Journal of Apicultural Research 16(3) : 131-142 (1977)

COMPARATIVE BIOMETRICAL INVESTIGATION ON DIPLOID DRONES OF THE HONEYBEE

I. THE HEAD *

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Manuscript received for publication 28 *June* 1976

Summary

Altogether 9815 measurements were made on the head and its parts in 269 haploid and 295 diploid drones, 109 queens, 248 and workers. All individuals originated from 12 queens of *Apis mellifera ligustica*, *A. m. adansonii*, their backcrosses and some hybrids.

The head, and all its parts and appendages measured, were larger in diploid drones than in haploid drones. But relationships with the same characters in queens and workers were different; some diploid drone characters were super-male, others were intersex, and others were caste characters.

Introduction

After a method of rearing diploid drones of *Apis mellifera* had been established (Woyke, 1969*a*), it was possible to make comparative studies on them. Preliminary measurements of morphological characters of approximately 300 diploid drones were presented by Woyke (1971*a*) at the 23rd International Beekeeping Congress, but the 6 tables submitted were unfortunately omitted from the published paper; the full details were, however, included in the final report for the USDA (Woyke, 1971*b*).

In 1967 Kerr and Nielsen had suggested that homozygous X/X males are more female-like than haploid males, but Woyke (1971*a*, 1971*b*) showed that diploid drones show many super-male characters. Exceptionally, the testes are much smaller (Woyke, 1973), the mean volume being commonly one-tenth that for haploid drones. But testes of diploid drones of *Apis mellifera adansonii* were comparatively larger, with a volume 0·2 to 0·5 of that for haploids originating from the same queens (Woyke, 1974). The number of chromosomes found in spermatocytes, and the DNA content in spermatids, were found to be twice as high in diploid drones as in haploids (Woyke, 1975).

Patches of diploid drone tissue in mosaic drones were described before diploid drones had been reared. Rothenbuhler (1957) found that the diameter of diploid facets in mosaic drones was approximately one-eighth greater than that in haploids, although this was not confirmed by Drescher and Rothenbuhler (1964).

Recently Chaud-Netto (1973, 1975) reported investigations on different characters of *Apis mellifera adansonii* diploid drones. Surprisingly, the characters of diploid drones determined by individual measurements, or by counts on 16-20 individuals (number of chromosomes, number of spermatozoa, weight of testes, number of hooks on the hind wing, etc.) fell into two separate groups, or into a dimodal distribution. Of the two groups (or modes) for diploid drones, one was typical for haploid drones.

Materials and Methods

Most bees investigated were reared in 1967-68 in the apiary of the Department of Genetics, University of São Paulo, Brazil, but the hybrids were reared in Poland. Table 1 shows

* This investigation was supported by a research grant from the Fundacão de Amparo á Pesquisa do Estado de São Paulo, Brazil, and from USDA authorized by Public Law 480.

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the total number of diploid and haploid drones, and of queens and workers, that were used; they all originated from 12 queens. Altogether, 295 diploid drones were investigated. Owing to injury, some characters were measured on 1 or 2 fewer individuals. A total of 9815 measurements of the head and its parts were made.

The following races and crosses were used:

1. *Apis mellifera adansonii*, all mother-queens being sisters mated to brothers;
2. *Apis mellifera ligustica*, all mother-queens being sisters mated to brothers;
3. backcross of Italian queens to drones from F_1 hybrid queens of the two above races (the mother-queens were sisters of the Italians, but two (125, 131) were mated to drones from one F_1 queen and the third (167) to drones from another one);
4. three hybrid queens, mated to their brothers, but not related to each other or to any other queen investigated.

Both backcrosses and hybrids are referred to in this paper as crosses between the different races.

Each queen was inseminated instrumentally with the semen of one drone only. Queen excluders were kept on hive entrances until the queen started to lay eggs, and usually for much longer.

Only queens producing brood of 50% survival rate were used for further investigations. Three queens of each combination were selected. Queens inseminated with semen of 1 drone only (1/8 to 1/10 of the normal amount in natural or instrumental insemination) may start by laying unfertilized eggs in worker cells, or otherwise do this much sooner than queens normally inseminated do. Therefore it was necessary to eliminate immediately any queen producing brood in worker cells that the bees sealed with drone cappings. If this was not done, haploid drones would be reared as diploids. The diploid drones were reared from larvae taken from worker cells by Woyke's method (1969*a*, 1969*b*).

The haploid drones, as well as queens and workers, were reared normally. Combs or cells were caged a few days before emergence of the adults, which were then killed and preserved in 70% alcohol. Before preservation, the newly emerged drones were dissected, and their diploidy verified by the small size of the testes. Later, measurements were made of the head and its parts (Fig. 1) with a micrometer eyepiece in a stereoscopic microscope.

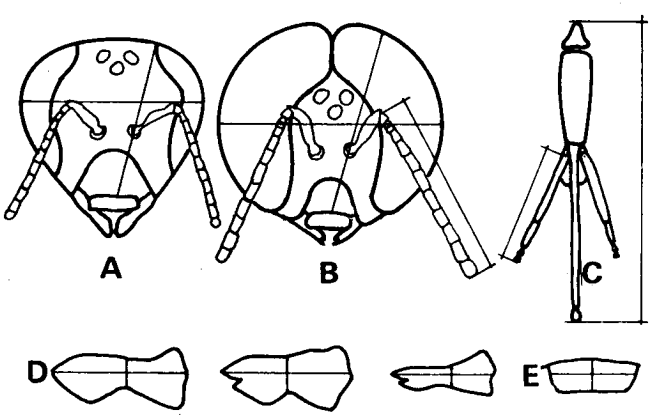

FIG. 1. Identification of characters measured.

Length and width of head shown in A (female) and B (male), also length of antennal flagellum. Length of labium and of labial palp shown in C. Length and width of mandibles shown in D (*left to right* : worker, queen, drone), and of labrum in E.

The insects were not boiled before being fixed (because the reproductive organs would also be studied), and therefore the length of the labium can be compared only within the material investigated, and not with measurements on specimens prepared by other methods.

Student's t-test was applied to find statistically significant differences between means. The following designations are used in the Tables: *se*, standard error of the mean; o, no statistical difference; x, $P < 0{\cdot}05$, i.e. significant; xx, $P < 0{\cdot}01$, i.e., highly significant; xxx, $P < 0{\cdot}001$, i.e. very highly significant. Different letters against two means indicate that they are significantly different.

Results

Fig. 2 represents a diploid drone. It looks slightly larger and more stocky, and it has a larger head, then the familiar haploid drone.

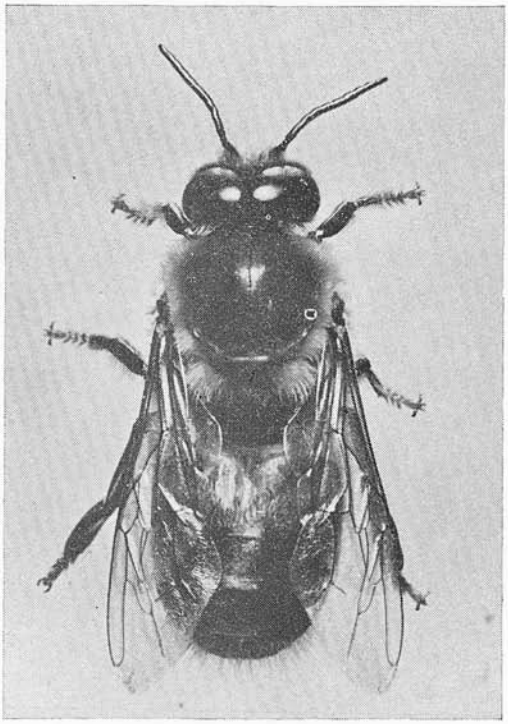

FIG. 2. Diploid drone honeybee (*Apis mellifera*) about 4×.

Table 2 and Table 3 show that the mean length and width of the head were once larger in queens and once in workers. The overall average length was almost identical for queens and workers, the width greater for queens. Both types of drone had a head larger than the female head. The head was significantly larger in diploid than in haploid drones originating from all queens except one hybrid. The larger head of the diploid drone is one of the characters by which it can be distinguished from the haploid drone, often visually. The diploid drone head thus showed a super-male character.

TABLE 1. Numbers of bees measured.

Race	*Queen no.*	*Diploid drones*	*Haploid drones*	*Queens*	*Workers*
African	128	25	23	8	8
	141	25	25	12	25
	146	24	25	12	25
Italian	144	25	25	2	8
	154	23	—	15	25
	155	23	25	—	7
Backcross	125	25	25	15	25
	131	25	25	13	25
	167	25	25	11	25
Hybrids	273	25	21	—	25
	439	25	25	9	25
	582	25	25	12	25
Total		295	269	109	248

The diameter of middle ocellus of the queen was mostly larger than that of the worker (Table 4), but the difference was not statistically significant. Ocelli of both types of drone were much larger than those of the females, and the mean diameters were always larger in diploid than in haploid drones, but differences between only 5 of 11 pairs of means were significant. The overall mean diameter of ocelli of diploid drones was highly significantly greater than that of haploids.

In the compound eye, the mean size of the facets (estimated from the sum of the length of 10 facets) was always greater in the queen than in the worker (Table 5). Facets were almost twice as long in both types of drone as in the females. Facets of diploid drones originating from all the queens were very highly significantly larger than those of haploid drones. The length of diploid facets was on average 1·12 that of haploids (1/8 longer). This character is quite useful for distinguishing haploid from diploid drones: in all the drones, very few values overlapped, and these were for drones originating from two queens only. The mean range of the length of 10 facets was mostly 0·339—0·433 mm in haploids and 0·440—0·500 mm in diploids.

The average length of the antennal flagellum was greater in all worker groups than in the corresponding queen groups (Table 6). The overall mean was very highly significantly greater for workers than for queens. Thus a shorter flagellum is characteristic of the female better developed sexually. In both types of drone the flagellum was almost 1·5 times as long as in the females. In one backcross and one hybrid cross the flagellum of diploid drones was significantly shorter than that of haploids. But in all other groups, either there was no significant difference between the two groups, or diploids had a significantly longer antennal flagellum than haploids.

Tables 7 and 8 show that the labrum of queens was longer and wider than that of workers. It was smaller in both types of drone than in females. But the diploid drones had a significantly longer labrum than the haploids, in all except two crosses (queens 167, 273), where the differences were not significant. The mean width of the labrum was significantly greater in diploid drones than in haploids (or there was no significant difference). No mean width significantly smaller in diploid than in haploid drones was found. So the size of the labrum of diploid drones was between the small labrum of haploid drones and the large female labrum: it shows an intersex character.

TABLE 2. Length of head (mm) of diploid and haploid drones, and of queens and workers.

In this and subsequent Tables, *se* = standard error of mean; o = difference not statistically significant; x = $P<0{\cdot}05$, xx = $P<0{\cdot}01$, xxx = $P<0{\cdot}001$; different letters before overall means signify that the differences between them are significant.

Race	Queen no.	Diploid drones	Haploid drones	Difference Dip−Hap	Queens	Workers
		Mean ± se	Mean ± se		Mean ± se	Mean ± se
African	128	4·00 ± 0·017	3·92 ± 0·017	0·08 xx	3·31 ± 0·042	3·55 ± 0·020
	141	4·10 ± 0·022	3·90 ± 0·016	0·20 xxx	3·31 ± 0·029	3·14 ± 0·023
	146	4·00 ± 0·016	3·71 ± 0·017	0·29 xxx	3·32 ± 0·029	3·27 ± 0·013
Italian	144	4·10 ± 0·019	3·92 ± 0·016	0·18 xxx	3·35 ± 0·062	3·44 ± 0·047
	154	4·07 ± 0·015	— —	—	3·22 ± 0·035	3·33 ± 0·032
	155	4·06 ± 0·028	3·85 ± 0·016	0·21 xxx	— —	3·27 ± 0·027
Backcross	125	3·94 ± 0·025	3·69 ± 0·023	0·25 xxx	3·34 ± 0·023	3·24 ± 0·009
	131	4·02 ± 0·019	3·74 ± 0·020	0·28 xxx	2·24 ± 0·023	3·25 ± 0·017
	167	3·98 ± 0·028	3·89 ± 0·014	0·09 xx	3·40 ± 0·030	3·08 ± 0·026
Hybrid	273	3·68 ± 0·030	3·62 ± 0·022	0·06 o	— —	3·35 ± 0·008
	439	3·98 ± 0·015	3·78 ± 0·023	0·20 xxx	3·23 ± 0·032	3·34 ± 0·013
	582	3·79 ± 0·014	3·68 ± 0·029	0·11 xx	3·22 ± 0·032	3·31 ± 0·014
Overall mean		*a*3·98 ± 0·009	*b*3·79 ± 0·009	0·19 xxx	*c*3·29 ± 0·011	*c*3·30 ± 0·009

TABLE 3. Width of head (mm) of diploid and haploid drones, and of queens and workers. See Table 2 for symbols.

African	128	4·56 ± 0·021	4·42 ± 0·011	0·14 xxx	3·87 ± 0·047	3·97 ± 0·015
	141	4·63 ± 0·018	4·44 ± 0·012	0·19 xxx	3·91 ± 0·030	3·78 ± 0·015
	146	4·54 ± 0·015	4·21 ± 0·027	0·33 xxx	3·86 ± 0·022	3·75 ± 0·016
Italian	144	4·55 ± 0·017	4·43 ± 0·013	0·12 xxx	3·83 ± 0·049	3·88 ± 0·039
	154	4·58 ± 0·021	— —	—	3·81 ± 0·026	3·82 ± 0·020
	155	4·50 ± 0·018	4·27 ± 0·022	0·23 xxx	— —	3·77 ± 0·022
Backcross	125	4·39 ± 0·023	4·19 ± 0·021	0·20 xxx	3·75 ± 0·021	3·64 ± 0·009
	131	4·51 ± 0·017	4·24 ± 0·017	0·27 xxx	3·77 ± 0·012	3·64 ± 0·013
	167	4·44 ± 0·030	4·32 ± 0·018	0·12 xx	3·92 ± 0·015	3·67 ± 0·011
Hybrid	273	4·35 ± 0·020	4·39 ± 0·022	−0·04 o	— —	3·76 ± 0·008
	439	4·43 ± 0·013	4·36 ± 0·015	0·07 xxx	3·85 ± 0·016	3·78 ± 0·017
	582	4·54 ± 0·031	4·39 ± 0·033	0·15 xx	3·77 ± 0·025	3·78 ± 0·012
Overall mean		*a*4·50 ± 0·008	*b*4·33 ± 0·008	0·17 xxx	*c*3·83 ± 0·009	*d*3·77 ± 0·007

TABLE 4. Diameter of middle ocellus (mm) of diploid and haploid drones, and of queen and workers. See Table 2 for symbols.

Race	Queen no.	Diploid drones Mean ± se	Haploid drones Mean ± se	Difference Dip−Hap	Queens Mean ± se	Workers Mean ± se
African	128	0·341 ± 0·0012	0·331 ± 0·0008	0·010 xxx	0·272 ± 0·0021	0·268 ± 0·0018
	141	0·338 ± 0·0012	0·336 ± 0·0010	0·002 o	0·271 ± 0·0015	0·267 ± 0·0008
	146	0·337 ± 0·0010	0·330 ± 0·0009	0·007 xxx	0·267 ± 0·0010	0·265 ± 0·0008
Italian	144	0·331 ± 0·0019	0·330 ± 0·0005	0·001 o	0·264 ± 0·0000	0·264 ± 0·0000
	154	0·332 ± 0·0007	— —	—	0·265 ± 0·0009	0·266 ± 0·0006
	155	0·330 ± 0·0008	0·330 ± 0·0006	0·000 o	— —	0·266 ± 0·0014
Backcross	125	0·326 ± 0·0009	0·325 ± 0·0009	0·001 o	0·266 ± 0·0010	0·257 ± 0·0011
	131	0·331 ± 0·0006	0·322 ± 0·0014	0·009 xxx	0·266 ± 0·0012	0·256 ± 0·0010
	167	0·331 ± 0·0008	0·325 ± 0 0009	0·006 xxx	0·266 ± 0·0014	0·256 ± 0·0011
Hybrids	273	0·329 ± 0·0010	0·329 ± 0·0009	0·000 o	— —	0·258 ± 0·0014
	439	0·321 ± 0·0012	0·324 ± 0·0013	0·003 o	0·258 ± 0·0013	0·255 ± 0·0016
	582	0·328 ± 0·0008	0·332 ± 0·0009	0·004 xx	0·258 ± 0·0013	0·262 ± 0·0008
Overall mean		*a*0·332 ± 0·0007	*b*0·328 ± 0·0008	0·004 xx	*c*0·265 ± 0·0012	*c*0·261 ± 0·0009

TABLE 5. Mean length of 10 facets of the compound eye (mm) of diploid and haploid drones, and of queens and workers. See Table 2 for symbols.

African	128	0·424 ± 0·0030	0·399 ± 0·0028	0·025 xxx	0·246 ± 0·0039	0·244 ± 0·0018
	141	0·445 ± 0·0020	0·417 ± 0·0019	0·028 xxx	0·241 ± 0·0024	0·231 ± p·0013
	146	0·458 ± 0·0014	0·417 ± 0·0018	0·041 xxx	0·248 ± 0·0015	0·231 ± 0·0013
Italian	144	0·458 ± 0·0010	0·421 ± 0·0010	0·037 xxx	0·261 ± 0·0033	0·244 ± 0·0022
	154	0·487 ± 0·0008	— —	—	0·260 ± 0·0022	0·254 ± 0·0007
	155	0·486 ± 0·0008	0·421 ± 0·0009	0·065 xxx	— —	0·248 ± 0·0014
Backcross	125	0·473 ± 0·0018	0·408 ± 0·0014	0·065 xxx	0·255 ± 0·0017	0·249 ± 0·0015
	131	0·464 ± 0·0027	0·412 ± 0·0017	0·052 xxx	0·252 ± 0·0014	0·248 ± 0·0014
	157	0·468 ± 0·0026	0·410 ± 0·0015	0·058 xxx	0·254 ± 0·0017	0·247 ± 0·0012
Hybrids	273	0·460 ± 0·0055	0·416 ± 0·0027	0·044 xxx	— —	0·255 ± 0·0021
	439	0·489 ± 0·0014	0·444 ± 0·0014	0·045 xxx	0·257 ± 0·0021	0·244 ± 0·0016
	582	0·463 ± 0·0040	0·414 ± 0·0017	0·049 xxx	0·250 ± 0·0020	0·248 ± 0·0010
Overall mean		*a*0·466 ± 0·0026	*b*0·416 ± 0·0016	0·05 xxx	*c*0·251 ± 0·0019	*d*0·245 ± 0·0015

TABLE 6. Length of antennal flagellum (mm) of diploid and haploid drones, and of queens and workers. See Table 2 for symbols.

Race	Queen no.	Diploid drones	Haploid drones	Difference Dip−Hap	Queens	Workers
		Mean ± se	Mean ± se		Mean ± se	Mean ± se
African	128	4·34 ± 0·024	4·33 ± 0·025	0·01 o	2·86 ± 0·022	3·07 ± 0·010
	141	4·50 ± 0·022	4·40 ± 0·020	0·10 xx	2·93 ± 0·014	3·01 ± 0·010
	146	4·48 ± 0·016	4·30 ± 0·027	0·18 xxx	2·89 ± 0·011	3·01 ± 0·015
Italian	144	4·35 ± 0·029	4·37 ± 0·019	−0·02 o	2·93 ± 0·063	3·05 ± 0·017
	154	4·37 ± 0·015	— —	—	2·87 ± 0·036	3·02 ± 0·018
	155	4·42 ± 0·027	4·28 ± 0·029	0·14 xxx	— —	3·08 ± 0·013
Backcross	125	4·27 ± 0·023	4·18 ± 0·025	0·09 x	2·87 ± 0·011	3·01 ± 0·007
	131	4·25 ± 0·026	4·23 ± 0·026	0·02 o	2·92 ± 0·021	2·99 ± 0·006
	167	4·28 ± 0·028	4·36 ± 0·019	−0·08 x	2·99 ± 0·022	3·02 ± 0·010
Hybrids	273	4·38 ± 0·023	4·41 ± 0·023	−0·03 o	— —	3·14 ± 0·013
	439	4·24 ± 0·016	4·38 ± 0·017	−0·14 xxx	3·01 ± 0·024	3·02 ± 0·010
	582	4·47 ± 0·013	4·46 ± 0·016	0·01 o	2·87 ± 0·017	3·02 ± 0·008
Overall mean		*a*4·36 ± 0·008	*b*4·34 ± 0·008	0·02 xxx	*c*2·92 ± 0·008	*d*3·04 ± 0·004

TABLE 7. Length of labrum (mm) of diploid and haploid drones, and of queens and workers. See Table 2 for symbols.

African	128	0·999 ± 0·009	0·945 ± 0·008	0·054 xxx	1·225 ± 0·018	1·192 ± 0·011
	141	0·999 ± 0·009	0·933 ± 0·007	0·066 xxx	1·240 ± 0·006	1·091 ± 0·006
	146	0·982 ± 0·008	0·901 ± 0·009	0·081 xxx	1·224 ± 0·010	1·057 ± 0·010
Italian	144	1·041 ± 0·011	0·997 ± 0·006	0·044 xx	1·246 ± 0·035	1·163 ± 0·014
	154	1·038 ± 0·007	— —	—	1·173 ± 0·012	1·177 ± 0·009
	155	1·011 ± 0·012	0·930 ± 0·007	0·081 xxx	— —	1·108 ± 0·016
Backcross	125	0·986 ± 0·010	0·924 ± 0·008	0·062 xxx	1·202 ± 0·007	1·103 ± 0·004
	131	0·964 ± 0·011	0·908 ± 0·006	0·056 xxx	1·220 ± 0·006	1·115 ± 0·004
	167	0·949 ± 0·009	0·956 ± 0·009	−0·007 o	1·196 ± 0·009	1·072 ± 0·004
Hybrids	273	0·952 ± 0·009	0·934 ± 0·006	0·018 o	— —	1·093 ± 0·006
	439	0·989 ± 0·007	0·959 ± 0·009	0·030 x	1·167 ± 0·012	1·120 ± 0·004
	582	1·146 ± 0·009	1·099 ± 0·015	0·047 xx	1·194 ± 0·010	1·090 ± 0·005
Overall mean		*a*1·003 ± 0·0042	*b*0·955 ± 0·0041	0·040 xxx	*c*1·202 ± 0·0043	*d*1·102 ± 0·003

TABLE 8. Width of labrum (mm) of diploid and haploid drones, and of queens and workers. See Table 2 for symbols.

Race	Queen no.	Diploid drones	Haploid drones	Difference Dip − Hap	Queens	Workers
		Mean ± se	Mean ± se		Mean ± se	Mean ± se
African	128	0·336 ± 0·0051	0·322 ± 0·0044	0·014 x	0·345 ± 0·008	0·324 ± 0·005
	141	0·333 ± 0·0026	0·308 ± 0·0038	0·025 xxx	0·398 ± 0·006	0·335 ± 0·004
	146	0·324 ± 0·0050	0·292 ± 0·0044	0·032 xxx	0·385 ± 0·010	0·347 ± 0·003
Italian	144	0·296 ± 0·0042	0·298 ± 0·0039	−0·002 o	0·296 ± 0·014	0·308 ± 0·008
	154	0·309 ± 0·0047	— —	—	0·348 ± 0·005	0·341 ± 0·004
	155	0·312 ± 0·0046	0·297 ± 0·0036	0·015 x	— —	0·332 ± 0·007
Backcross	125	0·293 ± 0·0023	0·286 ± 0·0021	0·007 x	0·298 ± 0·006	0·331 ± 0·003
	131	0·309 ± 0·0051	0·289 ± 0·0031	0·020 xx	0·352 ± 0·009	0·332 ± 0·002
	167	0·292 ± 0·0042	0·298 ± 0·0046	−0·006 o	0·340 ± 0·010	0·324 ± 0·004
Hybrids	273	0·313 ± 0·0043	0·311 ± 0·0052	0·002 o	— —	0·354 ± 0·003
	439	0·318 ± 0·0033	0·322 ± 0·0052	−0·004 o	0·302 ± 0·007	0·332 ± 0·004
	582	0·292 ± 0·0040	0·297 ± 0·0055	−0·005 o	0·361 ± 0·007	0·336 ± 0·002
Overall mean		*a*0·311 ± 0·0015	*b*0·302 ± 0·0014	0·009 xxx	*c*0·343 ± 0·0037	*d*0·333 ± 0·001

TABLE 9. Length of mandibles (mm) of diploid and haploid drones, and of queens and workers. See Table 2 for symbols.

African	128	1·05 ± 0·007	1·02 ± 0·007	0·03 xx	1·23 ± 0·016	1·41 ± 0·004
	141	1·05 ± 0·006	1·01 ± 0·004	0·04 xxx	1·26 ± 0·009	1·29 ± 0·005
	146	1·06 ± 0·006	1·00 ± 0·009	0·06 xxx	1·25 ± 0·010	1·32 ± 0·004
Italian	144	1·06 ± 0·006	0·99 ± 0·007	0·07 xxx	1·25 ± 0·000	1·40 ± 0·017
	154	1·06 ± 0·008	— —	—	1·19 ± 0·014	1·37 ± 0·009
	155	1·04 ± 0·007	0·99 ± 0·007	0·05 xxx	— —	1·34 ± 0·012
Backcross	125	1·04 ± 0·006	0·99 ± 0·003	0·05 xxx	1·30 ± 0·008	1·32 ± 0·006
	131	1·06 ± 0·008	0·99 ± 0·006	0·07 xxx	1·29 ± 0·014	1·35 ± 0·005
	167	1·06 ± 0·008	1·05 ± 0·007	0·01 o	1·29 ± 0·008	1·35 ± 0·005
Hybrids	273	1·08 ± 0·007	1·07 ± 0·008	0·01 o	— —	1·39 ± 0·005
	439	1·09 ± 0·005	1·08 ± 0·006	0·01 o	1·26 ± 0·013	1·37 ± 0·006
	582	1·04 ± 0·006	1·07 ± 0·005	−0·03 xxx	1·23 ± 0·012	1·37 ± 0·003
Overall mean		*a*1·06 ± 0·002	*b*1·02 ± 0·003	0·04 xxx	*c*1·26 ± 0·005	*d*1·36 ± 0·003

TABLE 10. Width of mandibles (mm) of diploid and haploid drones, and of queens and workers. See Table 2 for symbols.

Race	Queen no.	Diploid drones	Haploid drones	Difference Dip−Hap	Queens	Workers
		Mean ± se	Mean ± se		Mean ± se	Mean ± se
African	128	0·215 ± 0·005	0·199 ± 0·004	0·016 x	0·400 ± 0·009	0·322 ± 0·003
	141	0·224 ± 0·004	0·216 ± 0·004	0·008 o	0·423 ± 0·008	0·315 ± 0·005
	146	0·200 ± 0·005	0·192 ± 0·004	0·008 o	0·435 ± 0·009	0·296 ± 0·003
Italian	144	0·218 ± 0·004	0·205 ± 0·004	0·013 x	0·388 ± 0·013	0·297 ± 0·006
	154	0·200 ± 0·004	— —	—	0·389 ± 0·009	0·288 ± 0·005
	155	0·209 ± 0·004	0·189 ± 0·003	0·020 xxx	— —	0·304 ± 0·008
Backcross	125	0·196 ± 0·002	0·196 ± 0·003	0·000 o	0·392 ± 0·003	0·282 ± 0·003
	131	0·217 ± 0·005	0·198 ± 0·004	0·019 xx	0·388 ± 0·006	0·305 ± 0·006
	167	0·214 ± 0·005	0·215 ± 0·004	−0·001 o	0·386 ± 0·004	0·304 ± 0·003
Hybrids	273	0·224 ± 0·005	0·228 ± 0·004	−0·004 o	— —	0·313 ± 0·004
	439	0·234 ± 0·004	0·207 ± 0·003	0·027 xxx	0·456 ± 0·013	0·306 ± 0·004
	582	0·240 ± 0·005	0·247 ± 0·004	0·007 o	0·440 ± 0·010	0·317 ± 0·003
Overall mean		*a*0·216 ± 0·001	*b*0·208 ± 0·001	0·008 xxx	*c*0·410 ± 0·004	*d*0·304 ± 0·001

TABLE 11. Length of labium (mm) of diploid and haploid drones, and of queens and workers. See Table 2 for symbols.

African	128	4·03 ± 0·044	3·78 ± 0·064	0·25 xx	3·70 ± 0·091	5·95 ± 0·025
	141	3·93 ± 0·075	3·56 ± 0·082	9·37 xx	3·88 ± 0·074	5·96 ± 0·034
	146	3·98 ± 0·023	3·58 ± 0·039	0·40 xxx	3·78 ± 0·043	5·87 ± 0·037
Italian	144	4·25 ± 0·047	3·84 ± 0·072	0·41 xxx	3·88 ± 0·049	6·45 ± 0·222
	154	4·16 ± 0·033	— —	—	3·79 ± 0·046	6·31 ± 0·057
	155	4·18 ± 0·044	3·45 ± 0·081	0·73 xxx	— —	— —
Backcross	125	4·14 ± 0·034	3·83 ± 0·040	0·31 xxx	3·94 ± 0·041	6·09 ± 0·045
	131	4·05 ± 0·050	3·78 ± 0·040	0·27 xxx	3·77 ± 0·098	6·12 ± 0·022
	167	3·92 ± 0·068	3·96 ± 0·057	−0·04 o	3·40 ± 0·036	6·22 ± 0·048
Hybrids	273	3·91 ± 0·048	3·98 ± 0·041	−0·07 o	— —	5·94 ± 0·038
	439	4·35 ± 0·062	3·75 ± 0·080	0·60 xxx	3·71 ± 0·123	6·00 ± 0·093
	582	3·84 ± 0·044	3·80 ± 0·043	0·04 o	3·60 ± 0·058	6·07 ± 0·027
Overall mean		*a*4·06 ± 0·017	*b*3·75 ± 0·021	0·31 xxx	*b*3·73 ± 0·030	*c*6·08 ± 0·019

TABLE 12. Length of labial palpus (mm) of diploid and haploid drones, and of queens and workers. See Table 2 for symbols.

Race	Queen no.	Diploid drones	Haploid drones	Difference Dip−Hap	Queens	Workers
		Mean ± se	Mean ± se		Mean ± se	Mean ± se
African	128	1·80 ± 0·015	1·71 ± 0·029	0·09 xx	1·54 ± 0·031	2·46 ± 0·035
	141	1·85 ± 0·013	1·69 ± 0·020	0·16 xxx	1·52 ± 0·016	2·38 ± 0·011
	146	1·80 ± 0·013	1·69 ± 0·017	0·11 xxx	1·47 ± 0·018	2·44 ± 0·008
Italian	144	1·82 ± 0·015	1·72 ± 0·016	0·10 xxx	1·48 ± 0·000	2·40 ± 0·006
	154	1·77 ± 0·009	— —	—	1·49 ± 0·018	2·39 ± 0·015
	155	1·85 ± 0·020	1·67 ± 0·019	0·18 xxx	— —	— —
Backcross	125	1·79 ± 0·019	1·66 ± 0·013	0·13 xxx	1·53 ± 0·017	2·42 ± 0·009
	131	1·72 ± 0·017	1·64 ± 0·015	0·12 xxx	1·47 ± 0·018	2·37 ± 0·008
	167	1·77 ± 0·022	1·78 ± 0·018	−0·01 o	1·56 ± 0·011	2·43 ± 0·008
Hybrids	273	1·76 ± 0·020	1·81 ± 0·016	−0·05 o	— —	2·53 ± 0·005
	439	1·94 ± 0·013	1·72 ± 0·022	0·22 xxx	1·62 ± 0·013	2·48 ± 0·015
	582	1·78 ± 0·015	1·75 ± 0·013	0·03 o	1·55 ± 0·016	2·47 ± 0·009
Overall mean		*a*1·81 ± 0·006	*b*1·71 ± 0·006	0·09 xxx	*c*1·52 ± 0·007	*d*2·43 ± 0·005

TABLE 13. Size (mm) of different head parts of haploid (H) and diploid (D) drones and of queens (Q) and workers (W), arranged in increasing sequence.

Head part	Smallest	Larger		Largest	D character
Length of head	Q 3·29	W 3·30	H 3·79	D 3·98	super-male
Width of head	W 3·77	Q 3·83	H 4·33	D 4·50	super-male
Diameter of middle ocellus	W 0·261	Q 0·265	H 0·328	D 0·332	super-male
Length of 10 facets	W 0·245	Q 0·251	H 0·416	D 0·466	super-male
Length of antennal flagellum	Q 2·92	W 3·04	H 4·34	D 4·36	super-male
Length of labrum	H 0·955	D 1·003	W 1·102	Q 1·202	intersex
Width of labrum	H 0·302	D 0·311	W 0·333	Q 0·343	intersex
Length of mandibles	H 1·02	D 1·06	Q 1·26	W 1·36	intersex
Width of mandibles	H 0·208	D 0·216	W 0·304	Q 0·410	intersex
Length of labium	Q 3·73	H 3·75	D 4·06	W 6·08	caste
Length of labial palpus	Q 1·52	H 1·71	D 1·81	W 2·43	caste

Queen mandibles were shorter but very highly significantly wider than those of workers (Table 9, Table 10); both types of drone had smaller mandibles than the females. The mean length for diploid drones was significantly lower than that for haploids in one hybrid cross only. In diploids of pure race, and of some crosses, all mean lengths were highly significantly greater than in haploids. The mandibles were significantly wider in diploids than in haploids, or there was no significant difference between them. The overall mean length and width of mandibles were significantly greater in diploids than in haploids. So mandible size in diploid drones also shows an intersex character.

The lengths of the labium and the labial palp are highly correlated; both are about 1·6 times as great in workers as in queens (Table 11, Table 12). Both averages were highly significantly greater in diploid drones than in haploids (in all groups except three crosses of different races where there was no significant difference). The overall mean lengths of the labium and labial palp were very highly significantly greater in diploid drones than in haploids. The most interesting result, however, is that the lengths of the labium and the labial palp in both types of drone were intermediate between the lengths in the queen and in the worker. The mean lengths found in haploid drones are closer to those in the queen, and those in diploid drones are closer to those in the worker. In this respect, the diploid drone shows a caste-like character.

Discussion and Conclusions

Results are summarized in Table 13. The head and its parts and appendages were larger in diploid than in haploid drones, but their dimensions bore different relationships to those in the queen and worker:

(*a*) For the size of the head and of its parts, including the antennal flagellum, the sequence (in increasing size) was Q/W, H, D: diploid drones thus showed super-male characters.

(*b*) For the size of the upper mouthparts (labrum, mandibles) the sequence was H, D, Q/W; diploid drones showed an intersex character.

(*c*) For the length of lower mouthparts (labium, labial palp), the sequence was Q, H, D, W ; the diploid drone was closer to the worker, and the haploid drone closer to the queen: the drones showed caste characters.

All three types of character (super-male, intersex, caste) were thus found in the head of the diploid drone.

Of the characters studied in this paper, three were investigated by Chaud-Netto (1973, 1975). For length and width of head, he found no significant difference between haploid and diploid drones, whereas the results reported here show highly significant differences between all groups of haploid and diploid drones. He found a significantly shorter antennal flagellum in diploid than in haploid drones, whereas here the diploid antennal flagellum was found to be the same as, or highly significantly longer than, that in the haploid drone. Characters of the head of diploid and possibly triploid workers were found by Chaud-Netto to be similar to or much smaller than those of diploid workers originating from 3 sister *A. m. adansonii* queens. The antennal flagellum of possibly triploid workers, which are considered to be more masculinized, was significantly shorter than that of diploid workers. But in the honeybee a shorter antenna signifies feminization, not masculinization. There are thus significant differences between the results presented by Chaud-Netto (1973, 1975) and Woyke (1971*a*, 1971*b*) and in the present paper, although the investigations used the same material in the same apiary. A possible explanation of these differences will be put forward in the final paper of the present series, after further data have been presented.

Acknowledgements

I would like to thank Professor W. E. Kerr for providing me with the facilities for conducting this investigation in his Department in Brazil. I thank also Dr. L. Gonçalves for the use of some of his Africanized and Italian queens.

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