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Review article

Apis mellifera capensis: an essay on the subspecific classification of honeybees

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Abstract – The history of the classification of *Apis mellifera capensis* is traced. The distributions of the traits thelytoky, ovariole number and spermatheca size of workers are given. Thelytoky in workers extends over 240 000 km^2 and the ratio of female/male progeny in laying worker offspring is clinal. Ovariole numbers are also clinal but spermatheca size is not. Allozymically, southern African honeybees are homogeneous; but differ in mtDNA haplotypes and nuclear DNA diversity. Morphometric analyses yield three distinct morphoclusters (*A. m. capensis*, *A. m. scutellata*, and *unnamed mountain bees*). Conventional morphometric classification is incongruous with the mode of parthenogenesis and distribution of mtDNA and nuclear DNA diversity in the honeybees of southern Africa. The terms "*A. m. capensis*" and "*A. m. scutellata*" are only meaningful if the precise geographical origins of the bees are specified.

***Apis mellifera capensis* / *Apis mellifera scutellata* / classification / biogeography / thelytoky**

1. INTRODUCTION

This review summarizes data accumulated over the years from various workers on the variation of morphological, physiological and biochemical traits in the honeybees of southern Africa, and examines them with regard to their congruity with current concepts of the two "subspecies" *Apis mellifera capensis* Escholtz and *Apis mellifera scutellata* Lepeletier. However, compilation of the various traits seems to bear on a more generally troubling question which is the "subspecies" concept as such. Although not only *A. m. capensis* is fraught with difficulties in the incongruous geographical distribution of its traits, this honeybee has been studied in quite considerable detail and is an excellent example of the fuzziness of subspecific definitions in general. It is of particular interest that several seemingly decisive traits associated

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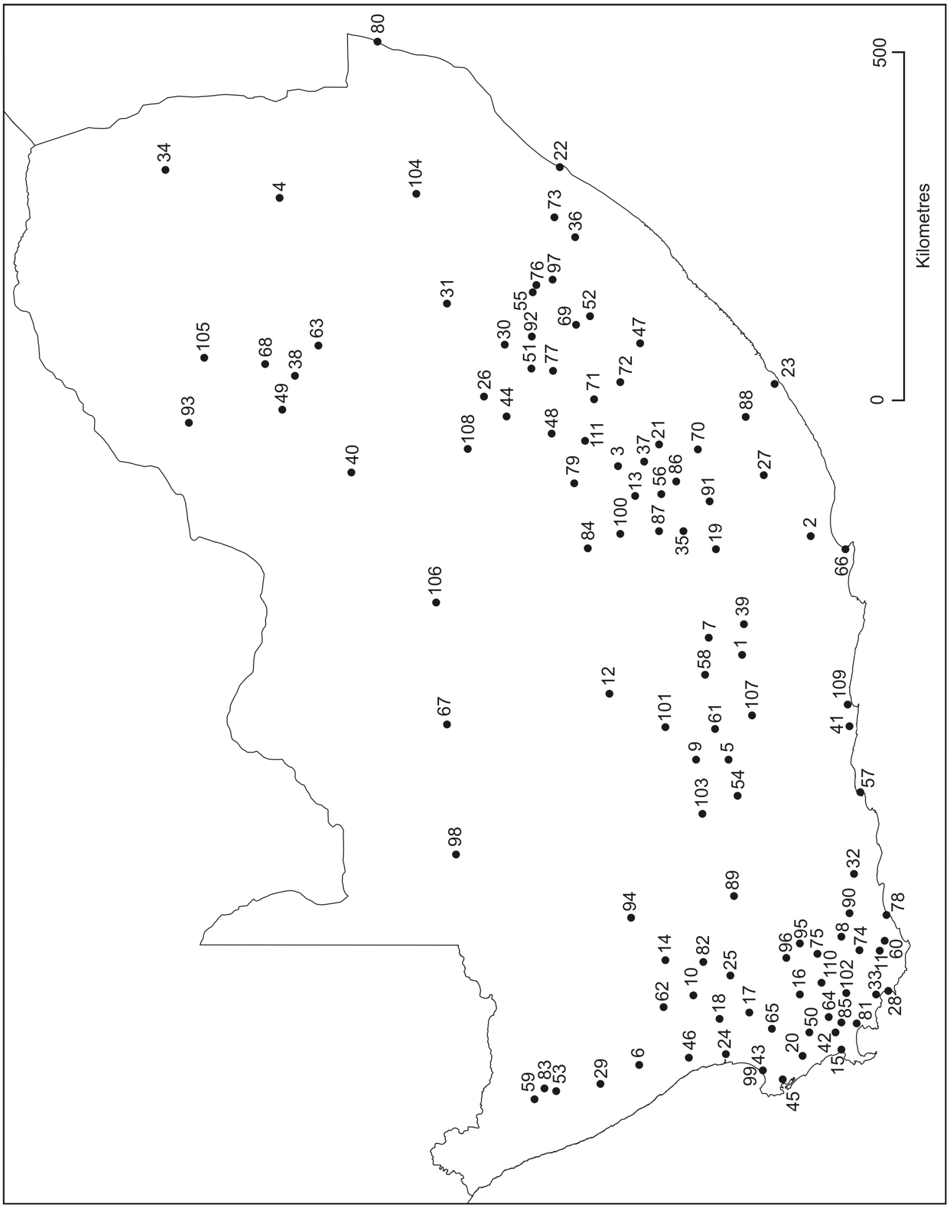
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with parthenogenetic reproduction in worker bees are at odds with purely morphological definitions of a subspecies.

Thelytoky in laying workers of Cape honeybees was evident in a late 19th century paper (de Villiers, 1883) which reported that worker brood could be produced by a colony of bees whose queen was confined to a cage; but, that such brood actually derived from laying workers was first recognized by Onions (1912, 1914). These results were confirmed by Trollip (1912), Terrell (1912) and Jack (1916). Terrell (1912) further reported that he obtained mated queens from worker-laid eggs. Because thelytoky is a rare occurrence in other subspecies of *A. mellifera* (Mackensen, 1943), its high frequency in the Cape honeybee established it as a singular curiosity amongst honeybees; but, an awareness of its reproductive peculiarities diffused very slowly in the apicultural literature (Kerr and Laidlaw, 1956; Kerr and Portugal Araújo, 1958; Anderson, 1963).

A few years later, Ruttner had turned his attention to the classification and biogeography of honeybees and gradually sifted and refined a suite of some 36 morphological characters with which he subsequently analyzed the honeybees of the world using sophisticated multivariate statistical methods of analysis (Ruttner, 1988). Ruttner encountered many difficulties such as shortage of data for some areas, irreconcilable anomalies, as well as the scientific decision/discretion problems of deciding cutoff points for a particular taxon. The methodology was systematic and metrically precise, coupled with a deep knowledge of honeybee biology. Ruttner's view (1976) was that "… a geographic race may be defined as a group of bees similar in morphology, behaviour and physiology, and characterized by a specific geographical distribution". This approach is particularly apparent in the context of *A. m. capensis*, one of Ruttner's more intractable problems. Even with multivariate methods he was unable to separate *A. m. capensis* from *A. m. scutellata* on morphometric criteria alone (Ruttner, 1976, 1977, 1988).

Thus, a well defined suite of morphological characters adequate for distinguishing the honeybee populations of southern Africa remained elusive. Ruttner then introduced new characters to develop a working definition of *A. m. capensis* (Ruttner, 1976, 1977, 1988): (1) the laying workers of the Cape honeybee could reproduce diploid offspring thelytokously; (2) such workers

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Figure 1. Reference map for the 111 localities in southern Africa for which data are given in subsequent figures and tables. 1. Aberdeen, 2. Addo, 3. Aliwal North, 4. Badplaas, 5. Beaufort West, 6. Bitterfontein, 7. Boesmanskop, 8. Bonnievale, 9. Booiskraal, 10. Botterkloof , 11. Bredasdorp, 12. Britstown, 13. Burgersdorp, 14. Calvinia, 15. Cape Town, 16. Ceres, 17. Citrusdal, 18. Clanwilliam, 19. Cradock, 20. Darling, 21. Dordrecht, 22. Durban, 23. East London, 24. Elandsbaai, 25. Elandsvlei, 26. Ficksburg, 27. Fort Beaufort, 28. Gansbaai, 29. Garies, 30. Ha Lejone, 31. Harrismith, 32. Heidelberg, 33. Hermanus, 34. Hoedspruit, 35. Hofmeyr, 36. Ixopo, 37. Jamestown, 38. Johannesburg, 39. Kendrew, 40. Klerksdorp, 41. Knysna, 42. Kraaifontein, 43. Laaiplek, 44. Ladybrand, 45. Langebaan, 46. Lutzville, 47. Maclear, 48. Mafeteng, 49. Magaliesberg, 50. Malmesbury, 51. Marakabei, 52. Matatiele, 53. Mesklip, 54. Middelwater, 55. Mokhotlong, 56. Molteno, 57. Mosselbaai, 58. Murraysburg, 59. Nababeep, 60. Napier, 61. Nelspoort, 62. Nieuwoudtville, 63. Nigel, 64. Paarl, 65. Piketberg, 66. Port Elizabeth, 67. Postmasburg, 68. Pretoria, 69. Qacha's Nek, 70. Queenstown, 71. Quiteng, 72. Rhodes, 73. Richmond, 74. Riviersonderend, 75. Sandvlei, 76. Sani Top, 77. Semonkong, 78. Skipskop, 79. Smithfield, 80. Sodwana Bay, 81. Somerset West, 82. Sonop, 83. Springbok, 84. Springfontein, 85. Stellenbosch, 86. Sterkstroom, 87. Steynsburg, 88. Stutterheim, 89. Sutherland, 90. Swellendam, 91. Tarkastad, 92. Thaba-Tseka, 93. Thabazimbi, 94. Tontelbos, 95. Touwsrivier, 96. Tweeriviere, 97. Underberg, 98. Upington, 99. Velddrif, 100. Venterstad, 101. Victoria West, 102. Villiersdorp, 103. Vonkfontein, 104. Vryheid, 105. Warmbad, 106. Warrenton, 107. Wiegenaarspoort, 108. Winburg, 109. Wittedrif, 110. Worcester, 111. Zastron.

Table I. Summary statistics of the morphometric and non-morphometric traits when analysed in terms of the morphoclusters (traditionally considered "subspecies").

	capensis	**transitional**	***scutellata***	**mountain**	**Tests**
Sample size *n*	28	10	64	9	
Mean morphometric variance	4.53	5.11	4.25	3.66	F = 3.39 (3,106 df) $P = 0.0253$*
No. of high morphometric variances	3 ($n = 28$)	4 ($n = 10$)	7 ($n = 63$)	0 ($n = 9$)	Chi-square^2 = 8.26 (3 df) $P = 0.0410$*
No. of high pheromonal variances	2 ($n = 18$)	3 ($n = 8$)	5 ($n = 29$)	---	Chi-square^2 = 2.63 (2 df) $P = 0.2686$
Ovariole number					
high	8	2	5	---	Chi-square^2 = 17.94 (2 df)
low	0	0	19	---	$P = 0.0001$**
DELW[1] frequencies					
yes	28	10	22	0	Chi-square^2 = 52.87 (3 df)
no	0	0	42	9	$P < 0.0001$**
Nuclear DNA allele mean frequencies	($n = 1$)	($n = 3$)	($n = 15$)		$F_{queen} = 0.29$ (2,16 df) $P = 0.7500$
queen	3.0	4.3	4.3	---	$F_{drone} = 0.01$ (2,16 df)
drone	7.0	7.0	7.2	---	$P = 0.9872$
mtDNA haplotype frequencies					Chi-square^2 = 0.78 (4 df) $P = 0.9415$
QQ	3	1	13	---	
mixed	1	0	6	---	
Q	0	0	1	---	

[1] DELW = diploid eggs from laying workers; * $P < 0.05$, ** $P < 0.01$.

have well developed spermathecae; and (3) Cape workers have many ovarioles. This approach seemed to allow the definition of *A. m. capensis* and, to some extent, supported a traditional, somewhat intuitive idea that Cape bees were blackish, rather docile with workers that could lay diploid eggs parthenogenetically (Anderson et al., 1971). This was methodologically broader in scope than that traditionally used in insect morphometrics (Daly, 1985). Ultimately, it led others to question the meaningfulness of morphometrically defined subspecific categories in honeybees (Hepburn and Radloff, 1998; Hepburn, 2000).

While a more biological working definition for the Cape honeybee was thus formulated (Ruttner, 1976, 1977), this did not, de facto, delimit the occurrence of this bee. Its distribution was thought to be more or less coincident with all or part of the winter rainfall region between Cape Town and Port Elizabeth (Kerr and Portugal Araújo, 1958; Anderson, 1963, 1977; Tribe, 1983) and led to differences of opinion that varied by thousands of km^2 (Fig. 1, localities 16 and 66). Ruttner (1976, 1977) began with this expanded view (giving the Cape bee a distribution of about 115 000 km^2) but in time reduced it to the Cape Peninsula, an area of less than 7000 km^2 (Ruttner, 1986, 1988). These ideas naturally lead to an account of the Cape honeybee, as a subspecific category. This essay is based on the analysis of the relevant published

Table II. Summary statistics of the morphometric and non-morphometric traits when analysed in terms of the modes of parthenogenesis of laying workers.

	Thelytoky	**Arrhenotoky**	**Tests**
Sample size *n*	60	51	
Mean morphometric variance	4.76	3.86	$t = 4.53$ (108 df) $P < 0.0001$**
No. of high morphometric variances	12 ($n = 60$)	2 ($n = 50$)	Chi-square$^2 = 6.29$ (1 df) $P = 0.0122$* Fisher exact: $P = 0.0191$*
No. of high pheromonal variances	9 ($n = 45$)	1 ($n = 10$)	Chi-square$^2 = 0.55$ (1 df) $P = 0.4583$ Fisher exact: $P = 0.6684$
Ovariole number			
high	14	1	Chi-square$^2 = 23.07$ (1 df) $P < 0.0001$**
low	2	17	Fisher exact: $P < 0.0001$**
Morphocluster			
capensis	28	0	
transitional	10	0	Chi-square$^2 = 52.87$ (3 df) $P < 0.0001$**
scutellata	22	42	
mountain	0	9	
Nuclear DNA allele mean frequencies	($n = 15$)	($n = 4$)	
queen	4.47	3.50	$t_{queen} = 1.06$ (17 df) $P = 0.3044$
drone	7.40	6.25	$t_{drone} = 0.98$ (17 df) $P = 0.3422$
mtDNA haplotype frequencies	8	9	Chi-square$^2 = 2.90$ (2 df) $P = 0.2349$
QQ	1	6	
mixed	0	1	
Q			

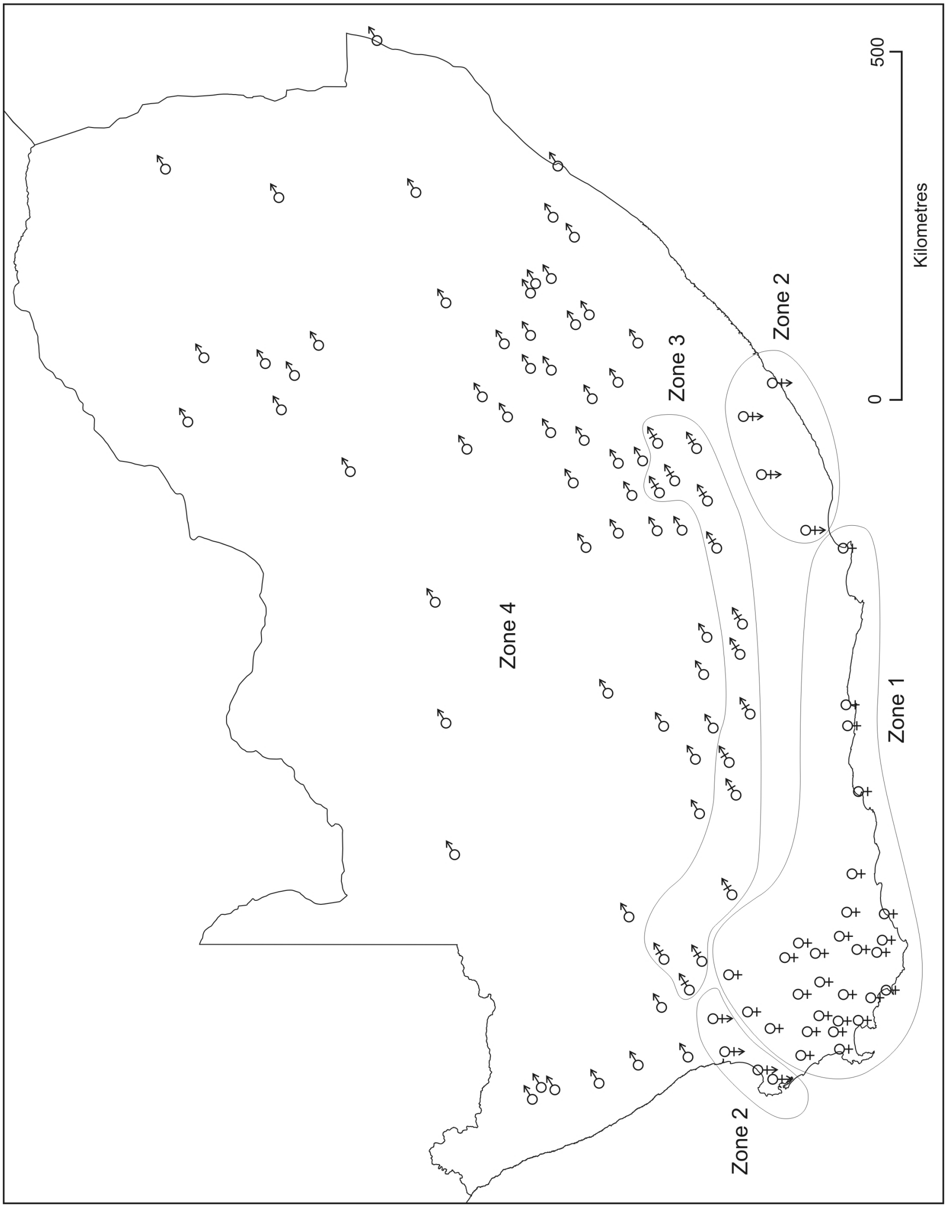
* $P < 0.05$, ** $P < 0.01$.

literature, hence there were no formal “Materials and Methods” as such beyond a few fresh calculations (Tabs. I and II) and the preparation of new maps. All of the localities referred to are given in Figure 1.

2. RESULTS AND DISCUSSION

2.1. Parthenogenesis in laying worker bees

The distribution of thelytokous parthenogenesis in laying workers (DELW), crucial to the Ruttner (1976, 1977, 1988) definition of the Cape bee, was discovered in two phases: that empirical data available to Ruttner, about 1975, on which he basically formulated his own view of the Cape honeybee; and, data obtained since then. Most of the information published in the first half of the 20th century on Cape bees was virtually unknown and extremely inaccessible outside South Africa. In any event, early records for the geographical distribution of the gene DELW show that this trait centred on the Cape Peninsula but Eastern Cape Province records extended this as far east as the Keiskamma Valley (about 50 km west of locality 23 in Fig. 1; Onions, 1912; Gough, 1928; Davidson, 1933). Subsequent to the suggestion that Cape bees might extend as far as the Suurberge mountains (Tribe, 1983), this was experimentally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confirmed on the basis of diploid eggs laid by workers (DELW) in colonies from Port Elizabeth, Grahamstown, Alicedale and East London (triangular area bounded by localities 23, 27 and 66 in Fig. 1; Hepburn et al., 1988; Hepburn, 1989; Hepburn and Crewe, 1990; Neumann et al., 2000).

Subsequent to the report that DELW occurs widely in the Eastern Cape Province (Hepburn et al., 1988; Hepburn, 1989), this trait was systematically investigated in field experiments in situ at various localities where colonies were dequeened and all their combs removed and replaced with empty combs that had been deep-frozen. A month later the formerly queenless, broodless colonies were examined for queens or laying workers and the sexes of all progeny determined (Hepburn and Crewe, 1990; Neumann et al., 2000). The current known distribution of the gene DELW based on survey data with an average interlocality resolution of less than 100 km is shown in Figure 2. Very simply, thelytokous parthenogenesis or DELW occurs in honeybee colonies extending from the Atlantic coast of South Africa from Vanrhynsdorp-Calvinia in the west to Queenstown-East London in the east (Fig. 1, localities 14, 23 and 70). Thus DELW occurs in an area of some 235 000 km^2, bounded in the interior by the Nuweveldberge and Stormberge ranges of the Drakensberg mountains (a west-east line between localities 2 and 95 of Fig. 1; cf. also Fig. 2).

Allied to thelytoky is the frequency of haploid and diploid progeny obtained from laying workers. The known frequency distributions for female/male progeny on a geographical basis show that there is a southern zone where the ratio of females to males is effectively 1:0; on the next tier both sexes occur but females dominate at a ratio of 0.75:0.25; in a third zone where both sexes occur males dominate at 0.25:0.75; and finally, there is a fourth zone of pure arrhenotoky with a ratio of 0:1 (Fig. 2). Thus the frequency distribution of sex ratios in laying worker progeny is clinal in nature As one moves from areas of high female: male ratios through evenly mixed female/male progeny produced by laying workers to pure arrhenotoky, the switchover is a very gradual one, highly suggestive of a polygenically inherited trait. This also applies to ovariole number (cf. below).

2.2. Ovarioles and spermathecae

Number of ovarioles and size of the spermatheca in worker bees were also considered as a useful diagnostic criteria for *A. m. capensis* (Kerr and Portugal Araújo, 1958; Anderson, 1963, 1977; Ruttner 1976, 1977, 1981, 1988). Indeed, Ruttner (1977) showed that both ovariole number and spermathecal size decreased clinally along a 400 km transect from Cape Town eastwards to Knysna (west-east line between localities 15 through 41 in Fig. 1). Also, the spermathecae of workers from Cape Town were twice the size of those of European subspecies of *A. mellifera*. Ultimately, he limited the designation "*A. m. capensis*" to colonies whose worker bees had, on average, more than five

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Figure 2. Geographical distribution of the zones of thelytoky and arrhenotoky in worker bees of southern Africa. Zone 1 consists of thelytokous worker bees where the female/male sex ratio is close to 1:0 and designated by symbol for females; zone 2 consists of thelytokous bees with an average F/M ratio of 0.75:0.25, designated by female symbol with cross-bar; zone 3 consists of bees still expressing thelytoky but the F/M ratio changes over to about 0.25:0.75 (the reverse of zone 2), designated by male symbol with cross-bar; zone 4 consists of entirely arrhenotokous bees where the F/M ratio is 0:1, designated by male symbol (data from several sources, summarised in Hepburn and Crewe, 1991; Hepburn et al., 1998).

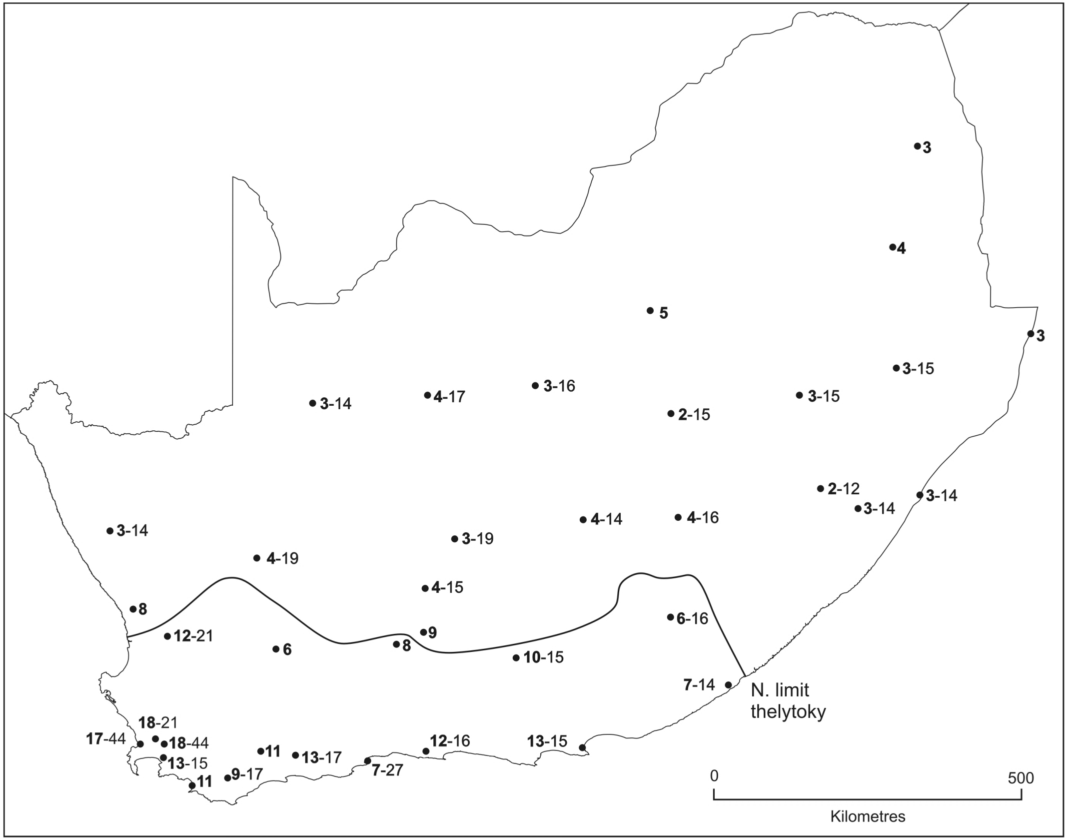

Figure 3. Geographical distribution of numbers of ovarioles/ovary (in bold type numerals) and spermatheca size (not bold numerals) in worker bees of southern Africa (data from several sources, summarised in Hepburn and Crewe, 1991; Hepburn et al., 1998). Note that these data reflect the natural distribution of ovariole numbers and spermatheca size prior to the inadvertent spread of Cape bees throughout the country sometime around 1992.

ovarioles/ovary and a spermathecal diameter of 0.30 mm (values not reached in temperate subspecies of *A. mellifera* – Hess, 1942; Velthuis, 1970). The then available database was meagre, with precise measurements for Prince Albert (about 100 km north of Port Elizabeth), Lutzville and Victoria West (localities 46, 57 and 101 in Fig. 1; Anderson, 1963, 1977) and a slightly larger data set extending from Cape Town to Knysna (localities 15 and 41 of Fig. 1; Ruttner, 1977).

Subsequently Hepburn and Crewe (1990) systematically analysed southern African honeybees for numbers of ovarioles (Fig. 3) and for spermathecal size.The distribution of ovarioles/ovary shows some very clear trends. Over the 1200 km west-east span between Cape Town and East London, ovariole values decrease from 17 to 7, another 200 km further east to Port St Johns this drops to only 1. Moving 100 km northwards, another west-east transect of about 1000 km between Clanwilliam and Queenstown yielded ovariole numbers ranging from 12 down to 6. On a third, west-east transect about 100 km north and parallel to the second one, ovariole number at Garies is only 3 and remains close to this value across the country to Durban. All localities north of this line showed ovariole values of about 3. So there is a gradual decline in ovariole numbers moving from west to east on the two southern transects as well as a gradual decline from south to north (Fig. 3). That ovariolar asymmetry within bees might confound interpretations had been raised (Anderson, 1963), but further analyses of very large samples established that there is no bilateral asymmetry in the average number of ovarioles (Velthuis, 1970). The data also show that there is an excellent correspondence between the distribution of the trait DELW, measured by the sex ratios of thelytokous offspring and ovariole number: the higher the ratio of female progeny, the higher the ovariole number (Figs. 2 and 3).

The spermatheca is usually vestigial in or absent from workers of temperate *A. mellifera* (Hess, 1942). By contrast, the spermathecae of workers bees from the Cape Peninsula are quite large (Onions, 1912, 1914), at about 0.5 mm (Jack, 1916) and those of queens about 1.4 mm (Anderson, 1963). But this organ is quite variable because in one study spermathecal size in worker bees from Stellenbosch ranged between 0.065 to 0.65 mm (Anderson, 1963) and in another study from 0.15 to 0.59 mm (Ruttner, 1977). Moreover, in a broad survey of spermathecal size in worker bees across South Africa, Hepburn and Crewe (1990, 1991) found that workers with large spermathecae certainly occur at the Cape Peninsula (Cape Town, Grabouw, Stellenbosch – near localities 15 and 85 of Fig. 1) but so do very small ones in the same area (Fairfield, Elim, Gansbaii – localities near 28 of Fig. 1). Likewise, the spermathecae of workers from the far northern Transvaal (localities near 105 in Fig. 1) match those of the Cape Peninsula (Hepburn and Crewe, 1990). There are no discernible geographical patterns of variation in the spermathecal size of worker honeybees in southern Africa; neither relationships between spermathecal diameter and the distribution of the trait DELW; nor, for the distribution of ovariole number.

2.3. Pheromones

Another characteristic of worker bees from the Cape Peninsula is their ability to secrete a pheromone from the mandibular gland rich in 9-ODA, normally a trait of queens (Hemmling et al., 1979, Wossler 2002) but which can be induced if such bees are placed together with worker bees of different races (Crewe and Velthuis, 1980) or become queenless (Hepburn et al., 1991). Because the mandibular gland of Cape Town worker bees is twice the volume of that of *A. m. carnica*, Ruttner (1988) suggested that this difference in gland size might be used to discern *A. m. capensis* from other bees. Subsequent measurements of mandibular gland volume of worker bees sampled throughout southern Africa showed that there was no significant difference among them (Hepburn, 1990). Nonetheless, the development of a queenlike bouquet in laying workers remains established for worker bees from the Cape Peninsula (Hemmling et al., 1979; Crewe and Velthuis, 1980), and the Eastern Cape Province (Hepburn, 1992) and is known to be absent from bees in northern areas of South Africa (Crewe and Velthuis, 1980; Jackson, 1982).

The pheromonal bouquet of the mandibular glands of queen bees presents a somewhat different picture. Because the trait DELW and high ovariole numbers were found in workers in the Eastern Cape Province (Hepburn and Crewe, 1991) as well as the ability of such workers to develop queenlike bouquets (Hepburn, 1992), it is possible that queen pheromones might also differ geographically. Indeed, the 9ODA: 10HDA ratios of queens from the Cape Town/Stellenbosch area (localities 15 and 85 of Fig. 1) are significantly higher than those of queens in the Transvaal (localities 36 and 68 of Fig. 1; Crewe, 1984, 1988).

A principal components analysis of the sting pheromones of southern African worker bees revealed that they formed a single, diffuse cluster (Hepburn et al., 1994). Other recent discoveries have shown that worker bees from the Cape Peninsula have queen-like abdominal tergal glands and that bees of northern South Africa do not (Wossler and Crewe, 1999; Wossler et al., 2000). These results lead to a not yet answerable but highly pertinent question: how do all of these pheromonal traits vary throughout southern Africa? Biogeographical analyses of the complete repertoire of pheromones of the bees of southern Africa could well prove highly informative.

2.4. Allozyme variation

The heritability of allozymes is mendelian and their phenotypic expression not subject to environmental effects. Thus they are potentially very useful probes in the analysis of honeybee populations. Although few of the allozyme systems of honeybees have proven polymorphic, malate dehydrogenase has a range of morphs the frequency distributions of which correspond reasonably well with biometrically defined races (Ruttner, 1988). In southern Africa those bees classified as *A. m. capensis* and *A. m. scutellata* (Cape Peninsula and Transvaal samples respectively) are monomorphic and homozygous for the fast form of malate dehydrogenase, Mdh-100 (Nunamaker and Wilson, 1981; Sylvester, 1982; Nunamaker et al., 1984, 1986; Sheppard and Huettel, 1988). Further investigations confirmed these basic results as well as for bees of the fynbos biome; and, the occurrence of Mdh heterozygotes at two localities can be explained as resulting from foreign (and presumably failed) introductions (Hepburn, 1990). There is no other published data on allozyme variation that bear on the differentiation of the honeybee populations of southern Africa.

2.5. Mitochondrial and nuclear DNA

Mitochondrial DNA has become a standard probe for the study of honeybee populations and offers the dual advantages of small and highly conserved molecules (Smith, 1991). Recent analyses have shown that the mtDNA profiles of the honeybees of Africa share a common mitotype defined by a combination of some 22 restriction sites (Smith, 1991; Garnery et al., 1992). In a series of recent analyses, Smith (1988, 1991) and (Garnery et al., 1992, 1995) demonstrated that restriction site polymorphisms and fragment length variations were adequate to separate the major *Apis* lineages; but, when their data were subjected to cluster analysis, none of the putative subspecies of Africa could be differentiated using mtDNA (Hepburn and Radloff, 1998). Subsequently, Sheppard et al. (1996) described several unique haplotypes from putative subspecies of African honeybees on a continental scale.

Nonetheless, the power of mtDNA as a probe stimulated three regional studies of southern African honeybees (Moritz et al., 1994, 1998; Hepburn et al., 2000). The rationale was based on the fact that laying workers of Cape honeybees produce female offspring which, in the absence of any recombination (Moritz and Haberl, 1994), result in both mtDNA and nuclear DNA clones. Workers of northern *A. m. scutellata* only reproduce arrhenotokously and drones make no contribution to the mitochondrial gene pool. The observed haplotypes, based on their Q-repeat sequences (Fig. 4), demonstrate that the single Q-repeat, varying in frequency, is characteristic of *A. m. scutellata* honeybees of northern South Africa and virtually absent from areas considered to be occupied by *A. m. capensis* or transitional group bees (that is, bees with thelytoky). The QQ-haplotype is ubiquitous in *A. m. capensis* areas and declines, clinally, northwards. With a single exception, the QQQ-haplotype is absent from *A. m. capensis* areas and is distributed intermittently among transitional group bees and in *A. m. scutellata* areas (Moritz et al., 1994). Finally, the frequency distributions of eight different mitochondrial restriction length patterns obtained from the non-coding region of COI-COII by a DraI restriction were measured for bees from localities defined morphometrically and reproductively as "transitional" and from the mountain bee morphocluster obtained from Lesotho, but there were no observable differences between these two groups (Hepburn et al., 2000).

Turning to the analysis of nuclear DNA, Moritz et al. (1998) analysed variation in 20 alleles at the Z-locus of queens and drones. Heterogeneity in the nuclear DNA fractions was minimal in classically defined *A. m. capensis* and *A. m. scutellata* areas and maximal in the transitional zone between them. Comparing the DNA data, the results show that greatest allelic diversity in nuclear DNA for both queens and drones occurs within a 100 km radius of Jamestown/Smithfield (localities 37 and 79 of Fig. 1); in contrast to this, significant changes in the frequency distribution of the Q- and QQ-repeats in mtDNA only begin north of the heterogeneous nuclear DNA area (Fig. 4).

2.6. Morphometrics

2.6.1. Formation of morphoclusters

Subsequent to the description of *A. m. capensis* by Escholtz (1822), the first study actually based on quantitative morphological comparisons of southern African bees was that of Alpatov (1933) who distinguished *A. m. capensis* from *A. m. scutellata*, but the interlocality sample distance between Stellenbosch and Pretoria is more than 1000 km. Somewhat later two important, albeit very different, studies (Maa, 1953; DuPraw, 1964, l965) concluded that all the bees of central and southern Africa are a single subspecies of *A. mellifera* with a high degree of colour polymorphism. This conclusion is of interest because of totally different methodological approaches. In the first report, Maa (1953) analysed all species and subspecies of *Apis* using classical, descriptive taxonomic methods; in the second, DuPraw (1964, 1965) made a major contribution to classification by incorporating the then newly developed multivariate methods of statistical analysis and applying them to honeybees. The effect of his contribution has proven to be an important philosophical challenge to the typological thinking inherent in the Linnaean system of nomenclature.

The early morphometric studies of southern African honeybees conducted by

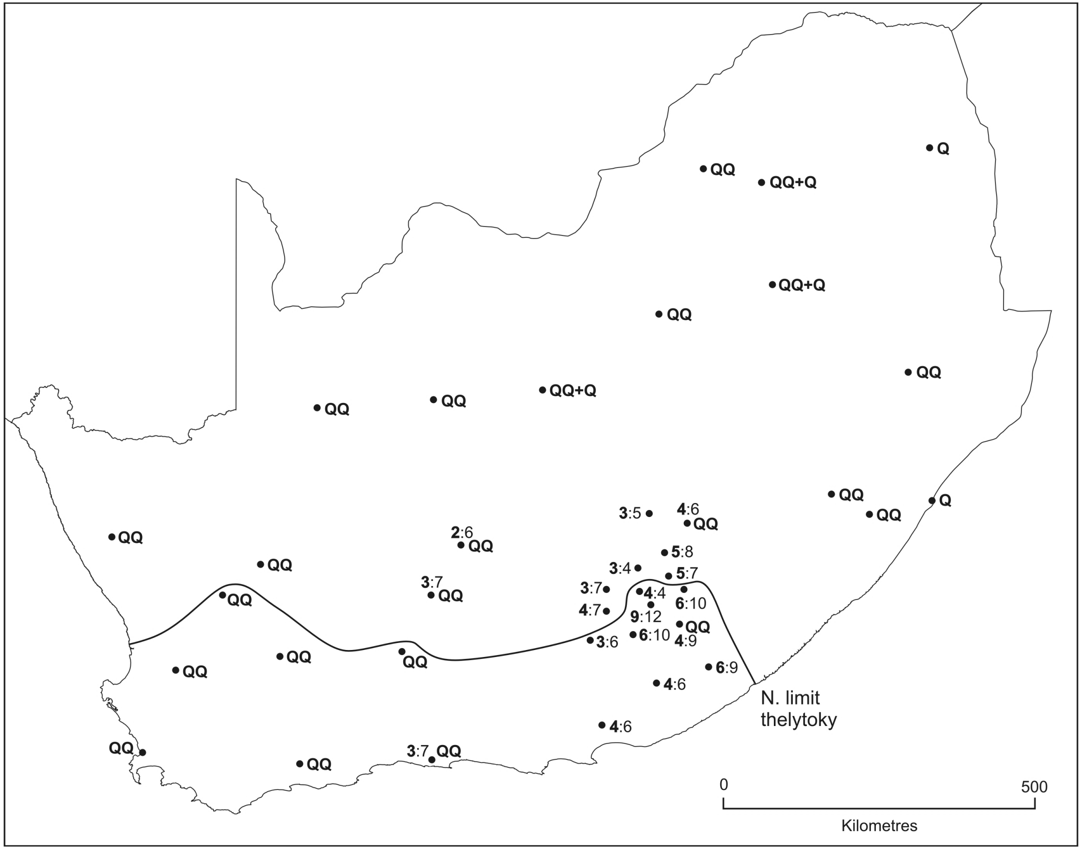

Figure 4. Geographical distribution of mtDNA haplotypes (QQ- and Q- repeat sequences) and nuclear DNA alleles at the Z-locus in queens (bold type numerals) and drones (not bold numerals) in the honeybees of southern Africa (from Moritz et al., 1994, 1998).

Ruttner (1976), like those of DuPraw (1965), did not yield a distinct "*A. m. capensis*" morphocluster. In fact, Ruttner's (1976) plots of the distribution of African honeybees in a system of coordinates of discriminant factors demonstrate that those bees considered to be *A. m. capensis* did not form a distinct morphocluster and were scattered amongst the morphoclusters of various other morphometrically distinct African subspecies. Given the well developed spermatheca and numerous ovarioles of Cape Peninsula bees, Ruttner (1976) concluded that there must have been widespread hybridization amongst the bees of southern Africa (a view endorsed by Moritz and Kauhausen, 1984). From this point in time Ruttner consistently emphasised the reproductive traits of worker bees in defining the limits of *A. m. capensis* (Ruttner, 1976, 1977, 1981, 1986, 1988, 1992).

In their initial attempts to further define the Cape honeybee and plot its distribution, Hepburn (1990) and Hepburn and Crewe (1990, 1991) began with the assumption that *A. m. capensis* could be defined by the criteria suggested by Ruttner (1976, 1977): thelytoky, high ovariole numbers and a large spermatheca in worker bees (as well as other traits – isozymes, mandibular glands, colour and size), but specifically excluding any morphometric data. They systematically investigated these traits at a 200 km interlocality sampling distance resolution throughout southern Africa and duly plotted the measurements obtained (Hepburn and Crewe, 1990, 1991). While these results enhanced the database on the relative distributions of these traits, the results still begged the question: do these characteristics relate to morphometrically definable bees in southern Africa?

To answer this question a morphometric analysis of 3440 worker honeybees from 172 colonies and 32 localities was performed (the same samples previously investigated biologically – Hepburn, 1990; Hepburn and Crewe, 1990, 1991). A principal components analysis of 36 morphological characters (the standard characters of Ruttner, 1988) yielded two distinct morphoclusters. Those bees which had been defined a priori as "hybrids" (intermediate ovariole numbers and mixed worker/drone laying worker progeny) fell in between or among the two morphoclusters obtained (Crewe et al., 1994). A subsequent linear discriminant function analysis produced the same two clusters using only 10 of the original 36 characters and confirmed the presence of morphologically transitional bees as well. The latter principally differed from the former with respect to intercolonial variance. Thus, *A. m. capensis* could be defined morphometrically. A point of particular importance was the conclusion by Crewe et al. (1994) that the morphometric data were geographically consistent with the reproductive and other biological data. It eventuated that this conclusion was premature.

2.6.2. Morphoclusters and distance

Shortly after publication of the Crewe et al. (1994) study, parallel investigations of these same populations revealed extensive variations in pheromones and the frequency distributions of the mtDNA and nuclear DNA profiles of these honeybees (Hepburn et al., 1994; Moritz et al., 1994, 1998 – cf. section on DNA above). This seemed to require a far more thorough re-examination of the morphometrics of *A. m. capensis*, *A. m. scutellata* and their possible "hybrids" (actually, transitional zone bees) at a finer sampling distance resolution (Radloff and Hepburn, 1998). This was achieved (following the amalgamation of the Ruttner database at Oberursel with that of Hepburn and Radloff at Grahamstown) in a further analysis of 8743 worker honeybees from 442 colonies and 104 localities which provided an interlocality sampling resolution better than 100 km (Hepburn et al., 1998a).

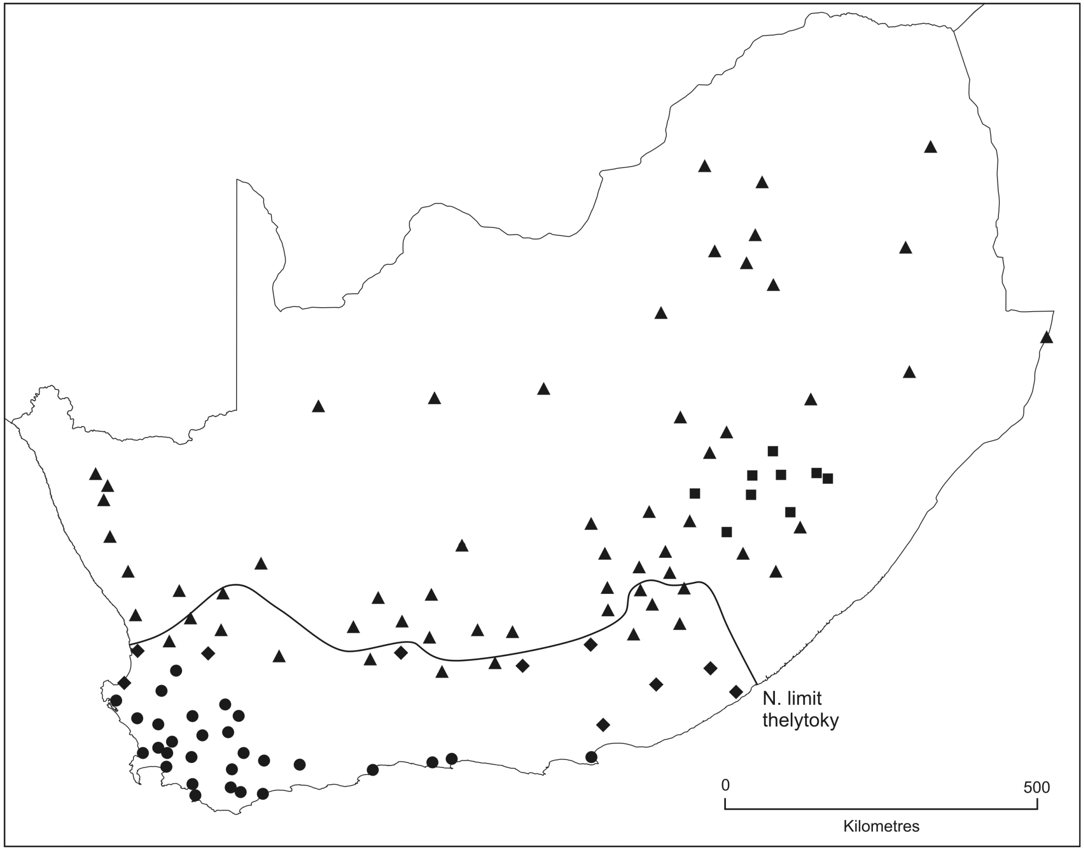

Figure 5. Geographical distributions of the three morphoclusters of honeybees in southern Africa: *capensis* (circles), *scutellata* (triangles) and *mountain* (squares) morphoclusters obtained in multivariate morphometric analyses (from Hepburn et al., 1998a; Hepburn, 2000). The "transitional" zone bees (diamonds) derive from the exclusion from or overlap of bees in the ellipses of morphometrically defined morphoclusters.

A graph of the factor analysis of this enlarged data set revealed two morphoclusters: (1) colonies from the southern Western Cape and Eastern Cape Provinces formed one group; and (2) the remaining colonies forming another group. A stepwise discriminant analysis confirmed the separation of the two clusters and when confidence ellipses at the 90% level were calculated and plotted, bees from several localities either fell beyond the bounds of the ellipses or occupied the small area of overlap between the ellipses. All of these transitional bees were then interpreted as morphometrically defined "hybrids" with significantly higher values of morphometric variance than those bees of either morphocluster (Hepburn et al., 1998a). It was further noted that within the morphometrically defined clusters that morphometric variance was significantly greater at some localities within the same cluster than between clusters or even for some localities within the transitional zone.

During the course of publication of the above paper, additional, parallel studies were undertaken within South Africa using essentially the same data set as that of Hepburn et al. (1998a). New emphasis was directed on the mountain bees of the Drakensberg range in the Eastern Cape Province in the one instance (Steele et al., 1998) and on their continuance within the Kingdom of Lesotho on the other (Hepburn et al., 1998b; Radloff and Hepburn, 1999). The combined effects of these studies thus focused on that area of the Eastern Cape Province which contained many of the morphocluster-excluded transitional bees near the Drakensberg mountains in the report of Hepburn et al. (1998a) and the bees of Lesotho which had not been previously sampled. The interlocality distance resolution in sampling for both of these two adjacent areas was improved to 50 km. The Steele et al. (1998) study confirmed the occurrence of the morphometric transitional zone reported by Hepburn et al. (1998a) which was again confirmed by Radloff and Hepburn (1999). However, two additional morphometric investigations of the honeybees of the Lesotho mountains exposed another distinct morphocluster of mountain bees (Radloff and Hepburn, 1999; Hepburn et al., 2000) previously suspected on the basis of their aerodynamic properties (Hepburn et al., 1998b).

Piecing together the composite morphometric results obtained from about 9849 worker honeybees representing 497 colonies from 111 localities with an average interlocality sampling distance resolution of about 50 km, the current morphometrically defined distribution of subspecies of the honeybees of southern Africa consists of *A. m. capensis*, *A. m. scutellata* and a third *mountain* morphocluster in Lesotho (to which a formal scientific name has not been assigned). There is also a morphometric group of transitional bees that derive from the exclusion from or overlap between the confidence ellipses of other well-defined morphoclusters (Fig. 5).

Traditionally, the three morphoclusters obtained from the discriminant function analyses would be regarded as three subspecies: *A. m. capensis*, *A. m. scutellata*, and the unnamed Drakensberg *mountain* group. The "transitional" bees cannot be considered as "hybrids" in the strict genetic sense because the honeybee populations of southern Africa are entirely contiguous. If one is only concerned with morphometric definitions then three such subspecies can be unequivocally defined for southern Africa. But, because the multivariate approach is concerned with defining probability contours it is clearly of interest to probe more deeply into the variance characteristics of these different bee groups. For example, bees of the capensis morphocluster at Malmesbury are morphometrically significantly more variable than those 50 km away at Stellenbosch (localities 50 and 85 of Fig. 1); the same degree of difference occurs within the *scutellata* morphocluster group comparing variances from Hofmeyr and Sterkstroom (localities 35 and 86 of Fig. 1). Likewise, some *capensis* morphocluster localities (Swellendam, locality 90 of Fig. 1) have significantly higher morphometric variances than occur in the morphometrically transitional area (Touwsrivier locality 95 of Fig. 1). Clearly morphoclusters may contain variance domains larger than those in transitional areas, thus belying the notion of morphocluster homogeneity (Radloff et al., 2002).

2.7. Character incongruity

The relationships between the honeybees at those localities which constitute solely morphometrically defined morphoclusters with clusters derived from other biological characters are not at all congruous. To consider three reproductive traits amongst worker bees, one of the most striking points of discord concerns expression of DELW. A comparison of Figures 2 and 3 shows that, if solely morphometric definitions are used to define subspecies, then one obtains the following kinds of bee groups in southern Africa: (1) thelytokous *capensis*, (2) thelytokous transitional bees, (3) thelytokous *scutellata*, (4) arrhenotokous *scutellata* and (5) arrhenotokous *mountain bees*. Another reproductive characteristic, ovariole number, is admittedly higher in the *capensis* morphocluster area than elsewhere; but, it nonetheless remains significantly higher within the transitional zone than in both the thelytokous or the arrhenotokous *scutellata* areas. Moreover, there are significant differences between the ovariole number and female/male sex ratios of laying worker progeny among the morphometrically defined *capensis*, *scutellata* and transitional areas.

The geographical distributions of both the mtDNA and nuclear DNA profiles further reflect the lack of accord between morphocluster distribution and DNA distribution. One specific haplotype of mtDNA, "a1" extends several hundred kilometres beyond the limits of the *capensis* morphocluster well into morphometrically defined *scutellata* territory; and, just the reverse occurs for a haplotype within the *scutellata* area. Similarly, while the greatest heterogeneity in nuclear DNA centres on the morphometrically defined transitional area adjacent to all three morphocluster areas, greatest mtDNA diversity actually occurs to the north in the arrhenotokous *scutellata* area (Fig. 4).

Lastly, the summary statistics relating to variances of the morphometric and non-morphometric traits grouped according to morphoclusters (comprised of three categories and the transition zone bees) vis-a-vis modes of parthenogenesis (comprised of thelytoky and arrhenotoky) are compared (Tabs. I and II). In the first instance, there is a significant association between mode of parthenogenesis and morphocluster composition (Chi-square^2 = 52.87, 3 df, $P < 0.0001$). The mean morphometric variance is significantly higher in both the thelytoky cluster (Tab. II; t = 4.53, 108 df, $P < 0.0001$) and the *capensis* cluster and the transitional group (Tab. I; F = 3.39, 3,106 df, $P = 0.0253$). Also the incidence of significantly high morphometric variance domains is greatly increased in both the thelytoky cluster (Chi-square^2 = 6.29, 1 df, Fisher exact: $P = 0.0191$) and the transitional group (Chi-square^2 = 8.26, 3 df, $P = 0.0410$). In the case of ovariole numbers, the incidence of significantly high values shifts significantly towards the thelytoky cluster because thelytoky and high ovariole number are highly correlated (Chi-square^2 = 23.07, 1 df, Fisher exact: $P < 0.0001$).

Perhaps not surprising at all are the results obtained from comparisons of the morphoclusters (traditional subspecies) themselves. Obviously, the morphocluster approach yields *capensis*, *scutellata*, and *mountain* bees as traditionally defined as well as several transitional bees. On the other hand, within the two parthenogenetic groups, the thelytokous one contains those bees which are morphometric *capensis*, *scutellata* and transitional bees in a ratio of about 3:1:2. Pheromonal variances do not differ significantly within and between morphocluster or parthenogenetic cluster groups. The same applies to the more limited data on frequency variation in nuclear and mitochondrial DNA (Tabs. I and II). Thus these two features, pheromones and DNA, fluctuate entirely independently of the other traits.

3. CONCLUSIONS

The concatenation of the entire series of traits: morphological, reproductive, pheromonal and DNA reveals the structure of a highly complex, continuous population of honeybees in which gene frequencies vary from trait to trait, often over large distances and beyond any kind of statistically-defined cluster boundary that one might choose. The differences in allelic frequency distribution are simply not area-specific, nor do traits migrate in blocks. These complex patterns evoke fundamental questions. Do they result from random admixture and genetic drift? Or, are they products of some level of selection and local adaptations?

Unequivocal answers cannot yet be given, but *A. m. capensis, A. m. scutellata* and the transitional zone bees exhibit unexpectedly different propensities for and susceptibility to reciprocal colonial invasiveness (for biological details see Neumann et al., 2001; Calis et al., 2002; Martin et al., 2002; Moritz, 2002; Neumann and Hepburn, 2002; Pirk et al., 2002; Reece, 2002). Coupled with north-south oscillations of climate between decades within the transitional zone (Preston-Whyte and Tyson, 1988), the situation appears similar to "tension zones" in which clines are maintained by a balance between dispersal and selection against hybrids (Barton and Hewitt, 1985).

The inescapable conclusion is that although honeybees may be "frog-marched" into subspecific categories with formal trinomial scientific names (with the residual outliers being statistically "transitional" by definition and thus not within the ken of the International Rules of Zoological Nomenclature), these categories are of necessity artefactual and seriously obfuscate the biological ranges of naturally occurring characters. Such categories cannot be natural kinds because they have no unique properties (Locke, 1689; Kripke, 1972; Putnam, 1975). Alternatively, the honeybees of southern Africa can be further subdivided and refined into some 40-odd "groups" but this would merely further cloud what is after all a genetically continuous population. At present, the only way the term or name "*A. m. capensis*" (or *A. m. scutellata* for that matter) can be accurately meaningful is to precisely qualify a bee's geographical point of origin: this would then immediately inform us both of a particular honeybee's morphocluster membership, mode of worker parthenogenesis and other biological traits.

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We are grateful to R.M. Crewe, S. Fuchs, P. Kryger, P. Neumann and C.W.W. Pirk for reviewing this manuscript; and especially acknowledge the late Professor F. Ruttner who first stimulated us to examine the bees of this region some 15 years ago.

Résumé – *Apis mellifera capensis* : essai sur la classification subspécifique des abeilles domestiques. *Apis mellifera capensis* Escholtz présente un intérêt particulier car la parthénogenèse thélytoque des

ouvrières pondeuses donne naissance à une descendance femelle diploïde. Lors d'analyses multivariées faites sur les abeilles africaines, Ruttner (1975 et suivantes) a trouvé que les abeilles du Cap ne formaient pas un morphogroupe distinct et ne pouvaient pas être séparées avec précision d'autres sous-espèces plus distinctes sur des bases morphologiques. Par conséquent il a défini *A. m. capensis* d'après trois caractères particuliers aux ouvrières du Cap : la thélytoquie, le nombre élevé d'ovarioles et une spermathèque bien développée.

La répartition de la parthénogenèse thélytoque a été maintenant déterminée expérimentalement et se rencontre dans une aire d'environ 235 000 km^2 qui traverse les parties méridionales des Provinces du Cap orientale et occidentale (Fig. 2). Pourtant la thélytoquie n'est pas un phénomène « tout ou rien » et le rapport descendance femelle/descendance mâle (rapport F/M) des ouvrières suit une distribution clinale. Dans la partie la plus méridionale de la région côtière l'Afrique du Sud, le rapport F/M est effectivement de 1 200 km plus au nord le rapport F/M tombe à 0,75:0,25 ; encore 200 km plus loin le rapport est inversé 0,25:0,75 et encore plus au nord le rapport tombe finalement à 0:1. Le nombre d'ovarioles chez les ouvrières présente la même distribution. Le nombre d'ovarioles diminue d'ouest en est le long de la côte sud et aussi du sud vers le nord (Fig. 3). En ce qui concerne la taille de la spermathèque il n'y a pas de distribution cohérente ni à l'intérieur ni à travers la zone sensée être occupée par *A. m. capensis*.

Les ouvrières des deux Provinces du Cap, occidentale et orientale, sont capables de modifier le bouquet de la sécrétion des glandes mandibulaires du type ouvrière au type reine. Cela s'exprime régulièrement lorsqu'elles deviennent orphelines ou lorsqu'elles sont introduites dans des colonies d'une autre sous-espèce d'*A. mellifera*. Les glandes tergales abdominales des ouvrières de l'abeille du Cap sont également du type reine. Ces deux caractères sont absents chez *A. m. scutellata* vers le nord. De même le rapport 9ODA:10ODA est significativement plus grand chez les reines de l'abeille du Cap que chez les voisines situées au nord. Les données disponibles sont insuffisantes pour interpréter ces différences biogéographiques.

Les analyses de variation allozymique chez les abeilles d'Afrique du sud ont montré qu'elles étaient assez homogènes. Néanmoins les analyses d'ADNmt ont établi qu'une seule répétition-Q, ainsi qu'une autre séquence haplotype-QQQ, est absente de l'aire de thélytoquie ; au contraire l'haplotype-QQ se rencontre partout dans la province méridionale du Cap et diminue de façon clinale vers le nord (Fig. 4). Les analyses d'ADN nucléaire ont établi que la plus grande diversité allélique à la fois chez les reines et les mâles se rencontre dans une région considérée comme étant de transition d'un point de vue morphométrique entre les abeilles du Cap et les voisines situées au nord (Fig. 4).

Avec une amélioration énorme dans la résolution de la distance d'échantillonnage entre localités, il est devenu pour la première fois possible d'obtenir deux morphogroupes séparés d'abeilles d'Afrique du Sud. En outre, des analyses morphométriques encore plus détaillées, ont peut-être établi la présence dans le sud de l'Afrique de trois morphogroupes distincts : (i) les abeilles de la région méridionale du Cap, (ii) les abeilles du nord de l'Afrique du Sud et (iii) un groupe en montagne, les trois groupes convergeant dans une zone commune de transition définie du point de vue morphométrique (Fig. 5).

La principale difficulté pour assigner aux abeilles d'Afrique du Sud des limites significatives provient de l'incongruence de base entre les morphogroupes, les groupes biologiques (ouvrière reproductrice) et les groupes obtenus par les analyses d'ADNmt et d'ADN nucléaire. Le compromis le plus parcimonieux entre la morphométrie et la biologie de la reproduction fournirait cinq types d'abeilles pour la région : (i) *A. m.*

capensis thélytoque, (ii) abeilles thélytoques de transition, (iii) *A. m. scutellata* thélytoque, (iv) *A. m. scutellata* arrhénotoque et (v) abeilles des montagnes arrhénotoques. L'ensemble des caractères morphologiques, de reproduction, phéromonaux et d'ADN révèlent la structure d'une population d'abeilles hautement complexe et continue, dans laquelle les fréquences géniques varient d'un caractère à l'autre. Les différences de distribution dans les fréquences alléliques ne sont pas spécifiques à une région et le système trinominal de nomenclature ne peut s'en accommoder.

Actuellement le seul moyen pour que le nom d'*A. m. capensis* (ou d'*A. m. scutellata*) puisse avoir un sens est de qualifier précisément le lieu de son origine géographique au sein de l'Afrique du Sud. Ceci nous informe immédiatement de l'appartenance à un morphogroupe donné, du type de parthénogenèse des ouvrières et des autres caractères biologiques.

***Apis mellifera capensis* / *Apis mellifera scutellata* / classification / biogéographie / thélytoquie / Afrique du Sud**

Zusammenfassung – *Apis mellifera capensis*: Ein Essay zur subspezifischen Klassifikation von Honigbienen. *Apis mellifera capensis* Escholtz ist wegen ihrer thelytoken Parthenogenese von besonderem Interesse, durch die eierlegende Arbeiterinnen diploide weibliche Nachkommen erzeugen. Unter Anwendung von multivariaten Analysen auf afrikanischen Honigbienen zeigte Ruttner (1975 et seq.), dass die Kaphonigbienen keinen distinkten Morphokluster bilden und hierdurch morphologisch nicht eindeutig von anderen Subspezies abgegrenzt werden konnten. Als Folge definierte er *A. m. capensis* auf Grundlage von drei für Kaparbeiterinnen typischen Eigenschaften: Thelytokie, hohe Anzahl von Ovariolen und eine gut entwickelte Spermatheka.

Die Verbreitung der thelytoken Parthenogenese wurde zwischenzeitlich auf experimenteller Grundlage geklärt. Diese kommt in einem Gebiet von 235 000 km^2 vor, das sich über die südlichen Teile der westlichen und östlichen Kapprovinzen erstreckt (Abb. 2). Allerdings ist Thelytokie keine „alles oder nichts“ Erscheinung, sondern es besteht eine klinale Verteilung des Verhältnisses von Arbeiterinnen erzeugter weiblicher oder männlicher Nachkommen (F/M). In den südlichsten Teilen der Küstenregion von Südafrika ist das F/M Verhältnis effektiv 1:0. 200 km weiter nördlich fällt das F/M Verhältnis auf 0,75:0,25 ab, in weiteren 200 km ist es mit 0,25:0,75 umgekehrt, noch weiter nördlich erreicht es endlich 0:1. Auch die Ovariolenanzahlen zeigen ein klinales Verbreitungsmuster. Zum Einen nimmt die Ovariolenzahl entlang der südlichen Küste von Westen nach Osten ab, zum Anderen von Süden nach Norden (Abb. 3). Bezüglich der Spermathekalgröße besteht dagegen weder innerhalb noch über das angenommene Verbreitungsgebiet von *A. m. capensis* hinaus ein klares Muster.

Arbeiterinnen sowohl der westlichen als auch der östlichen Kapprovinz sind in der Lage, das Bouquet ihrer Mandibeldrüsen von arbeiterähnlich zu königinnenähnlich zu ändern. Dies tritt regelmäßig auf, sobald ihre Völker weisellos werden oder die Arbeiterinnen in Völker anderer Unterarten von *A. mellifera.* eingesetzt werden. Ebenso werden die abdominalen Tergaldrüsen der Arbeiterinnen königinnenähnlich. Diese beiden Charakterzüge fehlen bei der nördlicheren *A. m. scutellata*. Ähnlich ist das Verhältnis von 9ODA zu 10ODA bei den Kaphonigbienen signifikant größer als bei ihren nördlichen Nachbarn. Für eine biogeografische Deutung dieser Trends reichen die Daten bislang allerdings nicht aus.

Analysen allozymatischer Variation südafrikanischer Bienen haben gezeigt, dass diese relativ einheitlich sind. mtDNA Analysen dagegen zeigten, dass ein einzelnes Q-repeat sowie ein weiterer QQQ-Haplotyp im thelytoken Bienengebiet fehlt; wogegen der QQ-Haplotyp in der südlichen Kapprovinz überall vorkommt und nach Norden klinal abnimmt (Abb. 4). Analysen

nuklearer DNA zeigten, dass die höchste allelische Diversität sowohl bei Königinnen als auch bei Drohnen in einer morphometrisch definierten Übergangszone zwischen den Kapbienen und ihren nördlichen Nachbarn anzutreffen ist (Abb. 4).

Im Zuge einer bedeutenden Verbesserung der räumlichen Sammeldichte war es nun erstmalig möglich, zwei getrennte Morphokluster der südafrikanischen Bienen zu erhalten. Darüber hinaus belegten weitergehende morphometrische Analysen, dass im südlichen Afrika drei getrennte Morphokluster vorkommen: (1) die Bienen der südlichen Kapregion, (2) die Bienen des nördlichen Südafrika, und (3) eine Gruppe von Bergbienen. Alle drei treffen in einer gemeinsamen morphologisch definierten Übergangszone aufeinander (Abb. 5).

Das Hauptproblem bei der Zuweisung von bedeutungsvollen Grenzen zwischen den Bienen Südafrikas liegt in dem grundsätzlichen Problem der fehlenden Übereinstimmung zwischen morphometrischen Gruppen und biologischen Gruppen entsprechend der Reproduktion der Arbeiterinnen, sowie den Gruppierungen nach der mitochondrialen oder Kern DNA. Der sparsamste Kompromiss zwischen Morphometrie und Reproduktionsbiologie würde innerhalb der Region zu 5 verschiedenen Bienengruppen führen: (1) thelytoke *A. m. capensis*, (2) thelytoke Übergangsbienen, (3) thelytoke *A. m. scutellata*, (4) arrhenotoke *A. m. scutellata* und (5) arrhenotoke Bergbienen.

Der gesamte Satz von morphologischen, reproduktiven, pheromonalen sowie DNA Charakterzügen erschließt die Struktur einer hochkomplexen und kontinuierlichen Population von Honigbienen, wobei die Genhäufigkeiten zwischen den Eigenschaften variieren. Die Verbreitung der Allelhäufigkeiten ist nicht Gebietsspezifisch und kann durch das trinomische Nomenklatursystem nicht wiedergegeben werden. Zur Zeit ist der einzige Sinn, in dem die Namen *A. m. capensis* oder *A. m. scutellata* bedeutsam verwendet werden können, die genaue Bezeichnung der Lage der geographischen Entstehung innerhalb des südlichen Afrika. Diese wäre gleichzeitig informativ über den Status einer Biene bezüglich ihrer morphometrischen Clusterzugehörigkeit, ihren Modus von Arbeiterinnenreproduktion sowie ihrer anderen biologischen Eigenschaften.

***Apis mellifera capensis* / *A. m. scutellata* / Klassifikation / Biogeographie / Thelytokie**

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