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The genus *Rubus* in South Africa. I. Chromosome numbers and geographical distribution of species

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ABSTRACT

The geographical distribution of 14 of the *Rubus* species in South Africa is presented. Chromosome numbers of nine of the species were determined: six for the first time, one is confirmed and additional polyploid levels are described for the other two species.

It is demonstrated that the South African species of the subgenus *Idaeobatus* contain less diploid specimens and more polyploid specimens than their extra-African counterparts. This phenomenon could be attributed to hybridization between the subgenera *Eubatus* and *Idaeobatus*.

INTRODUCTION

The genus *Rubus* is spread over all continents and is found in most climatic regions. Focke (1910–1914) divided this genus into 12 subgenera of which only two are present in South Africa. All the representatives of the subgenus *Eubatus* Focke are introduced, whereas the subgenus *Idaeobatus* Focke contains both indigenous and introduced species.

Introduced *Eubatus* species all represent the subseries *Suberecti* of the series *Moriferi* and include the species *Rubus affinis* Wh. & N., *R. cuneifolius* Pursh., *R. pascuus* Bailey and *R. flagellaris* Willd. The introduced *Idaeobatus* species, *R. niveus* Thunb. and *R. phoenicolasius* Maxim., form part of the series *Nivei* of the section *Idaeanthi*. The indigenous *Idaeobatus* species include the sections *Rosifolii* (*R. rosifolius* Sm.), *Afromontani* (*R. immixtus* C.E. Gust.) and *Idaeanthi* [various species of the series *Afroidaei*, including *R. apetalus* Poir., *R. intercurrens* C.E. Gust., *R. longepedicellatus* (C.E. Gust.) C.H. Stirton, *R. pinnatus* Willd., *R. rigidus* Sm., *R. transvaliensis* C.E. Gust. and *R. ludwigii* Eckl. & Zeyh., with its subspecies *ludwigii* and *spatiosus* C.H. Stirton]. For the purpose of this study *R. adolfi-friederici* Engl., *R. ecklonii* Focke and *R. exsuccus* Steud. are included in *R. apetalus* Poir. because integration between these taxa renders the separation into distinct species impossible. Plants collected from a hybrid swarm in eastern Transvaal are included in *R.* × *proteus* C.H. Stirton.

The problems with *Rubus* taxonomy in South Africa are aggravated by the occurrence of apomixis, hybridization among indigenous species and between indigenous and introduced species, the variation produced by a breeding program and subsequent escape from cultivation of those plants and inadequate collected herbarium material. The aim of this study is, therefore, to provide cytogenetical evidence for the species delimitation in the South African species of *Rubus*. To achieve this goal, the results of a preliminary study on chromosome numbers and species distribution of the most important species are presented in this paper. Other papers in this series will include studies on meiotic chromosome behaviour, reproduction, hybridization and will be concluded with a cytotaxonomic study of the genus *Rubus* in South Africa.

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MATERIALS AND METHODS

The plants used in this study were collected throughout South Africa and transplanted under quarantine in the Pretoria National Botanical Garden. The following 35 plants, representing nine different species, were used:

Eubatus

Rubus affinis:

TRANSVAAL. — 2329 (Pietersburg): Dap Naude Dam (–DD), *Stirton 5746*.

R. cuneifolius:

NATAL. — 2929 (Underberg): 14 km from Swartberg to Underberg (–CD), *Stirton 8154*. 2930 (Pietermaritzburg): 3 km from Midmar Dam to Lions River (–CB), *Henderson & Gaum 93;* 5 km from Pietermaritzburg to Mooi River (–CB), *Liengme s.n.* 3029 (Kokstad): 11 km from Harding to Weza (–DB), *Stirton 8102*.

R. pascuus:

TRANSVAAL. — 2430 (Pilgrim's Rest): 1 km from Graskop to Sabie (–DD), *Henderson & Gaum 18, Stirton 9800, 9861 & 9868*.

R. flagellaris:

TRANSVAAL. — 2530 (Lydenburg): Kaapse Hoop (–DB), *Henderson & Gaum 2*.

Idaeobatus

R. apetalus:

TRANSVAAL. — 2430 (Lydenburg): Kaapse Hoop (–DB), *Henderson & Gaum 6*.

NATAL. — 2929 (Underberg): Clairmont Plantation (–DD), *G. Hemm s.n. a & b*. 2930 (Pietermaritzburg): Endeni Farm (–CC), *Wells 5000*.

R. longepedicellatus:

TRANSVAAL. — 2430 (Pilgrim's Rest): 1 km from Graskop to Sabie (–DD), *Henderson & Gaum 22, Stirton 9862.* 2530 (Lydenburg): 5 km from Lydenburg to Sabie (–AB), *Henderson & Gaum 36;* Brooklands (–BA), *Henderson & Gaum 14.*

R. pinnatus:

TRANSVAAL. — 2530 (Lydenburg): Brooklands (–BA), *Henderson & Gaum 15.*

NATAL. — 3029 (Kokstad): 4 km from Kokstad to Weza (–CB), *Arnold 1335.*

R. ludwigii:

NATAL. — 2929 (Underberg): Kamsberg Nature Reserve (–BD), *Henderson & Gaum 41.*

CAPE. — 3226 (Fort Beaufort): Hogsback (–DB), *Admiraal & Drijfhout 2940.*

R. × proteus:

TRANSVAAL. — 2430 (Pilgrim's Rest): Bourkes Luck (–DB), *Henderson & Gaum 27, 28, 31 & 32;* Mac-Mac Falls (–DD), *Henderson & Gaum 20;* 1 km from Graskop to Sabie (–DD), *Stirton 9798, 9865 & 9866.*

NATAL. — 2929 (Underberg): 25 km from Himeville to Boesmansnek (–DC): *Henderson & Gaum 50 & 51.* 3029 (Kokstad): Ngeli Forest (–DA), *Stirton 8135.*

R. transvaliensis × R. longepedicellatus:

TRANSVAAL. — 2530 (Lydenburg): Nelspruit (–BD), *Henderson & Gaum 10.*

TABLE 1.—Chromosome numbers of some South African *Rubus* species

Species	Plant No.	2n=
Eubatus		
Rubus affinis	*Stirton* 5746	28
R. cuneifolius	*Stirton* 8102	14
	Stirton 8154	14
	Liengme s.n.	21
	Henderson & Gaum 93	28
R. pascuus	*Henderson & Gaum* 18	21
	Stirton 9800	21
	Stirton 9861	28
	Stirton 9868	28
R. flagellaris	*Henderson & Gaum* 2	28
Idaeobatus		
R. apetalus	*G. Hemm* s.n. a	14
	G. Hemm s.n. b	28
	Henderson & Gaum 6	28
	Wells 5000	28
R. longepedicellatus	*Henderson & Gaum* 22	14
	Henderson & Gaum 14	28
	Stirton 9862	28
	Henderson & Gaum 36	35
R. pinnatus	*Henderson & Gaum* 15	14
	Arnold 1335	28
R. ludwigii	*Admiraal & Drijfhout* 2940	14
	Henderson & Gaum 41	14
R. × proteus	*Henderson & Gaum* 28	14
	Stirton 9866	21
	Stirton 9798	28
	Henderson & Gaum 27	28
	Henderson & Gaum 32	28
	Henderson & Gaum 51	28
	Stirton 9865	35
	Henderson & Gaum 20	35
	Henderson & Gaum 31	42
	Stirton 8135	49
	Henderson & Gaum 50	56
R. transvaliensis × *R. longepedicellatus*	*Henderson & Gaum* 10	28
Rubus species	*Henderson & Gaum* 24	28

Rubus species:

TRANSVAAL. — 2430 (Pilgrim's Rest): 5 km from Graskop to Sabie (–DD), *Henderson & Gaum 24.*

Specimens are housed in the National Herbarium, Pretoria (PRE). Chromosome counts were made from meiotic squashes in aceto-carmine (Darlington & LaCour, 1976). Between 20 and 25 cells per plant were studied.

Distribution maps were obtained by using the data of all *Rubus* specimens available on PRECIS (Pretoria computerized information system) (Gibbs Russell & Gonsalves, in press).

RESULTS AND DISCUSSION

All chromosome numbers determined were multiples of 7 and somatic chromosome numbers of 14, 21, 28, 35, 42, 49 and 56 were observed in the investigated South African *Rubus* species (Table 1). Polyploidy occurred in six of the nine species studied. The different *Rubus* species varied in regard to their geographical distribution.

a) The subgenus *Eubatus*

The most widespread of the introduced *Moriferi* was *Rubus affinis*. Specimens representing *R. affinis* were collected in the northern Transvaal, Swaziland, Natal and southern and western Cape (Fig. 1). However, the western Cape is the only place where this species invaded the natural vegetation and where this species is regarded as a weed. The somatic chromosome number of 28 for *R. affinis* (Gustafsson, 1933, 1939 & 1943; Heslop-Harrison, 1953) is confirmed.

R. cuneifolius is restricted to Natal, with the majority of specimens collected in western Natal (Fig. 1). In addition to the chromosome number of 2n = 14 for *R. cuneifolius* reported by Shoemaker & Sturrock (1959), polyploid forms with 21 and 28 somatic chromosomes were observed during this study.

R. pascuus was collected in the eastern Transvaal (Fig. 1). This species frequently hybridized with *R. longepedicellatus* and the hybrids are included in *R × proteus*. Since *R. pascuus* contains both triploid and tetraploid specimens, it may either represent a hybrid rather than a parental form or a diploid form might be present in South Africa.

Two *R. flagellaris* specimens were collected in the eastern Transvaal (Fig. 1). This species has a somatic chromosome number of 28 in contrast to the published chromosome numbers of 56 (Faasen & Nadeau, 1976) and 63 (Einset, 1947).

The geographical distribution of *R. affinis* and *R. cuneifolius* (Fig. 1) indicates that these species occupy different habitats. This suggests that they were differently adapted to the South African climate. The single specimens of *R. affinis* collected in Transvaal, Swaziland and Natal might suggest separate introductions. The occurrence of polyploidy in the subgenus *Eubatus* is restricted to eastern Transvaal and Natal.

b) The subgenus *Idaeobatus*

The introduced species of the subgenus *Idaeobatus* have a limited distribution. *R. niveus* is restricted to Swaziland and the adjacent Transvaal areas (Fig.

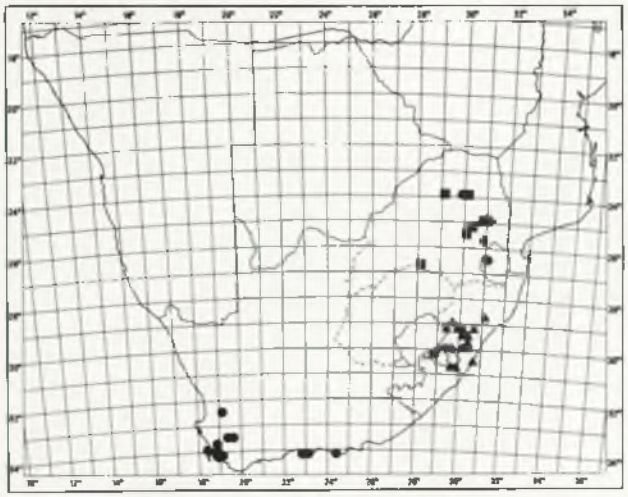

FIG. 1.—Geographical distribution of *Rubus affinis* ●, *R. cuneifolius* ▲, *R. pascuus* ■ and *R. flagellaris* ◆ in South Africa.

2). *R. phoenicolasius* is found in the central parts of Natal (Fig. 2).

The indigenous *R. rosifolius* is found in eastern Transvaal and Natal and a single specimen was found near Cape Town (Fig. 3). *R. immixtus* is found in the eastern Cape (Fig. 2).

The series *Afroidaei* is indigenous and contains species with variable distributions. *R. apetalus* specimens were collected in eastern Transvaal, Natal and the eastern Cape (Fig. 3). *R. longepedicellatus* is found mainly in eastern Transvaal but two specimens from southern Natal were also observed (Fig. 4). *R. pinnatus* is another widespread species and specimens from Transvaal, Natal and eastern, southern and western Cape are found in the National Herbarium (Fig. 5). *R. rigidus* has the widest distribution of all *Rubus* species in South Africa. This species is found in Transvaal, Natal, Orange Free State and eastern, southern and western Cape (Fig. 6). *R. ludwigii* is restricted to the mountainous parts of Transvaal, the Orange Free State, Natal and the Cape (Fig. 7). The hybrid species, *R.* × *proteus*, was collected in eastern Transvaal and Natal (Fig. 8).

No chromosome counts for any of the indigenous South African *Rubus* species were found in the literature. Therefore, new chromosome counts for the genus *Rubus* include the species *R. apetalus* (2n = 14 & 28), *R. longepedicellatus* (2n = 14, 28 & 35), *R. pinnatus* (2n = 14 & 28), *R.* × *proteus* (2n = 14, 21, 28, 35, 42, 49, & 56) and *R. ludwigii* (2n = 14).

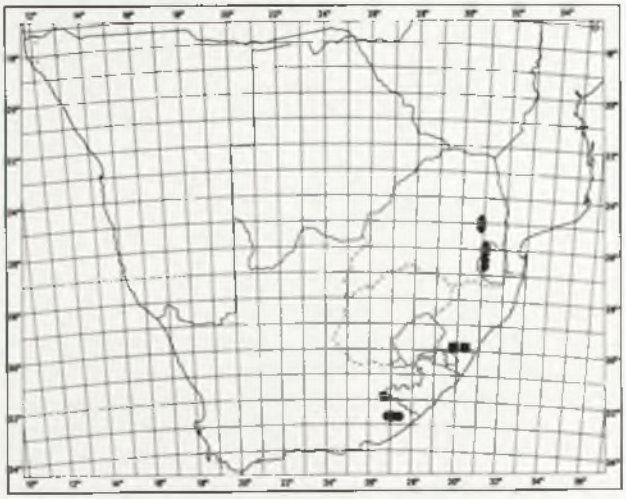

FIG. 2.—Geographical distribution of *Rubus niveus* ◆, *R. phoenicolasius* ■ and *R. immixtus* ● in South Africa.

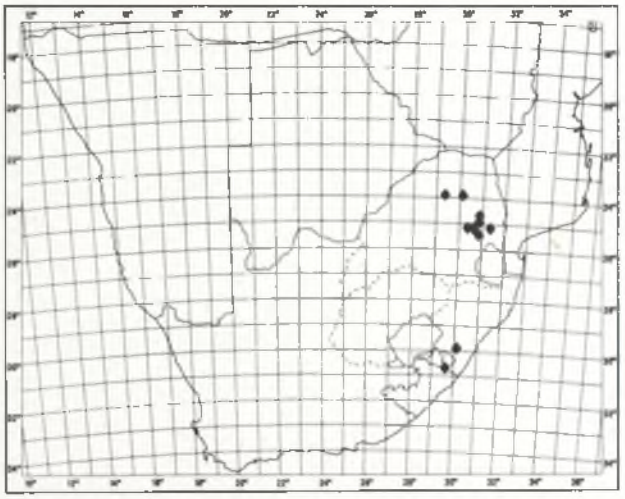

FIG. 4.—Geographical distribution of *Rubus longepedicellatus* ◆ in South Africa.

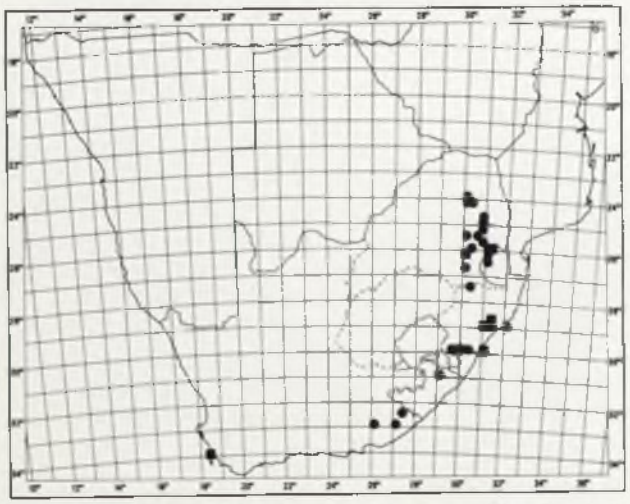

FIG. 3.—Geographical distribution of *Rubus rosifolius* ■ and *R. apetalus* ● in South Africa.

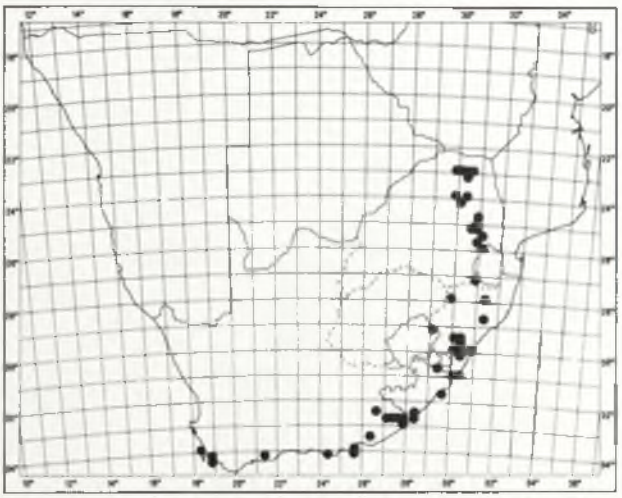

FIG. 5.—Geographical distribution of *Rubus pinnatus* ● in South Africa.

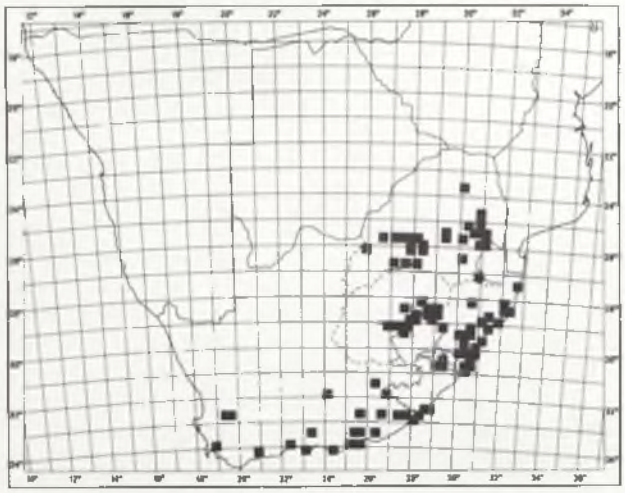

FIG. 6.—Geographical distribution of *Rubus rigidus* ■ in South Africa.

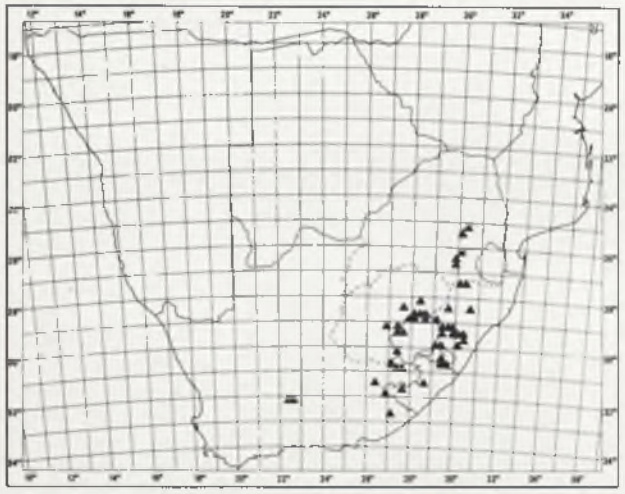

FIG. 7.—Geographical distribution of *Rubus ludwigii* ▲ in South Africa.

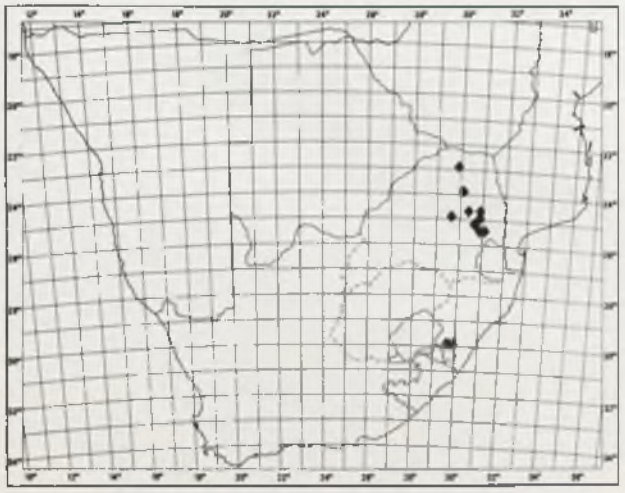

FIG. 8.—Geographical distribution of *Rubus* × *proteus* ◆ in South Africa.

No correlation can yet be found between chromosome number and geographical distribution, except that species with a high degree of polyploidy are present in the eastern Transvaal and Natal.

CONCLUSIONS

The genus *Rubus* has a basic chromosome number of 7 and a polyploid series exists, with plants varying from diploid to duodecaploid. The tetraploid frequency of the South African *Rubus* species is much higher than that of the extra-African species (the chromosome numbers of the extra-African species were obtained from Darlington & Wylie, 1955; Ornduff, 1967–1969; Fedorov, 1969; Moore, R.J., 1970–1977; Moore, D.M., 1982), whereas the frequency of diploids is much lower (Fig. 9a).

Previous chromosome studies indicated that the majority of species in the subgenus *Eubatus* are polyploids, whereas the majority of *Idaeobatus* species are diploid (Longley & Darrow, 1924; Gustafsson, 1933, 1934 & 1943; Brown, 1943; Einset, 1947; Heslop-Harrison, 1953; Varaama, 1954; Darlington & Wylie, 1955; Jinno, 1958a & b; Aalders & Hall, 1966; Ornduff, 1967–1969; Fedorov, 1969; Baquar & Askari, 1970; Moore, R.J., 1970–1977; Moore, D.M., 1982). The South African results indicated much higher triploid and tetraploid frequencies in the subgenus *Eubatus* (Fig. 9b). The South African *Idaeobatus* species have seven times more tetraploids than the extra-African species (Fig. 9c). Although the sample studied was not large enough to give a true representation of the South African *Rubus* population, the comparisons were made to indicate possible trends that will need further investigation.

These deviations from the extra-African pattern might possibly be attributed to hybridization. Hybridization between indigenous and naturalized species could have resulted in the formation of polyploid series especially in the subgenus *Idaeobatus*. The occurrence of diploid ($2n = 14$) *Eubatus* species in South Africa indicates sexual reproduction. The worldwide tendency for a very high frequency of diploid *Idaeobatus* species could have existed in South Africa. Since two previously allopatric sexually reproducing taxa became sympatric in South Africa, the elimination of geographical distribution as a reproductive isolation mechanism could have led to extensive hybridization and subsequent chromosome doubling.

The fact that polyploidy occurs mainly in the subgenus *Idaeobatus* could indicate introgression where backcrossing to the *Eubatus* parent were restricted. Polyploid forms of *R. cuneifolius* and *R. pascuus* suggest, however, that these species might be the only *Eubatus* species involved in hybridization. The fact that these species contain different ploidy levels and are relatively widespread, supports this theory. However, to determine the validity of this theory, the type of polyploidy in each species must be investigated and subsequently their modes of reproduction.

A hypothesis is consequently proposed that this diploid *Eubatus* species hybridized with the diploid

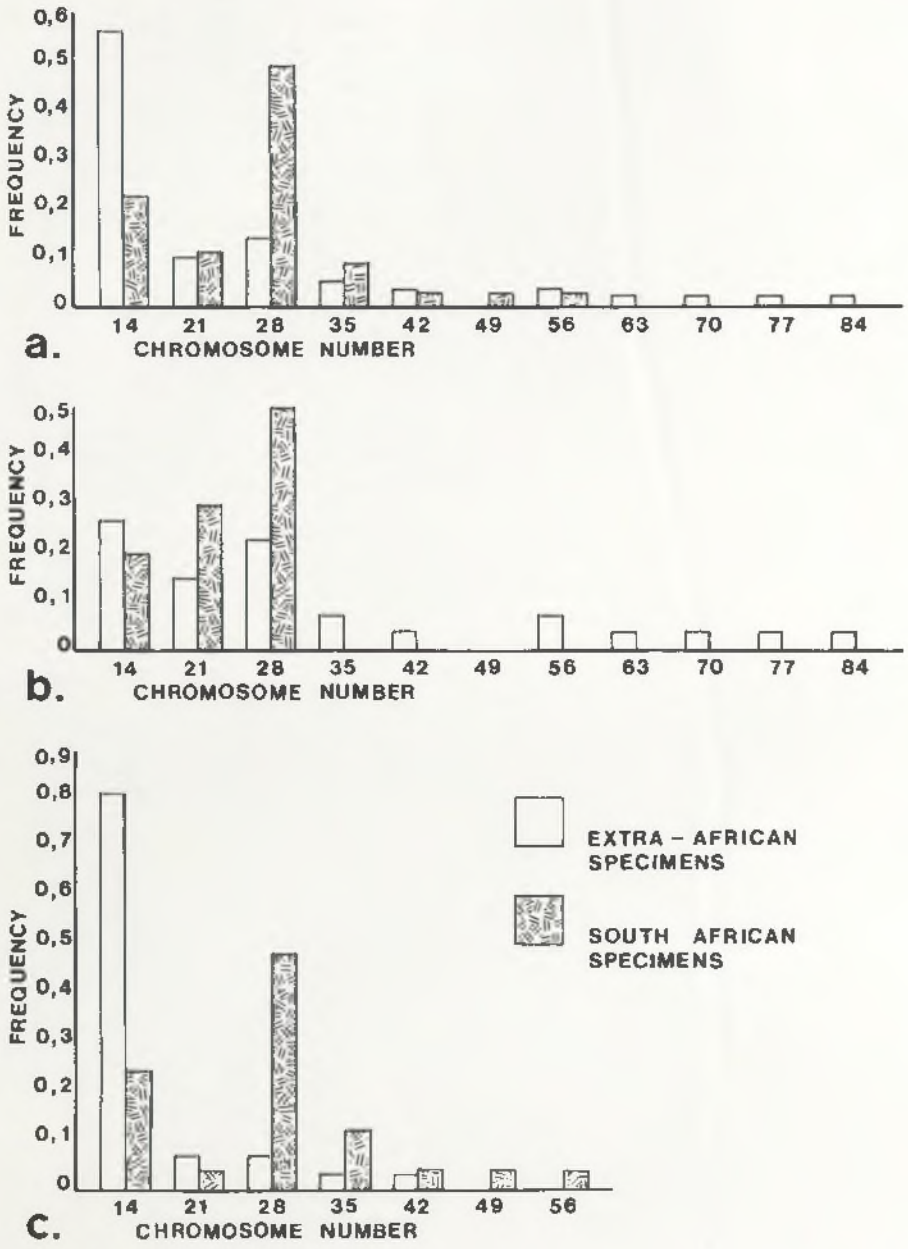

FIG. 9.—Comparison between frequencies in chromosome numbers between the South African and extra-African *Rubus* species (a), *Eubatus* species (b) and *Idaeobatus* species (c). (Shaded areas represent South African *Rubus* species, whereas unshaded areas represent extra-African *Rubus* species. These frequencies represent the number of species per polyploid level and not the number of chromosome counts.)

indigenous *Idaeobatus* species. The hybridization between two different subgenera, with possibly non-homologous or homoeologous genomes, would only succeed after chromosome doubling. It is, therefore, suggested that the high polyploid frequency in the South African *Idaeobatus* species is the result of intersubgeneric hybridization.

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UITTREKSEL

Die geografiese verspreiding van 14 van die Suid-Afrikaanse Rubus *spesies word weergegee. Chromosoomgetalle van nege spesies is vasgestel; ses hiervan word vir die eerste keer beskryf, een word bevestig en addisionele poliploïede vlakke word vir die ander twee spesies beskryf.*

Daar word aangetoon dat spesies van die Suid-Afrikaanse subgenus Idaeobatus *baie meer poliploïede plante bevat as wat chromosoomgetalle uit ander wêrelddele sou suggereer. Hierdie verskynsel kan moontlik toegeskryf word aan verbastering tussen die subgenera* Eubatus *en* Idaeobatus.

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