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Biosystematic revision of the native and naturalised species of *Rubus* L. (Rosaceae) in the Cape Floristic Region, South Africa

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ABSTRACT

Rubus L. is a highly diverse and taxonomically complex genus with a worldwide distribution. Although southern Africa is not a major centre of *Rubus* diversity, a number of indigenous and naturalised taxa have been recorded from the region, although their taxonomy, nomenclature and evolution are either confused or poorly studied at best. This paper represents the first results of a wider project focusing on the biosystematics of the southern African *Rubus* flora, and presents a taxonomic revision of the brambles of the Cape Floristic Region, including an estimation of ploidy levels. A total of eight taxa are recognised, including the two indigenous taxa *R. pinnatus* and *R. rigidus* agg., the four introduced species *R. armeniacus*, *R. bergii*, *R. rosifolius* and *R. titanus*, and two hybrids between indigenous and introduced taxa. *Rubus rigidus* agg. is an unresolved and variable species complex with at least two ploidy levels (5x, 6x). The hybrid taxon *R. bergii* × *R. rigidus* appears to be widespread and behaves as an independent apomictic complex. In addition, hybridization between *R. bergii* and *R. pinnatus* is relatively common in the contact zones between the two species. The two introductions *Rubus armeniacus* and *R. titanus* are recorded from South Africa for the first time. The invasive potential of the introduced species is regarded as low but the potential for hybridization by *R. bergii* seems to be high. An identification key, morphological descriptions, and notes on nomenclature, distribution and ecology are provided, and all taxa are illustrated.

1. Introduction

Rubus L. (brambles, blackberries, raspberries, dewberries etc.) is a large and diverse genus in the Rosaceae with a worldwide distribution, and includes thousands of published species names and infrageneric taxa (Gustafsson, 1943; Kurtto et al., 2010). It is traditionally divided into twelve subgenera (Focke, 1910–1914), although this classification is clearly artificial as many of the subgenera have been shown to be poly- or paraphyletic (Alice and Campbell, 1999). The species-level taxonomy is very controversial due to the frequent occurrence of facultative apomixis (asexual formation of seeds) and hybridization, particularly common in some of the subgenera (Weber, 1996; Sochor et al., 2015).

Current taxonomic treatments in Europe and North America, the two large regions with the highest diversity of apomictic brambles, approach the subject quite differently. The leading European paradigm, the so-called "Weberian batology" (from *batos* = the Greek for bramble), accepts a very narrow species delimitation that treats every apomictic genotype with a sufficiently extensive distribution area as a separate species (Weber, 1996; Holub, 1997), whereas the account of the genus in the Flora of North America adopts a much broader species concept (Alice et al., 2015) that groups several (probably many) different, often reproductively isolated genotypes, into more broadly circumscribed species based on morphological similarities, thereby rejecting the earlier, more detailed treatments by Bailey (1941–1945) and Davis et al. (1967).

Taxonomic and nomenclatural difficulties are the major reasons why *Rubus* is understudied or even neglected in many regions of the world, e.g. the southern Caucasus (Sochor and Trávníček, 2016), some parts of Europe (Kurtto et al., 2010), and also South Africa (Stirton, 1981a, 1981b; Henderson, 2011). Data on evolutionary mechanisms, modes of reproduction, and phylogenesis are also scarce outside Europe. This is despite the importance of the genus, not only as an integral component of many vegetation types and as a significant ecological element across the globe, but also as the source of valuable fruit crops and of expansive/invasive taxa. Several *Rubus* species have been introduced into various regions of the world, where they have become

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dangerous invaders, e. g. European *R. ulmifolus* Schott, *R. praecox* Bertol. or Caucasian *R. armeniacus* Focke in western North America, South America and Australia (Mazzolari et al., 2011; Clark et al., 2013; Bruckart et al., 2017) or *R. alceifolius* Poir. in many Indian Ocean islands and Australia (Amsellem et al., 2000).

South Africa is known for the occurrence of many alien brambles, some of which have substantial environmental and economic impact, particularly in the east of the region (Henderson, 2011; Sochor and Manning, pers. obs.). Their taxonomy in the subcontinent, however, is still much confused and even the distinction between native and naturalised taxa is not always clear (Stirton, 1981a, 1981b; Henderson, 2011). Literature on this topic is scarce and inadequate, and studies on herbarium material are not very helpful as collections are mostly incomplete, consisting usually of a single inflorescence or only a tip of the flowering stem. For proper determination it is necessary to study both sterile stems (i.e. first-year stems, also called 'primocanes') with their associated leaves, in combination with inflorescences, which usually develop on second-year stems ('floricanes'). The minimum herbarium specimens should thus comprise parts of first-year stems with at least two well-developed leaves attached (collected from the middle of the stem) plus one or more well developed inflorescences/infructescences (also from the middle of the stem).

The earliest, relatively modern account of *Rubus* in South Africa is that by Ecklon and Zeyher (1836), in which they enumerate nine species, including *R. bergii* (Cham. & Schltdl.) Eckl. & Zeyh., *R. chrysocarpus* Cham. & Schltdl., *R. fruticosus* L., *R. mundii* Cham. & Schltdl., *R. pinnatus* Willd., *R. rigidus* Sm. and *R. rosifolius* Sm. plus the two newly described taxa *R. ludwigii* Eckl. & Zeyh. and *R. pappei* Eckl. & Zeyh. This number was reduced to five by Harvey (1862) in his account of the genus for the *Flora capensis*, in which he recognised just three native species, *R. ludwigii* Eckl. & Zeyh., *R. pinnatus* Willd. (including *R. pappei*, treated here as an uncertain species) and *R. rigidus* Sm. (including *R. chrysocarpus* and *R. mundii* as varieties), as well as the introduced *R. fruticosus* var. *bergii* Cham. & Schltdl. and *R. rosifolius* Sm. Some additional specimens remained unassigned, including at least one potential hybrid collection. In contrast to this conservative treatment, Gustafsson (1934) described a further six native species, mainly from the eastern parts of the country, and recorded the occurrence of an additional two introduced species, but the status of several of these new taxa is uncertain. Since then some preliminary comments on the genus in southern Africa have been published (Stirton, 1981a, 1981b, 1984), as well as observations on the chromosome numbers, meiotic chromosome behaviour, reproduction and hybridization of some species (Spies et al., 1985, 1987; Spies and du Plessis, 1985, 1986). Our current knowledge of the genus in the subcontinent was summarised in an informal treatment provided by Henderson (2011), which enumerates 13 native and introduced taxa for South Africa. Current accounts of the genus in the Cape Floristic Region (CFR) list the three taxa *R. fruticosus*, *R. pinnatus* and *R. rigidus* (Bond and Goldblatt, 1984; Goldblatt and Manning, 2000; Manning and Goldblatt, 2012), without comment on their native status, although the former is a European introduction correctly treated under the name *R. bergii*.

An early reference to the occurrence of brambles in the CFR is found in C.P. Thunberg's account of his travels in the region in 1772–1775 (Forbes, 1986) in the context of their use as quickset hedges by European settlers in the region but it is not clear whether these were native species or plants introduced for the purpose. If the latter, then this is likely to be one of the original reasons for the introduction of European species into the country, presumably along with their value as a fruit crop. Certainly *R. bergii* was well established in the environs of Cape Town by the middle of the nineteenth century, when Harvey (1862) described it as the 'common bramble or blackberry of the Cape'. Partial hedges of *R. bergii* are still evident on roadsides and the edges of vineyards around Stellenbosch today, and may represent the remains of these early hedges.

In view of the inadequacies in our knowledge of the biosystematics of the South African bramble flora, we have undertaken a detailed study of the topic using both classical and modern cytogenetic/molecular approaches. This paper presents the first results of a wider project focusing on diversity, evolution and classification of the South African taxa of *Rubus*. In this contribution, we revise the genus *Rubus* in the CFR in terms of their taxonomy, nomenclature and ploidy levels, and provide descriptions, pictures and a key to species of this greatly overlooked plant group. No *Rubus* collections have been made from Namaqualand or the Roggeveld Escarpment, i.e. the so-called Extra Cape Flora of the CFR (Snijman, 2013), and the genus is thus restricted to the Core Cape Flora Region within the Greater Cape Floristic Region (Manning and Goldblatt, 2012).

2. Materials and methods

This work was based on field studies on and around the Cape Peninsula, and the adjacent Boland and Overberg of Western Cape, South Africa. We examined all specimens in BOL, NBG, PRE and SAM (acronyms after Thiers, 2018), the primary holdings of material from the Western Cape, as well as all relevant types. Only taxonomically unambiguous specimens from the CFR are cited. Descriptions were based on material collected in the field, supplemented by herbarium specimens and literature sources (Launert, 1978; Lingdi and Boufford, 2003) (only the latter two in the case of *R. rosifolius*).

DNA ploidy level was estimated from flow cytometric measurements using a BD Accuri C6 flow cytometer (BD Biosciences, Franklin Lakes, NJ, USA), staining with propidium iodide and *Solanum lycopersicum* and *Zea mays* as internal standards, as described in Sochor and Trávníček (2016). All voucher specimens are deposited in NBG and/or OL.

3. Results and discussion

Based on our field and herbarium studies, we recognise eight taxa and diagnosable hybrids of *Rubus* from the Cape Floristic Region (sensu Manning and Goldblatt, 2012), including the two native taxa *R. pinnatus* and *R. rigidus* agg., the four naturalised species *R. armeniacus*, *R. bergii*, *R rosifolius* and *R. titanus*, and the two hybrids *R. bergii* × *R. rigidus* and *R. bergii* × *R. pinnatus*. This is the first record of *R. armeniacus* and *R. titanus* in South Africa. Many other *Rubus* taxa, both native and introduced, are recorded from neighbouring eastern South Africa, and their occasional presence in the CFR cannot be excluded, particularly when taking into account the long history of blackberry cultivation in the region. We are, however, only able to recognise these eight taxa and hybrids with certainty as occurring in the CFR.

We provide an identification key, description and notes to each of the taxa, including the hybridogenous complex *R. bergii* × *R. rigidus*, which behaves as an independent evolutionary unit. The other hybrid, *R. bergii* × *R. pinnatus*, is mostly of clear intermediate phenotype and occurs together with its parents, and is therefore not described separately.

3.1. Key to native and naturalised Rubus species and hybrids in the Cape Floristic Region

1a. Petals white, flowers solitary or few in sparse inflorescence; sepals with long caudate tip; stem villous with long patent hairs; aggregate fruit bright red, usually of hundreds of small drupelets … **6.*R. rosifolius***

1b. Petals pink to white, flowers usually many in ± rich panicles; sepals acute to acuminate but not caudate; stem glabrous to tomentose with short hairs; aggregate fruit black, of up to tens of large drupelets:

2a. Leaves discolourous, grey/white stellate-tomentose beneath:

3a. Leaves pinnate or ternate, never palmate; stem tomentose with stellate hairs … **2.*R. rigidus*agg.**