

Portrait of the Cape honeybee, *Apis mellifera capensis*

HR Hepburn ^{1*}, RM Crewe ²

¹ Rhodes University, Department of Zoology and Entomology, Grahamstown;

² University of Witwatersrand, Department of Zoology, Johannesburg, South Africa

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Summary — The honeybees of southern Africa were assessed for expression of the trait, diploid eggs laid by workers, worker ovariole number, spermatheca size, worker size and allozymes of malate dehydrogenase. *A m capensis* is readily defined in terms of the first 2 of these traits and may further be separated from *A m scutellata* by a suite of biological characteristics associated with laying worker development and behaviour, queenless cell building, foraging, thermoregulation and docility. The Cape honeybee occurs in the fynbos biome along the southwest and south coasts of South Africa extending into the interior as far as the mountains bordering on the Klein Karoo. From here it hybridizes with *A m scutellata* to the next mountain ranges near latitude 32 where hybrids fall away. This border is a barrier where there are fundamental differences in topography, climate and vegetation which place the 2 races ecologically totally out phase and ensure the relative stability of *A m capensis* and *A m scutellata* as separate races.

***A m capensis* / behaviour / *A m scutellata* / biotope / review article**

INTRODUCTION

The remarkable honeybee trait, thelytoky by workers, was discovered in Cape honeybees by Onions (1912, 1914) and has often been confirmed (Kerr and Portugal Araujo, 1958; Anderson, 1963; Ruttner, 1988). Further studies have revealed the pheromonal (Ruttner *et al*, 1976; Hemmling *et al*, 1979; Crewe and Velthuis, 1980; Velthuis *et al*, 1990) and biological

versatility of Cape bees (Hepburn *et al*, 1988; Ruttner, 1988; Crewe *et al*, 1991), yet its definition and precise distribution remained elusive. In attempting to resolve the problem of defining so biologically distinct a race as *capensis* by traditional taxonomic methods, 3 biological traits have been identified: the occurrence in worker bees of i) the trait diploid eggs (thelytoky) laid by workers (DELW); ii) a well developed spermatheca; and iii) many ovari-

* Correspondence and reprints

oles per ovary (Kerr and Portugal Araujo, 1958; Ruttner, 1977). This new approach led to the view that unhybridized *capensis* was possibly restricted to the Cape Peninsula with transitory forms to the north and east (Moritz and Kauhausen, 1984; Ruttner, 1988). The important work of Ruttner (1977, 1988), coupled to recent discoveries that honeybees of the eastern Cape are actually *capensis*-like (Hepburn *et al*, 1988; Hepburn, 1989), led to a re-examination of this race (Hepburn and Crewe, 1990; Hepburn and Jacot Guillarmod, 1991) and, ultimately, to this review of the Cape honeybee.

collected from 20 workers per colony from about 6 colonies per locale. *In loco* measurements of the sex ratios (male progeny: female worker progeny) of laying worker progeny in queenless, broodless colonies pinpointed the distribution of the trait 'diploid eggs laid by workers' (DELW). These ratios should not be confused with those of normal reproductives (queen honeybees). Allelic and genotypic frequencies of isozymes of malate dehydrogenase were determined using isoelectric focusing (Nunamaker and Wilson, 1981). The 'sizes' of workers were assessed on the basis of constant dry weight values. Statistical analyses included the Kruskal-Wallis 1-way ANOVA (H values) and the calculation of Pearson's correlation coefficients. Significance is defined as $P < 0.05$.

METHODS

We sampled the worker honeybees of southern Africa (table I, fig 1) and measured ovariole number, spermatheca size, body size and surface area of the mandibular gland. Data were

RESULTS

The distribution of the trait DELW is crucial to the definition of *capensis* (Ruttner, 1988) and the sex ratios of known laying worker progeny (expression of DELW) are

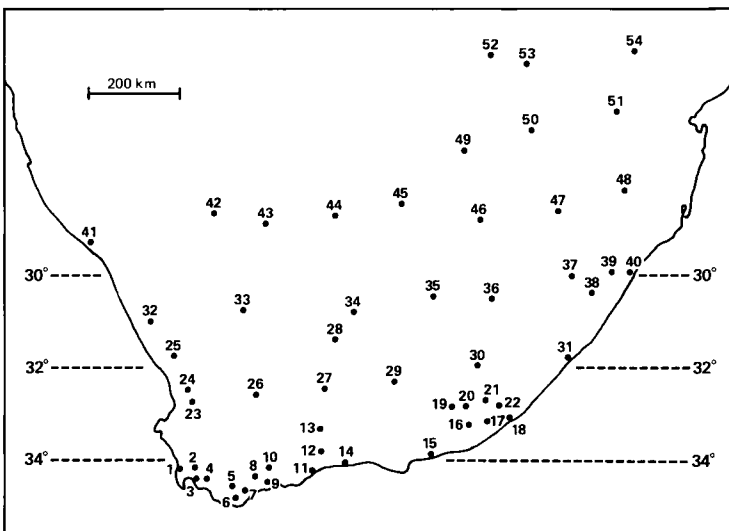


Fig 1. Localities in southern Africa at which honeybee colonies were assessed for the sex ratios of laying worker progeny, ovariole number, spermatheca size and bee dry weights. Results are given in table I.

given in table I. DELW extends along the seaward side of the mountains from about Calvinia-Vanrhynsdorp (locality 33) in the southwest, around the southern coast to about East London (locality 18) in the east (table I, fig 1). In the interior it is bounded by the Nuweveld and Stormberg mountain ranges (line joining locality points 33, 26–30 of figure 1; mountains 5–9, fig 2). Grouping the sex ratio (M/F) data into pure *capensis*, mixed and *scutellata*, 3 areas can be distinguished, respectively: i) a Cape Town-East London zone (fig 1, points 1–18), ii) a Clanwilliam-Queenstown zone (24–30) and iii) all points north of latitude 32 (fig 1). The relationship of the sex ratio of laying worker progeny to area (distinctness of groups) is highly significant ($H = 11.8$, $df = 2$ and $P < 0.002$).

The distribution of ovariole number for about 5 000 workers representing 45 localities is given in table I. Using the DELW

zones, average ovariole number is about 12 in the first zone, 9 in the second and north of latitude 32 (classical *scutellata* area) it drops to 3 ovarioles/ovary (table I). These 3 groups are significantly different from one another ($H = 29.4$, $df = 2$, $P < 0.05$). Moreover, the 3 groups based on ovariole number match those based on the sex ratios of laying worker progeny ($H = 11.8$, $df = 2$, $P < 0.002$). Variance for ovariole numbers (Hepburn and Crewe, 1990) significantly decreased ($H = 14.91$, $df = 2$, $P < 0.05$) between zone 1 and 2 and between zone 2 and above latitude 32, or from south to north.

Data on spermatheca size for about 2 500 bees representing 45 localities (table I) show that large spermathecae occur in the Cape Peninsula (localities 1–3) but so do small ones (localities 7 and 8). Spermathecae larger than those found at the Cape Peninsula occur further east along

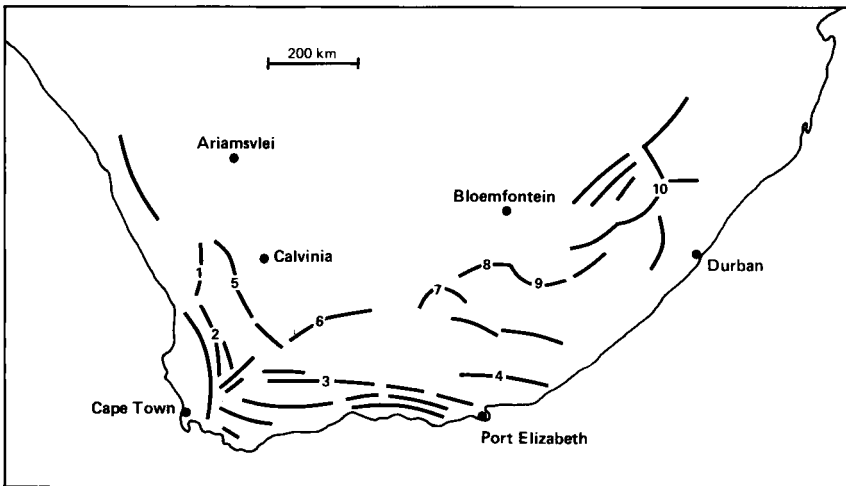


Fig 2. Geographical distribution of *A m capensis* in relation to *A m scutellata* and the major mountain ranges of southern Africa. *Capensis* occurs in the fynbos biome along the southwest and south coasts extending to the: 1, Bokkeveld; 2, Cedarberg; 3, Swartberg; and 4, Suurburg mountains. *Scutellata* extends southwards to the: 5, Roggeveldberg; 6, Nuweveldberg; 7, Sneeuberg; 8, Kikvorsberg and Bamboesberg; 9, Stormberg; and 10, Drakensberg mountain ranges. The zone of hybridization between *capensis* and *scutellata* is the region lying between mountain ranges 1–4 and 5–10.

Table 1. Distribution of the gene DELW, ovariole number, spermatheca size and constant dry weight of worker honeybees in southern Africa ^a.

<i>Locality</i>	<i>Laying worker^b progeny sex ratio (M/F)</i>	<i>Ovariole^c number</i>	<i>Spermatheca^d size (µm)</i>	<i>Dry weight (mg)</i>
1. Cape Town	a+	17.4 ± 4.9	21 ± 4	1.6 ± 0.3
2. Stellenbosch	a+	18.2	(44)	—
3. Somerset West	a+	—	(—)	—
4. Grabouw	a+?	12.7	(—)	—
5. Fairfield	a+?	11.1	(—)	—
6. Elim	a+?	11.4	(15)	—
7. Bredasdorp	a+?	8.9	26	—
8. Malgas	a+?	10.7	17	—
9. Witsand	a+?	12.0	42	—
10. Heidelberg	a+?	12.6 ± 4.1	(20 ± 4)	1.8 ± 0.2
11. Mossel Bay	a+?	6.8	—	—
12. Oudtshoorn	a+?	10.1	27	—
13. Prince Albert	a+?	14.9	15	—
14. Knysna	a+	11.8 ± 2.9	13 ± 2	2.0 ± 0.4
15. Port Elizabeth	a+	12.5 ± 2.8	15 ± 2	1.0 ± 0.8
16. Alicedale	a	—	—	—
17. Grahamstown	a	—	—	—
18. East London	a = b	7.1 ± 2.0	14 ± 3	2.3 ± 0.4
19. Longhope	a	—	—	—
20. Bedford	a	—	—	—
21. Fort Beaufort	a	—	—	—
22. Dudumashe	b+	—	—	—
23. Citrusdal	a+	—	—	—
24. Clanwilliam	a	11.5 ± 5.1	21 ± 3	1.4 ± 0.2
25. Lutzville	a?	8.2	15	—
26. Sutherland	a	6.4 ± 3.0	21 ± 2	1.6 ± 0.3
27. Beaufort West	b	7.9 ± 3.0	14 ± 2	1.9 ± 0.1
28. Victoria West	a?	4.2	15	—
29. Graaff Reinet	a=b	10.2 ± 3.1	15 ± 3	2.1 ± 0.1
30. Queenstown	b	6.0 ± 3.2	16 ± 5	3.4 ± 1.0
31. Port St Johns	b+?	1.3 ± 1.6	14 ± 4	2.6 ± 1.4
32. Garies	b+?	2.6 ± 2.7	14 ± 4	2.6 ± 0.9
33. Calvinia	a	4.3 ± 2.3	19 ± 4	2.8 ± 0.9
34. Britstown	b+	2.7 ± 1.9	19 ± 3	4.0 ± 1.0
35. Springfontein	b+	4.4 ± 1.2	14 ± 2	2.4 ± 0.6
36. Zastron	b+	3.8 ± 2.7	16 ± 4	3.5 ± 1.2
37. Underberg	b+	1.6 ± 1.2	12 ± 3	2.0 ± 0.2
38. Ixopo	b+	2.9 ± 1.1	14 ± 3	2.4 ± 0.6
39. Pietermaritzburg	b+	—	—	—
40. Durban	b+?	3.2 ± 1.7	14 ± 3	2.5 ± 0.6
41. Alexander Bay	b+?	2.6 ± 1.7	14 ± 4	2.2 ± 0.6
42. Ariamsvlei	b+?	3.0 ± 1.1	16 ± 7	2.9 ± 1.0
43. Upington	b+?	2.8 ± 2.7	14 ± 3	2.8 ± 0.5
44. Postmasberg	b+?	3.9 ± 2.9	17 ± 4	3.8 ± 1.3

45. Warrenton	b+?	3.3 ± 1.9	16 ± 7	3.1 ± 0.9
46. Wlnberg	b+?	2.3 ± 2.1	15 ± 4	4.1 ± 1.0
47. Harrismith	b+?	2.6 ± 1.1	15 ± 4	3.7 ± 1.2
48. Vryheid	b+?	3.1 ± 1.5	15 ± 5	2.6 ± 0.6
49. Klerksdorp	b+?	4.6 ± 2.3	19 ± 3	3.0 ± 0.9
50. Nigel	b+?	3.3 ± 1.4	14 ± 3	3.0 ± 1.0
51. Badplass	b+?	3.5 ± 1.8	19 ± 3	2.5 ± 0.7
52. Thabazimbi	b+?	2.9 ± 1.6	17 ± 3	3.3 ± 1.5
53. Warmbaths	b+?	3.1 ± 1.5	18 ± 5	2.8 ± 1.0
54. Hoedspruit	b+?	2.8 ± 1.2	18 ± 3	3.0 ± 1.2

^a Primary sources given by Hepburn and Crewe (1990); ^b Laying worker progeny is indicated as: a+ = pure *capensis*, a = predominantly *capensis*, a = b, b = predominantly *scutellata*, b+ = pure *scutellata*. When actual sex ratio data for laying worker progeny is missing, based on the position of the localities it is highly likely that the ratios will be as indicated by a "?". The sex ratios referred to here are male : female workers (arrhenotoky : thelytoky). ^c Values calculated for several data sets at some localities. ^d Bracketed values are approximate for more than one locality.

the south coast (localities 14 and 15) as well as among *scutellata* of the Transvaal (localities 49, 51–54) and many other localities. Tests of differences between zones for spermathecae showed them to be not significant ($H = 2.4$, $df = 2$, $P < 0.05$); nor was there a correlation between spermatheca size and ovariole number ($r = 0.4$ and $r^2 = 18\%$).

To preclude errors from posthumous shrinkage we estimated "size" in bees on the basis of constant dry weight (table I). The bees were heaviest in the north and weighed progressively less to the south. Bee weights from the DELW area are significantly less than those beyond the DELW area, indicating smaller bees to the south. Using the DELW zones, the 3 groups of bee weights were significantly different ($H = 14.0$, $df = 2$, $P < 0.05$) and were negatively correlated with ovariole number ($r = 0.66$). Because the volume of the *capensis* mandibular gland is larger than that of *carnica* (Ruttner, 1988) the surface area of this gland was assessed but no patterns emerged from this data (Hepburn, 1991).

Of 6 allozyme phenotypes for the Mdh-1 locus in honeybees (Nunamaker and Wil-

son, 1981), only 2 were found in the southern African samples and they corresponded with known bands (Nunamaker *et al*, 1984). Six bees from Cape Town (locality 1) and 2 from Queenstown (locality 30) had 3 bands, indicating heterozygosity for MDH m/F (there is historical proof of *ligustica* introductions at both localities). The homozygous genotype MDH M/M was not detected.

DISCUSSION

The Mdh-1 locus exhibited a very low degree of polymorphism suggesting that both *capensis* and *scutellata* are monomorphic for Mdh-1. However, analysis of mitochondrial DNA has demonstrated that both *capensis* and *scutellata* differ from European *mellifera* (Smith, 1988) and that there are other differences between these 2 African races (Meusel and Moritz, personal communication). The differences between the African races (base pair inserts, table II) may not be diagnostic, but merely represent a high level of variability within the populations.

The spectrum of sex ratios of laying worker progeny encountered in southern

Africa (table I) raises questions about the genetics of DELW. Onions (1912) reported that *ligustica* x *capensis* crosses yielded laying workers whose own progeny was female; but Kerr and Portugal Araujo (1958) obtained mixed sex progeny in similar crosses. Production of mixed progeny could be a result of the production of diploid and haploid eggs by a single individual or it could arise as a result of having a mixed population in which some workers had the DELW trait and others the HELW trait. The latter appears the more likely explanation in view of the mechanism for the expression of the DELW trait (Verma and Ruttner, 1983), but remains uncertain.

Tribe (1981, 1983) noted that laying workers of *capensis* x *scutellata* crosses produced workers whose own progeny was female. When this laying worker progeny was used to produce queens for successive *scutellata* crosses, the new generation of laying workers produced mixed progeny. These results reflect what occurs in nature in zone 2 for DELW in southern Africa. Recently, Ruttner (1988) reported on *capensis* queens crossed with drones produced from F₁ queens of a *capensis* x *carnica* cross so representing male F₂ gametes. Although there is a very low but natural frequency of DELW in temperate *mellifera* races (Mackensen, 1943; Woyke, 1986) the sex ratios of progeny of laying workers in Ruttner's cross were bimodally distributed, suggesting 2 alleles at one locus in *capensis* (Ruttner, 1988; Moritz, 1991).

On the strength of their measurements, Ruttner (1977, 1988) and Moritz and Kauhhausen (1984) thought that relatively homogeneous populations of *capensis* were probably restricted to the Cape Peninsula. The much larger data set now available (table I) indicates that a reasonably homogeneous population, based on DELW and ovariole number, is distributed in zone 1

(fig 1). Although the variance for these features decreases from south to north, the magnitude of the variance within the *capensis* area lacks the clinal characteristics for ovariole number that occurs in the hybrid zone between *capensis* and *scutellata* (table I; Hepburn and Crewe, 1990). The few genes necessary to control the expression of DELW and ovariole number (table I) may not be sufficient to elevate 2 populations to the level of races. However, there is a substantial body of additional biological data which separates *capensis* from *scutellata* (table II).

We interpret the full data (tables I and II) to mean that the Cape honeybee, *Apis mellifera capensis* is a biologically distinct, small, blackish bee race of the fynbos, a biome which extends along the coast of South Africa from about the level of Vanrhynsdorp in the west to somewhere near East London. It extends from the coast into the mountains (1, Bokkeveld; 2, Cedarberg; 3, Swartberg; and 4, Suurberg of figure 2). The African honeybee, *Apis mellifera scutellata* is a northern race whose southern limit is defined by mountains in the interior (5, Roggeveldberg; 6, Nuweveldberg; 7, Sneeuweberg; 8, Kikvorsberg and Bamboesberg; 9, Stormberg and 10, Drakensberg ranges of figure 2). This leaves a corridor or zone of hybridization between the Cape honeybee and the African honeybee of about 200 km breadth running between the Cape Fold mountains in the south and the Nuweveldberge and Drakensberge to the north (fig 2).

Given the distribution of *capensis*, *scutellata* and the hybrid zone between them, the origins of these 2 races, the stability and homogeneity of their populations and possible barriers that maintain them are of considerable theoretical and practical interest. These points can be at least partially realized by considering the physical and biological factors of their respective regions

(table III). The fynbos is a macchia-like biome of unique plant forms contained within about 70 000 km², the world's smallest floral kingdom (Bond and Goldblatt, 1984). Geologically the fynbos occurs in a belt of folded mountains of pre-Gondwanan origin which have been stable for about 65 million years. They descend sharply into coastal plains which experienced some 60 million years of periodic marine inundation. This contrasts sharply with the Great Karoo to the north which was defined by warping of the continental plate some 60 million years ago, and led to the shunting of all drainage to the north and leaving an arid region behind (Deacon *et al*, 1983).

The climates stabilized some 5 million years ago but included 0.1 million year cycles of glaciation, the last of which began some 70 000 years ago and ended perhaps 10 000 years ago (Deacon and Lancaster, 1988). The movements of plants and animals during interglacial periods and their isolation during glaciation in southern Africa are well documented (Deacon *et al*, 1983). Any of the cycles of Pleistocene glaciation in southern Africa could have isolated honeybee populations (Deacon and Lancaster, 1988) over time scales that have been proposed for the evolution of honeybee races (Ruttner, 1988).

The fynbos occurs on a patchwork of poorly differentiated soils unlike the well-developed latosols and clays the interior of the country (Lambrechts, 1979). Temperatures of the former region are moderate, those of the latter more severe and extreme (Schulze, 1965). Precipitation in the fynbos changes from winter rainfall in the west to evenly distributed in the east while that of the interior comes in summer (Schulze, 1965). The fynbos is a region of winds that regularly change seasonally unlike the highly variable ones in the interior karoo system (table III). Superimposed on

these landscapes are totally different vegetative systems. The fynbos has great floristic diversity and endemism whose flowering cycles match that of changing patterns of precipitation along an east-west gradient (Hepburn and Jacot Guillarmod, 1991). This stands in total contrast to that of the Nama-Karoo and Grassland biomes to the north (Rutherford and Westfall, 1985).

Significant features in the biology of the Cape honeybee such as brood cycles, winter migrations, swarming season, thermoregulation and foraging techniques (table II) are finely attuned to the cycles of flowering and precipitation as they unfold in the fynbos year (Hepburn and Jacot Guillarmod, 1991; also table III). Similarly, Moritz (1986) showed that where there is a high risk of losing the queen (table II) then thelytoky by workers is favoured. Where this risk is lower then it becomes more advantageous for workers to produce drones. Since climatic conditions at the time of reproductive swarming in *capensis* can result in a sharply increased probability of queen loss, they may have supplied the selection pressure that favoured the fixation of the trait DELW in *capensis*. Beyond the escarpment of the interior are the arid lands with their own unique plant communities stretching as far north as latitude 25 and perhaps further. Elements of the life history of the bees that live there, *scutellata*, are equally attuned to the vagaries of these totally different circumstances (Fletcher, 1978; Anderson *et al*, 1983).

The barrier to the mixing of these populations is the border between the 2 regions at which there is a total discontinuity of physical and biological factors so that ecological variables are completely out of phase. It is likely that southerly movements of *scutellata* are heavily restricted by limited resources under normal conditions and virtually precluded in the drought decades of the wet-dry cycles which occur, particu-

Table II. Biological characteristics of *A m capensis* and *A m scutellata*.

<i>Character</i>	<i>Capensis</i>	<i>Scutellata</i>	<i>Remarks</i>	<i>References</i> ^a
Worker ovarioles	10	5	Intermediate in hybrid zone	Table I
DELW gene	Present	Absent	Present, hybrid zone	Table I
Laying worker progeny	Diploid and haploid	Haploid	Diploid and haploid in hybrid zone	Table I
Laying worker, latency to	Short	Long	Values in Africa	1, 2
Laying worker has retinue	Yes	No		3, 4
Laying worker pheromones	Queen-like 9-ODA dominant	Worker-like 9-ODA trace		5, 6, 27
Laying worker types	Pheromonally queen-like, lays eggs or not; worker-like, lays eggs or not	Pheromonally worker-like, lays eggs or not		5, 6
Queenless bees fighting syndrome	Variable	Absent	Commoner in western Cape	1, 7
Queenless bees cell building	Worker-size	Drone-size		8, 9
Queenless broodless bees	New queen possible	New queen impossible	Several sequences possible in <i>capensis</i>	8, 10, 11
Queenless bees, acceptability of new queen	High rejection	High acceptance		12, 13
Queen mating flights, wind	Up to 14 m/s	5 m/s		7
Mating flights, queen loss	High	Low		7
Reproductive dominance	Very high	Low	In Africa	8, 14, 28

Invasiveness, other races	High	Low	In Africa, both high for other <i>mellifera</i> races	7, 8, 14, 15, 16
Inhibition of queen cells	By queens and laying workers	By queens only		2, 10, 17
Inhibition of worker ovarioles	By queens and laying workers	By queens only		2, 18
Colony growth	Sluggish	Rapid		10
Abscending migrations	Winter	Summer	In South Africa	14, 19
Foraging success	High in fynbos, low elsewhere	Low in fynbos, high elsewhere		14, 19, 20
Temperature regulation	Clusters well	Clusters poorly	<i>Capensis</i> similar to temperate <i>mellifera</i>	21
Dociility	Very high	Very low	Intermediate in hybrid zone	7, 15, 22
Worker colouration	Blackish	Yellowish	Highly variable	8, 23, 24
Propolis use	High	Lowish	Personal observations	
Worker tergal gland	Present	Absent		25
mtDNA	430 bp insert	270 bp insert	Absent from European <i>mellifera</i> races	26

a References. 1, Anderson, 1963; 2, Hastings, 1989; 3, Anderson, 1965; 4, Velthuis, 1985; 5, Ruttner *et al*, 1976; 6, Crewe and Velthuis, 1980; 7, Tribe, 1983; 8, Onions, 1912; 9, Whiffler and Hepburn, 1991a; 10, Anderson *et al*, 1983; 11, Hepburn *et al*, 1988; 12, Lundie, 1929; 13, Buys, 1984; 14, Johannsmeier, 1983; 15, Davidson, 1933; 16, Rinderer *et al*, 1985; 17, Whiffler and Hepburn, 1991b; 18, Hepburn *et al*, 1991; 19, Hepburn and Jacot Guillarmod, 1991; 20, Worswick, 1988; 21, Worswick, 1987; 22, Fletcher, 1978; 23, Guy, 1976; 24, Hepburn, 1989; 25, Billen *et al*, 1986; 26, Meusel and Moritz, 1991; 27, Crewe *et al*, 1991; 28, Moritz and Hillesheim, 1985.

larly in the hybrid zone. Likewise, there has never been any migratory beekeeping that involves crossing over from the zone of one race into that of another race. Thus,

capensis and *scutellata* are constrained ecologically as are the other biological races of *mellifera* in sub-Saharan Africa (Ruttner, 1988). The dynamics of the *capensis*

Table III. Physical and biological characteristics of areas naturally occupied by *capensis* and of *scutellata* areas bordering on the fynbos.

<i>Character</i>	<i>Capensis</i>	<i>Scutellata</i>	<i>Remarks</i>
Topography ^a	Mountains to coastal	Undulating plains to flat	Border between hybrid zone and <i>scutellata</i> mountainous
Soils ^a	Mainly rock, undifferentiated	Latosols, clays, or lime-rich	Hybrid zones as in <i>scutellata</i>
Climate ^b	Mediterranean	Semi-arid	Hybrid zone semi-arid
Temperature ^b extremes and fluctuation	Moderate	Severe	Hybrid zone severe
Precipitation ^b	Winter to year-round	Summer	Precipitation decreases on west-east gradient
Wind intensity ^b	Moderate to high	Low to moderate	Hybrid zone as in <i>scutellata</i>
Winds			
Summer	Southeast	Highly variable	Hybrid zone as in <i>scutellata</i>
Winter	Northwest	Northwest	for winter and summer
Biomes ^a	Fynbos	Nama-Karoo and grassland	Hybrid zone as in <i>scutellata</i>
Vegetation ^a type ^c	Grassy, dwarf shrub shrub-woodland	Grassy to dwarf shrubland	Hybrid zone as in <i>scutellata</i>
Floristic ^c diversity	Very high	Low/moderate	Hybrid zone as in <i>scutellata</i>
Floral ^c endemism	Very high	Low/moderate	Hybrid zone as in <i>scutellata</i>
Flowering ^d cycles			
Peak	Late winter and spring	Summer and autumn	
Low	Summer and mid-winter	Winter	

^a Rutherford and Westfall, 1985; ^b Schulze, 1965; ^c Bond and Goldblatt, 1984; ^d Hepburn and Jacot Guillarmod, 1991.

x *scutellata* hybrid zone offer opportunities for natural experiments in genetics and evolution that are unparalleled by any other region in which honeybees occur.

NOTE

The distributions of *capensis*, *scutellata* and their hybrids (fig 2) are fully supported by our recent morphometric analysis of bees from the same localities listed in table I, the results of which all be published in due course. A recent synthesis of the ecology of the Fynbos Biome, natural home of *capensis*, is now available as follows: Cowling R (1991) *The Ecology of Fynbos, Nutrients, Fire and Diversity*. Oxford, Cape Town.

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Résumé — Portrait de l'abeille du Cap.

En s'appuyant sur un vaste échantillonnage de colonies prélevées dans toute l'Afrique du Sud (fig 1), on définit la race *Apis mellifera capensis*, ou abeille du Cap, par 2 caractères essentiels, le caractère «œufs diploïdes pondus par les ouvrières» et un nombre élevé d'ovarioles chez les ouvrières (tableau I), et par une série d'autres caractéristiques biologiques. Elles comprennent, dans le cas de colonies orphelines, la possibilité latente de développer des ouvrières pondueuses et leur capacité à déclencher le comportement de cour à l'aide de substances semblables aux phéromones royales, les combats d'ouvrières entre elles, la construction des cellules et l'acceptation de reines introduites (tableau II).

Cette race diffère aussi des autres par les vols nuptiaux, la dominance de reproduction, la propension à envahir les colonies des autres races et la capacité des ouvrières pondueuses à inhiber la construction des cellules royales et le développement ovarien chez les autres ouvrières (tableau II). Elle se distingue également par la croissance des colonies, la désertion, le butinage, la régulation de la température, la docilité, l'utilisation de la propolis et, dans une certaine mesure, par la couleur (tableau II).

A m capensis est présente dans le biome fynbos, une formation végétale unique semblable au maquis de la région méditerranéenne, mais constituée de plantes totalement différentes. Cette région s'étend le long des côtes sud-ouest et sud de l'Afrique du Sud et est limitée à l'intérieur par 4 chaînes de montagnes, le Bokkeveld, Cedarberg, Swartberg et Suurberg (fig 2). *A m scutellata* se rencontre plus au Nord et ses limites méridionales sont les chaînes de montagnes du Roggeveldberg, Nuweveldberg, Sneeuwberg, Kikvorsberg, Bamboesberg, Stormberg et Drakensberg (fig 2). La région comprise entre la première chaîne de montagnes et la seconde est une zone d'hybridation entre les 2 races.

La barrière actuelle entre les 2 races (en fait la limite définissant l'extension d'*A m scutellata* vers le sud) présente des caractéristiques physiques et biologiques qui la définissent avec précision. Cette limite, qui est la frontière sud du grand Karoo, diffère radicalement du biome fynbos d'*A m capensis* par la structure géologique, les sols, le climat (température, précipitation et vents), ainsi que par la composition, la diversité, l'endémisme et la phénologie de la végétation (tableau III). La définition et la répartition d'*A m capensis* données ici tiennent compte de toutes les données connues.

***A m capensis* / article de synthèse/
comportement / physiologie / *A m scu-*
tellata / biotope**

Zusammenfassung — Portrait der Kapbiene (*Apis mellifera capensis*). Auf Grund einer umfassenden Probensammlung in der ganzen Südspitze von Afrika (Abb 1) wurde die Rasse der Kapbiene, *Apis mellifera capensis* vor allem nach zwei Hauptmerkmalen definiert, nämlich dem Merkmal diploide Eier von Arbeitsbienen und einer hohen Zahl von Ovariolen (Eischläuchen) bei Arbeiterinnen (Tabelle I), sowie nach einer Reihe anderer biologischer Eigenschaften. Diese umfassen bei weisellosen Völkern unter anderem die Latenzzeit bis zur Entstehung legender Arbeiterinnen sowie deren Fähigkeit, mittels königinnen-ähnlicher Pheromone die Bildung eines Hofstaates auszulösen, Kämpfe der Bienen untereinander, Zellbau und Annahme zugesetzter Königinnen (Tabelle II). Diese Rasse unterscheidet sich auch bei den Paarungsflügen, der Fortpflanzungsdominanz, ihrer Fähigkeit, in Völker anderer Rassen einzudringen sowie in der Fähigkeit legender Arbeiterinnen, die Ovaentwicklung bei anderen Arbeitsbienen und die Errichtung von Weiselzellen zu hemmen (Tabelle II). Unterscheidungsmerkmale dieser Rasse sind außerdem langsames Volkswachstum, geringere Neigung zum Ausziehen, Besonderheiten des Sammelns und der Temperaturregulierung (Anpassung an die lokale Tracht, Bildung einer Wintertraube), besondere Sanftmut, stärkere Verwendung von kittshartz und (zu einem gewissen Grad) dunklere Körperfärbung (Tabelle II). *A m capensis* kommt in der Fynbos-Region vor, einer einzigartigen Pflanzengesellschaft ähnlich der niedrigen immergrünen Buschvegetation des Mittelmeergebietes, aber zusammengesetzt aus

gänzlich anderen Pflanzen. Diese Region erstreckt sich entlang der Südwest- und Südküste Afrikas und ist gegen das Innere des Kontinents durch vier Bergzüge abgegrenzt, das Bokkeveld, Cedarberg, Swartberg und Suurberg (Abb 2). *A m scutellata* kommt weiter nördlich vor; ihre Südgrenze sind die Bergzüge des Roggeveldberg, Nuweveldberg, Sneewberg, Kikvorsberg, Bamboesberg, Stornberg und Drakensberg (Abb 2). Das Gebiet zwischen den ersten und den zweiten Bergzügen bildet eine Hybridzone zwischen den beiden Rassen. Die heutige Barriere zwischen den beiden Rassen (welche die südliche Begrenzung des Verbreitungsgebietes von *A m scutellata* bildet) ist physikalisch wie biologisch scharf markiert. Diese Grenzlinie, gleichzeitig die Südgrenze der Großen Karoo, unterscheidet sich radikal von der Fynbos-Zone von *A m capensis* in der Gestalt der Erdoberfläche, den Böden, dem Klima (Temperatur, Niederschlag und Wind) und der Zusammensetzung, Vielfalt, örtlichen Besonderheiten (Endemismen) und der Blütenbiologie der Pflanzenwelt (Tabelle III). Die hier für *A m capensis* gegebene Definition und Verbreitung schließt alle bisher bekannten Daten ein.

***Apis mellifera capensis* / Übersicht /
Verhalten / Physiologie / *Apis mellifera*
scutellata / Biotop**

REFERENCES

- Anderson RH (1963) The laying worker in the Cape honeybee, *Apis mellifera capensis*. *J Apic Res* 2(2), 85-92
- Anderson RH (1965) A method for controlled queen-rearing in colonies of the Cape honeybee (*Apis mellifera capensis*). *S Afr J Agric Sci* 8, 1163-1164
- Anderson RH, Buys B, Johannsmeier M (1983) *Beekeeping in South Africa*. Bulletin No 394, Department of Agriculture, Pretoria

- Billen JPJ, Dumortier KTM, Velthuis HHW (1986) Plasticity of honeybee castes. *Naturwissenschaften* 73, 332-333
- Bond P, Goldblatt P (1984) Plants of the Cape Flora. *J S Afr Bot suppl* No 13
- Buys B (1984) Cape worker-bees dislike African virgin queens. *S Afr Bee J* 56(3), 63
- Crewe RM, Velthuis HHW (1980) False queens: a consequence of mandibular gland signals in worker honeybees. *Naturwissenschaften* 67, 467-469
- Crewe RM, Wossler T, Allsopp MH (1991) Workers in queens clothing: why *capensis* workers become pseudoqueens. In: *Bees and Beekeeping in Southern Africa* (Anderson RW, Buys B, eds) Apimondia, Stellenbosch, 83-89
- Davidson GP (1933) *Apiculture in South Africa*. Central News Agency, South Africa
- Deacon J, Lancaster N (1988) *Late Quaternary Palaeoenvironments of Southern Africa*. Clarendon, Oxford
- Deacon WJ, Hendey QB, Lambrechts JJ (1983) *Fynbos Palaeoecology: A Preliminary Synthesis*. CSIR, Pretoria
- Fletcher DJC (1978) The African bee, *Apis mellifera adansonii*, in Africa. *Ann Rev Entomol* 23, 151-171
- Guy RD (1976a) Whence the Cape bee? Part 1. *S Afr Bee J* 48 (2), 7-8
- Guy RD (1976b) Whence the Cape bee? Part 2. *S Afr Bee J* 48 (3), 9-11
- Hastings H (1989) Two aspects of the biology of an African honeybee *Apis mellifera scutellata* (Hymenoptera, Apidae): laying workers and colony defence behaviour. Ph D thesis, University of Natal, Pietermaritzburg
- Hemmling C, Koeniger N, Ruttner F (1979) Quantitative Bestimmung der 9-oxodecensäure im Lebenszyklus der Kapbiene (*Apis mellifera capensis* Esch). *Apidologie* 10, 227-240
- Hepburn HR (1989) *Capensis* in the Eastern Cape. *S Afr Bee J* 61(4), 87-89
- Hepburn HR (1991) What and where is the Cape bee - an interim report. In: *Bees and Beekeeping in Southern Africa* (Anderson RH, Buys B, eds) Apimondia, Stellenbosch, 74-82
- Hepburn HR, Crewe RM (1990) Defining the Cape honeybee: reproductive traits of queenless workers. *S Afr J Sci* 86, 524-527
- Hepburn HR, Jacot Guillarmod A (1991) The Cape honeybee and the fynbos biome. *S Afr J Sci* 87, 70-73
- Hepburn HR, Nefdt RJC, Whiffler LA (1988) Queen loss in the Cape honeybee: the interactions of brood, laying workers (false queens?) and queen cells. *S Afr J Sci* 84, 778-780
- Hepburn HR, Magnuson P, Herbert L, Whiffler LA (1991) The development of laying workers in the Cape honeybee. *J Apic Res* (in press)
- Johannsmeier MF (1983) Experiences with the Cape bee in the Transvaal. *S Afr Bee J* 55, 130-138
- Kerr WE, Portugal Araujo V de (1958) Racas de abelhas de Africa. *Garcia de Orta* 6, 53-59
- Lambrechts JJN (1979) Geology, geomorphology and soils. In: *Fynbos Ecology: a Preliminary Synthesis* (Day J, Siegfried W, Louw GN, Jarmna ML, eds) CSIR, Pretoria, 16-26
- Lundie AE (1929) The rearing of queen-bees. *Bull Dept Agric Un S Afr* No 6
- Mackensen O (1943) The occurrence of parthenogenetic females in some strains of honeybees. *J Econ Entomol* 36, 465-470
- Moritz RFA (1986) Two parthenogenetical strategies of laying workers in honeybee populations (*Apis mellifera* L). *Entomol Gen* 11, 159-164
- Moritz RFA (1991) Natural and artificial selection in the Cape honeybee *Apis mellifera capensis*. In: *Bees and Beekeeping in Southern Africa* (Anderson RH, Buys B, eds) Apimondia, Stellenbosch, 63-73
- Moritz RFA, Kauhausen D 1984. Hybridization between *Apis mellifera capensis* and adjacent races of *Apis mellifera*. *Apidologie* 15, 211/222
- Moritz RFA, Hillesheim E (1985) Inheritance of dominance in honeybees (*Apis mellifera capensis* Escholtz). *Behav Ecol Sociobiol* 17, 87-89
- Nunamaker RA, Wilson WT (1981) Comparison of MDH allozyme patterns in the African honey bee (*Apis mellifera adansonii* L) and

- the Africanized populations of Brazil. *J Kans Entomol Soc* 54, 704-710
- Nunamaker RA, Wilson WT, Haley BE (1984) Electrophoretic detection of Africanized honey bees (*Apis mellifera scutellata* L) in Guatemala and Mexico based on male dehydrogenase allozyme patterns. *J Kans Entomol Soc* 57, 622-631
- Onions GW (1912) South African "fertile worker bees". *S Afr Agric J* 1, 720-728
- Onions GW (1914) South African "fertile" worker bees. *Agric J Un S Afr* 7, 44-46
- Rinderer TE, Hellmich RL, Danka RG, Collins AM (1985) Male reproductive parasitism: a factor in the Africanization of European honey-bee populations. *Science* 228, 1119-1121
- Rutherford MC, Westfall RH (1985) Biomes of southern Africa - an objective categorization. *Mem Bot Surv S Afr* No 54
- Ruttner F (1977) The problem of the Cape bee (*Apis mellifera capensis* Escholtz): parthenogenesis - size of population - evolution. *Apidologie* 8, 281-294
- Ruttner F (1988) *Biogeography and Taxonomy of Honeybees*. Springer, Berlin
- Ruttner F, Koeniger N, Veith HJ (1976) Queen substance bei eierlegenden Arbeiterinnen der Honigbiene *Apis mellifica* L. *Naturwissenschaften* 63, 434
- Schulze BR (1965) *Climate of South Africa*. No 8. Weather Bureau, Department of Transport, Pretoria
- Smith DR (1988) Mitochondrial DNA polymorphisms in five old world subspecies of honeybees and in new world hybrids. In: *Africanized Honey Bees and Bee Mites* (Needham GR, Page RE, Delfinado-Baker M, Bowman CE, eds) John Wiley, New York
- Tribe GD (1981) Cape honeybee behaviour. *S Afr Bee J* 53, 10-12
- Tribe GD (1983) What is the Cape bee? *S Afr Bee J* 55, 77-87
- Velthuis HHW (1985) The honeybee queen and the social organization of her colony. *Fortschr Zool* 31, 343-357
- Velthuis HHW, Ruttner F, Crewe RM (1990) Differentiation in reproductive physiology and behaviour during the development of laying worker honey bees. In: *Social Insects* (Engels W, ed) Springer, Berlin
- Verma S, Ruttner F (1983) Cytological analysis of the thelytokous parthenogenesis in the Cape honeybee (*Apis mellifera capensis* Escholtz). *Apidologie* 14, 41-57
- Whiffler LA, Hepburn HR (1991a) The queen in relation to wax secretion in honeybees. *J Comp Physiol* (in press)
- Whiffler LA, Hepburn HR (1991b) Inhibition of queen cell construction in the Cape honeybee, *Apis mellifera capensis*. *Apidologie* 22, 229-236
- Worswick PV (1987) Comparative study of colony thermoregulation in the African honeybee *Apis mellifera adansonii* Latreille and the Cape honeybee, *Apis mellifera capensis* Escholtz. *Comp Biochem Physiol* 86A, 95-102
- Worswick PV (1988) Comparison of nectar foraging efficiency in the Cape honeybee, *Apis mellifera capensis* Escholtz and the African honeybee, *Apis mellifera adansonii* Latreille in the Western Province. *S Afr J Zool* 23, 124-127
- Woyke J (1986) Sex determination. In: *Bee Genetics and Breeding* (Rinderer T, ed) Academic Press, New York