'stvo Akademii Nauk SSSR.

Buhk N., Zhao L., Li H. & Albach D. C. (2015): Molecular systematics and morphometrics in *Veronica* subsect. *Canae* (Plantaginaceae). – Pl. Syst. Evol. **301**: 1967–1979. https://doi.org/10.1007/s00606-015-1214-1

Buono D., Khan G., von Hagen K. B., Kosachev P. A., Mayland-Quellhorst E., Mosyakin S. L. & Albach D. C. (2021): Comparative phylogeography of *Veronica spicata* and *V. longifolia* (Plantaginaceae) across Europe: Integrating hybridization and polyploidy in phylogeography. – Frontiers Pl. Sci. (Online journal) **11**: 588354 (12 pp.). https://doi.org/10.3389/fpls.2020.588354

Coyne J. A. & Orr H. A. (2004): Speciation. – Sunderland (MA): Sinauer.

Cracraft J. (1987): Species concepts and the ontology of evolution. – Biol. & Philos. **2**: 329–346. https://doi.org/10.1007/BF00128837

Darwin C. (1859): On the origin of species by the means of natural selection. – London: John Murray. https://doi.org/10.5962/bhl.title.82303

De Jongh S. & Kern J. (1971): De variabiliteit van *Veronica hederifolia* L. in Nederland. – Gorteria **5**: 160–165.

De Queiroz K. (1999): The general lineage concept of species and the defining properties of the species category. – In Wilson R. A. (Ed.): Species – new interdisciplinary essays: pp. 49–89. – Cambridge & London: MIT Press.

De Queiroz K. (2005): A unified concept of species and its consequences for the future of taxonomy. – Proc. Calif. Acad. Sci. **56**: 196–215.

De Queiroz K. (2007): Species concepts and species delimitation. – Syst. Biol. **56**: 879-886. https://doi.org/10.1080/10635150701701083

De Queiroz K. & Donoghue M. J. (1988): Phylogenetic systematics and the species problem. – Cladistics **4**: 317–338. https://doi.org/10.1111/j.1096-0031.1988.tb00518.x

Dodoens R. (1578): A nievve herball; or, Historie of plantes. Translated by Henry Lyte. – London: Gerard Dewes. https://doi.org/10.5962/bhl.title.7107

Doostmohammadi M., Bordbar F., Albach D. C. & Mirtadzadini M. (2022): Phylogeny and historical biogeography of *Veronica* subgenus *Pentasepalae* (Plantaginaceae): Evidence for its origin and subsequent dispersal. – Biology **11**: 639 (27 pp.). https://doi.org/10.3390/biology11050639

Ellmouni F. Y., Karam M. A., Ali R. M. & Albach D. C. (2017): Molecular and morphometric analysis of *Veronica* L. section *Beccabunga* (Hill) Dumort. – Aquatic Bot. **136**: 95–111. https://doi.org/10.1016/j.aquabot.2016.09.010

Fick S. E. & Hijmans R. J. (2017): WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. – Int. J. Climatol. **37**: 4302–4315. https://doi.org/10.1002/joc.5086

Fischer M. A. (1967): Beiträge zur Cytotaxonomie der *Veronica hederifolia*-Gruppe (Scrophulariaceae). – Österr. Bot. Z. **114**: 189–233. https://doi.org/10.1007/BF01373910

Fischer M. A. (1970a): Zur Cytotaxonomie der Verwandtschaftsgruppe um *Veronica orientalis* Mill., emend. Ait. in der Türkei. – Österr. Bot. Z. **118**: 131–161. https://doi.org/10.1007/BF01373226

Fischer M. A. (1970b): Zur Cytotaxonomie von *Veronica chamaedrys* L., I.: subsp. *vindobonensis* M. Fischer, eine neue diploide Sippe. – Österr. Bot. Z. **118**: 206–215. https://doi.org/10.1007/BF01377857

Fischer M. A. (1972): Neue Taxa, Chromosomenzahlen und Systematik von *Veronica* subsect. *Acinifolia* (Römpp) Stroh. – Österr. Bot. Z. **120**: 413–437. https://doi.org/10.1007/BF01324625

Fischer M. A. (1973): *Veronica vindobonensis* M. Fischer (Zur Cytotaxonomie von *Veronica chamaedrys* agg., III.). – Österr. Bot. Z. **122**: 287–292. https://doi.org/10.1007/BF01441580

Fischer M. A. (1974): Beitrag zu einer systematischen Neubearbeitung der Gruppe um *Pseudolysimachion spicatum* (L.) Opiz (= *Veronica spicata* L.). – Phyton (Horn) **16**: 29–47.

Fischer M. A. (1975): Untersuchungen über den Polyploidkomplex *Veronica cymbalaria* agg. (Scrophulariaceae). – Pl. Syst. Evol. **123**: 97–105. https://doi.org/10.1007/BF00981768

Fischer M. A. (1977a): Taxa et Nomina Nova Generis Veronicae (Scrophulariaceae) Turciae. – Pl. Syst. Evol. **128**: 293–297. https://doi.org/10.1007/BF00984565

Fischer M. A. (1977b): Two new *Veronica* species (Scrophulariaceae) of Turkey and Iraq. – Pl. Syst. Evol. **128**: 237–241. https://doi.org/10.1007/BF00984560

Fischer M. A. (1978): *Veronica* L. – In Davis P. H. (Ed.): Flora of Turkey and the East Aegean Islands **6**: 689–753. – Edinburgh: University Press.

Fischer M. A. (1981): *Veronica*. – In Rechinger K. H. (Ed.): Flora Iranica. Flora des iranischen Hochlandes und der umrahmenden Gebirge **147**: 52–165. – Graz: Akademische Druck- und Verlagsanstalt.

Fischer M. A. (1982): *Veronica*. – In Pignatti S. (Ed.): Flora d'Italia **2**: 558–573. – Roma: Edagricole.

Fischer M. A. (1984): *Veronica fridericae*, a new species from Eastern Turkey. – Pl. Syst. Evol. **144**: 67–71. https://doi.org/10.1007/BF00990802

Fischer M. A. (1987): On the origin of *Veronica persica* (Scrophulariaceae) – a contribution to the history of a neophytic weed. – Pl. Syst. Evol. **155**: 105–132. https://doi.org/10.1007/BF00936294

Fischer M. A. (1991): *Veronica*. – In Strid A. & Tan K. (Eds.): Mountain Flora of Greece: pp. 209–234 – Edinburgh; Edinburgh University Press.

Fischer, M. A. (1997): Friedrich Ehrendorfer 70 – a life of pioneering devotion to botany and biosystematics. – Pl. Syst. Evol. **206**: 3–18. https://doi.org/10.1007/BF00987937

Fitzhugh K. (2009): Species as explanatory hypotheses: Refinements and implications. – Acta Biotheor. **57**: 201–248. https://doi.org/10.1007/s10441-009-9071-3

Fuchs L. (1543): New Kreüterbuch. – Basel: Michael Isingrin. https://www.bavarikon.de/object/BSB-HSS-00000BSB00017437

Gärtner C. F. (1849): Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. – Stuttgart: Hering & Comp. https://doi.org/10.5962/bhl.title.50413

Geisen S., Ten Hooven F. C., Kostenko O., Snoek L. B. & Van der Putten W. H. (2021): Fungal root endophytes influence plants in a species-specific manner that depends on plant's growth stage. – J. Ecol. **109**: 1618–1632. https://doi.org/10.1111/1365-2745.13584

Gerard J. (1597): The Herball; or, Generall historie of plantes. – London: Iohn Norton. https://doi.org/10.5962/bhl.title.99400

Grayer-Barkmeijer R. J. (1973): A chemosystematic study of *Veronica*: Iridoid glucosides. – Biochem. Syst. **1**: 101–110. https://doi.org/10.1016/0305-1978(73)90023-9

Graze H. (1933): Die chromosomalen Verhältnisse in der Sektion *Pseudolysimachia* Koch der Gattung *Veronica*. – Jahrb. Wiss. Bot. **77**: 507–559.

Härle A. (1932): Die Arten und Formen der *Veronica*-Sektion *Pseudolysimachia* Koch auf Grund systematischer und experimenteller Untersuchungen. – Biblioth. Bot. **26**: 1–86.

Hausdorf B. & Hennig C. (2020): Species delimitation and geography. – Molec. Ecol. Resources **20**: 950–960. https://doi.org/10.1111/1755-0998.13184

Heitz E. (1926): Der Nachweis der Chromosomen. Vergleichende Studien über ihre Zahl, Größe und Form im Pflanzenreich I. – Z. Bot. **18**: 625–681.

Herrmann D. (2021): Die *Veronica hederifolia*-Gruppe: Ploidie und Phylogenie innerhalb Europas. – Bachelor thesis, Carl von Ossietzky-Universität Oldenburg.

Hörandl E. (2022): Novel approaches for species concepts and delimitation in polyploids and hybrids. – Plants **11**: 204 (25 pp.). https://doi.org/10.3390/plants11020204

Huber A. (1927): Beiträge zur Klärung verwandtschaftlicher Beziehungen in der Gattung *Veronica*. I. Die Kernuntersuchungen in der Gattung *Veronica*. – Jahrb. Wiss. Bot. **66**: 359–380.

Juel H. O. (1891): Studier öfver *Veronica*-Blomman. – Acta Horti Berg. **1**: 1–20.

Kingsbury N. (2009): Hybrid: The history and science of plant breeding. – Chicago: University of Chicago Press. https://doi.org/10.7208/chicago/9780226437057.001.0001

Lehmann E. B. J. (1906): Wanderung und Verbreitung von *Veronica tournefortii* Gm. – Sitzungsber. Abh. Naturwiss. Ges. Isis Dresden **2**: 93–107.

Lehmann E. B. J. (1914): Über Bastardisierungsuntersuchungen in der *Veronica*-Gruppe *Agrestis*. – Z. Indukt. Abstammungs- Vererbungsl. **13**: 88–175.

Linné C. (1753): Species Plantarum. – Stockholm: L. Salvius. https://doi.org/10.5962/bhl.title.37656

Linné C. (1787): Amoenitates academicae: seu Dissertationes variae physicae, medicae botanicae antehac seorsim editae nunc collectae et auctae cum tabulis aeneis **3**. – Erlangae: sumtu Jo. Jacobi Palm. https://doi.org/10.5962/bhl.title.149146

López-González N., Bobo-Pinilla J., Gutiérrez-Larruscain D., Martínez-Ortega M. & Rojas-Andrés B. (2021): Hybridization as a biodiversity driver: The case of *Veronica* × *gundisalvi*. – Medit. Bot. **42**: e67901 (8 pp.). https://doi.org/10.5209/mbot.67901

Martínez Ortega M. M., Delgado L., Albach D. C., Elena-Rosselló J. A. & Rico E. (2004): Species boundaries and phylogeography of *Veronica* subsect. *Pentasepalae* (Scrophulariaceae) in the Western Mediterranean inferred from AFLP markers. – Syst. Bot. **29**: 965–986. https://doi.org/10.1600/0363644042451071

Mattioli P. A. (1568): I discorsi […] nelli sei libri di Pedacio Dioscoride Anazarbeo della materia medicinale. Hora di nuouo dal suo istesso autore ricorretti, & in più di mille luoghi aumentati. – Venetia: Appresso Vincenzo Valgrisi. https://doi.org/10.5962/bhl.title.120952

Mayr E. (1942): Systematics and the origin of species, from the viewpoint of a zoologist. – Cambridge, (MA, USA): Harvard University Press.

Mitchell K. A., Markham K. R. & Bayly M. J. (2001): Flavonoid characters contributing to the taxonomic revision of the *Hebe parviflora* complex. – Phytochemistry **56**: 453–461. https://doi.org/10.1016/S0031-9422(00)00397-6

Mouterde P. & Fischer M. A. (1984): *Veronica*. – In Mouterde P. (Ed.): Nouvelle Flore du Liban et der la Syrie **3**: 130–133. – Beyrouth: Dar el-Machreq SARL.

Nordenstam B. & Nilsson Ö. (1969): Taxonomy and distribution of *Veronica hederifolia* s. lat. (Scrophulariaceae) in Scandinavia. – Bot. Not. **122**: 233–247.

Olmstead R. G. & Reeves P. A. (1995): Evidence for the polyphyly of the Scrophulariaceae based on chloroplast *rbcL* and *ndhF* sequences. – Ann. Missouri Bot. Gard. **82**: 176–193. https://doi.org/10.2307/2399876

Omar K. & Elgamal I. (2021): IUCN Red List and species distribution models as tools for the conservation of poorly known species: A case study of endemic plants *Micromeria serbaliana* and *Veronica kaiseri* in South Sinai, Egypt. – Kew Bull. **76**: 477–496. https://doi.org/10.1007/s12225-021-09953-4

Öztürk A. & Fischer M. A. (1982): Karyosystematics of *Veronica* sect. *Beccabunga* (Scrophulariaceae) with special reference to the taxa in Turkey. – Pl. Syst. Evol. **140**: 307–319. https://doi.org/10.1007/BF02418899

Padilla-García N., Rojas-Andrés B. M., López-González N., Castro M., Castro S., Loureiro J., Albach D. C., Machon N. & Martínez-Ortega M. M. (2018): The challenge of species delimitation in the diploid-polyploid complex *Veronica* subsection *Pentasepalae*. – Molec. Phylogen. Evol. **119**: 196–209. https://doi.org/10.1016/j.ympev.2017.11.007

Ramsey J., Bradshaw H. D. & Schemske D. W. (2003): Components of reproductive isolation between the monkeyflower *Mimulus lewisii* and *M. cardinalis* (Phrymaceae). – Evolution **57**: 1520–1534. https://doi.org/10.1111/j.0014-3820.2003.tb00360.x

Rieseberg L. H. (2006): The nature of plant species. – Nature **440**: 524–527. https://doi.org/10.1038/nature04402

Rieseberg L. H. & Brouillet L. (1994): Are many plant species paraphyletic? – Taxon **43**: 21–32. https://doi.org/10.2307/1223457

Rojas-Andrés B. M., Albach D. C. & Martínez-Ortega M. M. (2015): Exploring the intricate evolutionary history of the diploid–polyploid complex *Veronica* subsection *Pentasepalae* (Plantaginaceae). – Bot. J. Linn. Soc. **179**: 670–692. https://doi.org/10.1111/boj.12345

Rojas-Andrés B. M., Rico E. & Martínez-Ortega M. M. (2016): A nomenclatural treatment for *Veronica* subsect. *Pentasepalae* (Plantaginaceae sensu APG III) and typification of several names. – Taxon **65**: 617–627. https://doi.org/10.12705/653.14

Rosenberg N. A. (2003): The shapes of neutral gene genealogies in two species: Probabilities of monophyly, paraphyly, and polyphyly in a coalescent model. – Evolution **57**: 1465–1477. https://doi.org/10.1111/j.0014-3820.2003.tb00355.x

Schlenker G. (1935): Experimentelle Untersuchungen in der Sektion *Beccabunga* Griseb. der Gattung *Veronica*. – Flora **130**: 305–350. https://doi.org/10.1016/S0367-1615(17)31868-2

Schmitz M. (1946): Zur Charakterisierung der Arten der *Veronica*-Gruppe *Agrestis* unter besonderer Berücksichtigung des Polyploidieproblems. – Diss. Universität Tübingen.

Simpson G. G. (1961): Principles of animal taxonomy. – Columbia Biological Series **20**. – New York: Columbia University Press.

Soltis D. E., Soltis P. S., Schemske D. W., Hancock J. F., Thompson J. N., Husband B. C. & Judd W. S. (2007): Autopolyploidy in angiosperms: Have we grossly underestimated the number of species? – Taxon **56**: 13–30. https://www.jstor.org/stable/25065732

Sousa-Silva R., Alves P., Honrado J. & Lomba A. (2014): Improving the assessment and reporting on rare and endangered species through species distribution models. – Global Ecol. Conservation **2**: 226–237. https://doi.org/10.1016/j.gecco.2014.09.011

Stuessy T. F. (2009): Plant taxonomy: The systematic evaluation of comparative data. – New York: Columbia University Press.

Swiatek L. & Druzynski J. (1968a): Aucubin content of medicinal plants of *Veronica* species. – Acta Polon. Pharm. **25**: 593–597.

Swiatek L. & Druzynski J. (1968b): Aucubin content in medicinals plants of the *Veronica* genus. – Acta Polon. Pharm. **25**: 597–600.

Taskova R. M., Albach D. C. & Grayer R. J. (2004): Phylogeny of *Veronica* – a combination of molecular and chemical evidence. – Pl. Biol. **6**: 673–682. https://doi.org/10.1055/s-2004-830330

Taskova R. M., Kokubun T., Garnock-Jones P. J. & Jensen S. R. (2012): Iridoid and phenylethanoid glycosides in the New Zealand sun hebes (*Veronica*; Plantaginaceae). – Phytochemistry **77**: 209–217. https://doi.org/10.1016/j.phytochem.2012.02.001

Těšitelová T., Jersáková J., Roy M., Kubátová B., Těšitel J., Urfus T., Trávníček P. & Suda J. (2013): Ploidy-specific symbiotic interactions: Divergence of mycorrhizal fungi between cytotypes of the *Gymnadenia conopsea* group (Orchidaceae). – New Phytol. **199**: 1022–1033. https://doi.org/10.1111/nph.12348

Toprak Z., Pfeil B. E., Jones G., Marcussen T., Ertekin A. S. & Oxelman B. (2016): Species delimitation without prior knowledge: DISSECT reveals extensive cryptic speciation in the *Silene aegyptiaca* complex (Caryophyllaceae). – Molec. Phylogen. Evol. **102**: 1–8. https://doi.org/10.1016/j.ympev.2016.05.024

Van Valen L. (1976): Ecological species, multispecies, and oaks. – Taxon **25**: 233–239. https://doi.org/10.2307/1219444

Wagstaff S. J. & Garnock-Jones P. J. (1998): Evolution and biogeography of the *Hebe* complex (Scrophulariaceae) inferred from ITS sequences. – New Zealand J. Bot. **36**: 425–437. https://doi.org/10.1080/0028825X.1998.9512581

Warren D. L., Glor R. E. & Turelli M. (2008): Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. – Evolution **62**: 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x

Wells T., Carruthers T., Muñoz-Rodríguez P., Sumadijaya A., Wood J. R. I. & Scotland R. W. (2021): Species as a heuristic: Reconciling theory and practice. – Syst Biol. **71**: 1233–1243. https://doi.org/10.1093/sysbio/syab087

Wells T., Carruthers T. & Scotland R. W. (2022): Heuristics, species, and the analysis of systematic data. – Trends Pl. Sci. **27**: 524–527. https://doi.org/10.1016/j.tplants.2022.03.013

Wiley E. O. (1978): The evolutionary species concept reconsidered. – Syst. Zool. **27**: 17–26. https://doi.org/10.2307/2412809

Yang Z. & Rannala B. (2010): Bayesian species delimitation using multilocus sequence data. – Proc. Natl. Acad. Sci. U.S.A. **107**: 9264–9269. https://doi.org/10.1073/pnas.0913022107

Zapata F. & Jiménez I. (2012): Species delimitation: Inferring gaps in morphology across geography. – Syst. Biol. **61**: 179–194. https://doi.org/10.1093/sysbio/syr084

Zündorf W. (1939): Zytogenetisch-entwicklungsgeschichtliche Untersuchungen in der *Veronica*-Gruppe *Biloba* der Sektion *Alsinebe* Griseb. – Z. Indukt. Abstammungs- Vererbungsl. **77**: 195–238. https://doi.org/10.1007/BF01739890

Received 19 September 2022
Revision received 11 October 2022
Accepted 14 October 2022
Published 20 December 2023

Zeitschrift/Journal: Neilreichia - Zeitschrift für Pflanzensystematik und Floristik Österreichs

Jahr/Year: 2023

Band/Volume: 13-14

Autor(en)/Author(s): Albach Dirk

Artikel/Article: What is a species in Veronica? Reflections on the occasion of Manfred A. Fischer’s 80th birthday 305-323