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REPRODUCTIVE ORGANS OF HAPLOID AND DIPLOID DRONE HONEYBEES*

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Summary

Altogether 301 haploid and 428 diploid drones originating from 33 queens were reared. More than 9500 measurements or counts were made on different reproductive organs of these drones, which were killed on their first day of adult life.

The mean length of the testes of haploid drones varied from 4·61 to 5·45 mm, and the mean volume from 10·16 to 14·27 mm^3. Significant differences were found between different parts of reproductive organs of haploid drones originating from different queens.

The testes of diploid drones are surrounded by well developed fatty tissue. The mean length of testes of diploid drones originating from different queens varied from 1·81 to 3·44 mm, and the volume from 1·00 to 4·16 mm^3; the variations in diploid drones were thus much greater than in the haploids. The mean testes volume of haploid drones from a given queen was commonly 10 times as great as that of diploid drones from the same queen. The diploids had about half as many of testicular tubules as the haploids, and their vesiculae seminales and mucus glands were 85–95 % the size of those of the haploids. No consistent differences were found between the sclerotized plates of the reproductive systems of haploid and diploid drones.

The mean dimensions of various reproductive organs of diploid drones originating from different queens differed significantly. The small size of the testes of diploid drones, one of the factors that make it difficult to collect their semen, might therefore be ameliorated by selective breeding.

Introduction

After the method of rearing diploid drones had been worked out (Woyke, 1969) and adult diploid drones reared, the most important problem outstanding was to obtain offspring of these drones. However, some difficulties were encountered in collecting the semen, and therefore the investigation described here was carried out. The reproductive organs of haploid and diploid drones have been compared, and the variability of these organs assessed in additional groups of haploid and diploid drones originating from different queens. Comparisons between different races will be reported and discussed later (Woyke, 1973).

The reproductive organs of haploid drones were described by Swammerdam (1737) and Réaumur (1740), and later by Siebold (1854), Leuckart (1855, 1868, 1885) and Girdwoyń (1875, 1876); a detailed study was also made by Arnhart (1937). Their development was described by Michaelis (1900) and Zander (1916), and their histology by Kozhevnikov (1891*a*, 1891*b*), Bishop (1920) and Woyke (1958*a*). Bishop also described changes in these organs during the pupal and imaginal stages. The functioning of the endophallus was studied by Woyke (1958*b*), and Woyke and Ruttner (1958). Our present knowledge concerning the reproductive organs of haploid drones is based chiefly on descriptions in books by Snodgrass (1910, 1956) and Zander (1911, 1951).

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A preliminary report on the reproductive organs of diploid drones was given by Woyke (1965*a*, 1965*b*).

Materials and Methods

The drones were reared from 33 queens, 23 of which produced diploid drones. Altogether 729 drones were investigated, 428 of which were diploids. More than 1000 testes, and about the same number of vesiculae seminales and mucus glands were measured; smaller numbers of other parts of the reproductive organs were measured. A total of more than 9500 measurements or counts were made. Different races of the honeybee *Apis mellifera* were used, as follows: *carnica* (C), *caucasica* (Ca), *ligustica* (L), *adansonii* (A), *mellifera* (M), *carnica* × *fasciata* (CF).

The haploid drones were reared normally in colonies, and the diploids by the method developed in this laboratory (Woyke, 1969). To evaluate the influence of rearing conditions in the incubator (a necessary procedure in rearing diploid drones), a group of haploid drones was also reared by this method, i.e. the first 2 days of their larval life were spent in an incubator. The combs with brood of both types of drones were screened shortly before the emergence of the adults, and then placed again in an incubator.

The drones were killed in the first day of their imaginal life and were dissected immediately in a 1% solution of NaCl. The prominent fat-body surrounding the testes of diploid drones was removed, but the outer membrane of the testes was left. The testes, vesiculae seminales and mucus glands were measured in the 1% saline solution immediately after dissection, using a microscope with an micrometer eyepiece. The length (l) and the width (w) were recorded and, where necessary, also a second diameter (the "thickness", t) at right angles to the "width". The volume was calculated using the formula:

$$\pi ltw/6. \quad \text{i.e. } 0{:}524ltw$$

Some testes were fixed and embedded in paraffin wax, and then sectioned with a microtome in order to measure diameters more exactly.

The sclerotized plates of the reproductive organs were measured in drones preserved in 70% alcohol, using the places of measurement indicated in Fig. 1.

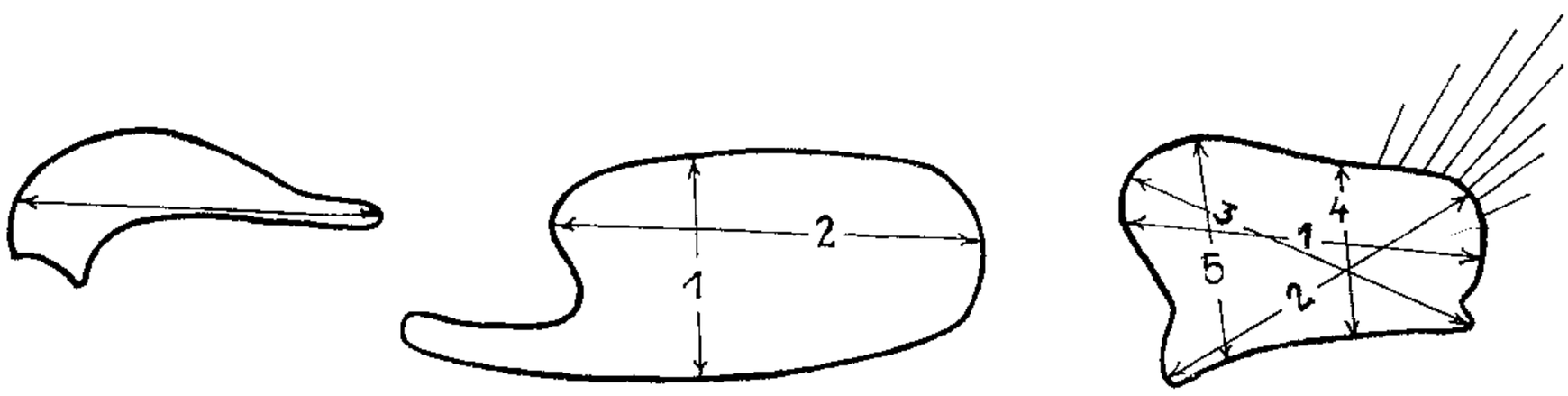

FIG. 1. Places of measurement of sclerotized plates of the drone reproductive organs : long plate of the bulb (left), penis valve (centre), lamina parameralis (right). Measurement no. 1 on the lamina parameralis was the greatest length of the plate, no. 4 was taken to the edge of the section with hairs, and no. 5 was the greatest width.

Results

1. Reproductive organs of haploid drones

(*a*) *Testes*

The data presented in Table 1 and Table 2 are arranged in order of increasing volume of the testes, as shown in the final column of Table 1.

TABLE 1. Mean dimensions of testes of haploid drones originating from various queens.

Queen No.	Race**	No. testes	Length (mm) Range	Length (mm) Mean ± s.e.*	Width (mm) Range	Width (mm) Mean ± s.e.*	Thickness (mm) Range	Thickness (mm) Mean ± s.e.*	Volume (mm³) Range	Volume (mm³) Mean ± s.e.*
81	C	20	4·5–4·9	4·61 ± 0·031	2·2–2·4	2·31 ± 0·016	1·8–1·9	1·83 ± 0·010	9·2–10·8	10·16 ± 0·125
82	C	20	4·7–5·1	4·90 ± 0·025	2·2–2·4	2·30 ± 0·016	1·7–1·8	1·75 ± 0·011	9·8–10·8	10·34 ± 0·088
59	Ca	20	4·1–5·1	4·62 ± 0·065	2·1–2·6	2·37 ± 0·028	1·9–2·2	2·03 ± 0·023	9·6–15·3	11·65 ± 0·343
83	M	20	4·5–5·3	4·90 ± 0·064	2·3–2·6	2·46 ± 0·023	1·8–2·0	1·90 ± 0·014	10·5–13·3	11·89 ± 0·206
73	L	20	5·1–5·5	5·32 ± 0·032	2·3–2·6	2·38 ± 0·022	1·8–2·1	1·92 ± 0·021	11·7–13·7	12·64 ± 0·137
84	M	20	5·2–5·8	5·45 ± 0·041	2·3–2·6	2·45 ± 0·026	1·8–2·1	1·94 ± 0·018	11·9–15·0	13·59 ± 0·187
72	L	20	5·0–5·9	5·29 ± 0·061	2·2–2·8	2·46 ± 0·035	1·8–2·3	2·06 ± 0·035	11·4–18·5	14·13 ± 0·513
60	Ca	20	4·7–5·6	5·25 ± 0·057	2·3–2·6	2·49 ± 0·026	1·9–2·3	2·08 ± 0·021	11·3–16·6	14·27 ± 0·290
Total		160								
Overall mean			4·1–5·9	5·04 ± 0·030	2·1–2·8	2·40 ± 0·011	1·7–2·3	1·94 ± 0·011	9·2–18·5	12·33 ± 0·152
L.s.d. (0·05)				0·084		0·032		0·032		0·43

* s.e. = standard error of mean.
** C = *A.m. carnica*; Ca = *A.m. caucasica*; L = *A.m. liguistica*; M = *A.m. mellifera*.

TABLE 2. Mean lengths and widths of vesiculae seminales and mucus glands of haploid drones from queens as in Table 1.

			Vesiculae seminales				*Mucus glands*			
			Length (mm)		Width (mm)		Length (mm)		Width (mm)	
Queen No.	Race**	No. measured	Range	Mean ± s.e.*	Range	Mean ± s.e.*	Range	Mean ± s.e.*	Range	Mean ± s.e.*
81	C	20	3·2–3·6	3·33 ± 0·026	0·50–0·60	0·54 ± 0·008	3·6–4·1	3·79 ± 0·031	1·0–1·2	1·12 ± 0·017
82	C	20	2·6–3·2	2·88 ± 0·042	0·55–0·60	0·59 ± 0·005	3·7–4·2	3·96 ± 0·029	1·0–1·2	1·12 ± 0·013
59	Ca	20	3·0–3·8	3·51 ± 0·048	0·55–0·70	0·60 ± 0·007	3·1–4·2	3·65 ± 0·078	1·0–1·4	1·27 ± 0·026
83	M	20	3·0–3·7	3·38 ± 0·043	0·60	0·60 ± 0·000	3·7–4·2	3·96 ± 0·032	1·1–1·3	1·21 ± 0·011
73	L	20	3·3–3·6	3·46 ± 0·021	0·55–0·60	0·57 ± 0·005	3·5–4·0	3·77 ± 0·031	1·1–1·2	1·19 ± 0·007
84	M	20	3·5–3·8	3·67 ± 0·016	0·55–0·60	0·58 ± 0·006	3·6–4·0	3·81 ± 0·027	1·2–1·3	1·21 ± 0·005
72	L	20	3·5–4·4	3·92 ± 0·052	0·55–0·70	0·66 ± 0·012	3·5–4·4	3·95 ± 0·057	1·2–1·5	1·29 ± 0·017
60	Ca	20	3·2–3·7	3·43 ± 0·033	0·55–0·60	0·58 ± 0·006	3·0–3·6	3·29 ± 0·037	1·1–1·4	1·21 ± 0·020
Total		160								
Overall mean			2·6–4·4	3·45 ± 0·030	0·50–0·70	0·59 ± 0·003	3·0–4·4	3·77 ± 0·023	1·0–1·5	1·20 ± 0·007
L.s.d. (0·05)				0·086		0·010		0·064		0·020

* s.e. = standard error of mean.
** C = *A.m. carnica*; Ca = *A.m. caucasica*; L = *A.m. ligustica*; M = *A.m. mellifera*.

The length of the testes (Table 1) ranged from 4·1 to 5·9 mm and, thus, the longest was 1·5 times as long as the shortest. The mean length for a group of drones originating from different queens ranged from 4·61 to 5·45 mm; differences between many means were significant (Table 1). The mean width ranged from 2·30 to 2·49 mm, and the mean thickness from 1·75 to 2·08 mm. Differences between many means were significant.

The volumes ranged from 9·2 mm^3 to 18·5 mm^3. Thus the largest testes had twice the volume of the smallest. The variation between the volumes of testes of drones originating from different queens was considerable. The difference between the smallest and the largest testes was lowest in drones originating from queen no. 82 (1 mm^3), and highest in drones from queen no. 72 (7·1 mm^3). The mean volumes ranged from 10·16 mm^3 to 14·27 mm^3; thus, one queen produced drones with a mean testes volume 40% greater than that of drones produced by another queen. In most cases the difference between the mean volumes of testes of drones produced by different queens was significant.

(*b*) *Vesiculae seminales*

Table 2 shows that there was variation in both length and width of the vesiculae seminales. The longest were 1·7 times as long as the shortest, and the widest 1·4 times as wide as the narrowest. Differences between many means were significant. The overall mean length was 3·45 mm and the mean width 0·59 mm.

(*c*) *Mucus glands*

The longest mucus gland was roughly 1·5 as long as the shortest, and the widest 1·5 as wide as the narrowest. Differences between many means were significant. The overall mean length was 3·77 mm and the mean width 1·20 mm.

2. Comparison of reproductive organs of haploid and diploid drones

(*a*) *Testes*

Fig. 2 shows the reproductive organs of a haploid drone and Fig. 4 those of a diploid drone. The greatest differences are between the testes. In both types of drone each testis has an outer tunic, whose outermost layer is composed of fat-cells, and outside this tunic is attached the fat-body. In haploid drones the fat-body is attached mainly to the anterior end of the testes; it is small, easy detachable, and usually lost during dissection and removal of the testes from the abdomen. In contrast, a large fat-body surrounds the testis of diploid drones (Fig. 4), probably incorporating part of the fat-cells found in the tunic of the haploid testis. The testes of diploid drones are much smaller than those of the haploids.

Since the haploids were reared normally in the colony, whereas the diploids spent the first 2 days of larval life in an incubator, the influence of this factor on the reproductive organs was investigated by comparing haploid drones reared in the two ways. The progenies of four queens were examined (Table 3). No significant differences were found between the widths and volumes of the testes of the progeny of any of the queens (I-N), but the mean lengths of the testes from the incubator-reared progeny of two queens (no. 212 and 929) were significantly greater than in those reared normally. The mean thickness of the testes of incubator-reared progeny of queen no. 212 was also greater than in the normally reared progeny, but the mean thickness for progeny of queen no. 91 was less in drones reared in an incubator than in those reared normally. The results, indicate therefore, that spending the first 2 days

TABLE 3. Mean dimensions of testes of haploid drones reared in normal conditions (N), or for 2 days in an incubator (I), and of diploid drones.

		Haploid drones (N)		*Haploid drones (I)*		*Difference (I–N)*	*Diploid drones*			
Queen No.	*Race***	*No. testes*	*Mean ± s.e.**	*No. testes*	*Mean ± s.e.**		*No. testes*	*Mean ± s.e.**	*% of N*	*% of I*
					Length (mm)					
63	L	54	4·55 ± 0·037	48	4·60 ± 0·034	0·05	54	1·86 ± 0·054	40·9	40·4
91	L	46	4·69 ± 0·051	42	4·70 ± 0·053	0·01	42	2·07 ± 0·034	44·1	44·0
212	L	40	5·01 ± 0·029	30	5·11 ± 0·028	0·10*s*	22	1·90 ± 0·038	37·9	37·2
929	Ca	16	5·08 ± 0·142	14	5·75 ± 0·060	0·67*s*	42	2·37 ± 0·035	46·7	41·2
Total		156		134			160			
Overall mean			4·77 ± 0·038		4·87 ± 0·038	0·10		2·06 ± 0·028	43·2	42·3
					Width (mm)					
63	L	54	2·24 ± 0·020	48	2·25 ± 0·020	0·01	54	1·18 ± 0·025	52·7	52·7
91	L	46	2·27 ± 0·028	42	2·26 ± 0·023	–0·01	42	1·27 ± 0·028	55·9	56·2
212	L	40	2·51 ± 0·011	30	2·50 ± 0·027	–0·01	22	1·30 ± 0·023	51·8	52·0
929	Ca	16	2·52 ± 0·099	14	2·54 ± 0·125	0·02	42	1·27 ± 0·057	49·6	49·2
Total		156		134			160			
Overall mean			2·35 ± 0·017		2·34 ± 0·020	–0·01		1·25 ±0·019	53·2	53·4
					Thickness (mm)					
63	L	54	1·88 ± 0·033	48	1·90 ± 0·026	0·02	54	0·92 ± 0·021	48·9	48·4
91	L	46	2·03 ± 0·024	42	1·94 ± 0·024	–0·09*s*	42	1·07 ± 0·017	52·7	55·2
212	L	40	1·86 ± 0·011	30	1·91 ± 0·017	0·05*s*	22	0·95 ± 0·022	51·1	49·7
929	Ca	16	1·87 ± 0·045	14	1·88 ± 0·040	0·01	42	0·85 ± 0·043	45·5	45·2
Total		156		134			160			
Overall mean			1·92 ± 0·016		1·92 ± 0·013	0·00		0·94 ± 0·016	49·0	49·0
					Volume (mm³)					
63	L	54	10·10 ± 0·199	48	10·23 ± 0·182	0·13	54	1·08 ± 0·071	10·7	10·6
91	L	46	11·32 ± 0·239	42	10·83 ± 0·291	–0·49	42	1·47 ± 0·047	13·0	13·6
212	L	40	12·23 ± 0·333	30	12·60 ± 0·523	0·37	22	1·21 ± 0·060	9·9	9·6
929	Ca	16	12·93 ± 0·858	14	14·97 ± 0·542	2·04	42	1·34 ± 0·058	10·4	9·0
Total		156		134			160			
Overall mean			11·30 ± 0·163		11·44 ± 0·198	0·14		1·27 ± 0·034	11·2	11·1

* s.e. = standard error of mean. *s* = significant, $P<0{\cdot}05$.
** Ca = *A.m. caucasica*; L = *A.m. ligustica*.

of larval life in an incubator did not influence the size of the testes of haploid drones in any consistent way.

Table 3 shows, however, that testes of diploid drones were much smaller than those of the haploids. The mean length, width and thickness of the diploid testes were about half those of the haploid testes, and the mean volume of the diploid testes was only about 11 % that of the haploids.

FIG. 2. Reproductive organs of a haploid drone.

FIG. 3. Reproductive organs of a haploid drone. Testicular tubules released by removing the membrane surrounding the testes.

FIG. 4. Reproductive organs of a diploid drone. Right testis surrounded by fatty tissue, left testis with fatty tissue removed.

FIG. 5. Reproductive organs of a diploid drone. Testicular tubules released by removing the membrane surrounding the testes.

TABLE 4. Mean number and size of testicular tubules in testes of haploid (H) and diploid (D) drones.

	Haploids (H)			*Diploids (D)*			
	No. measured	*Range*	*Mean ± s.e.**	*No. measured*	*Range*	*Mean ± s.e.**	*Difference D–H*
No. tubules/testes	16	172–256	214 ± 5·31	32	88–156	126 ± 3·74	–88*s*
Length (mm)	10	3·60–4·70	4·17 ± 0·111	32	1·01–2·81	1·74 ± 0·065	–2·43*s*
Width (mm)	10	0·08–0·13	0·10 ± 0·006	32	0·07–0·11	0·08 ± 0·0015	–0·02*s*
Diameter (mm) of transverse section	25	0·092–0·113	0·101	25	0·078–0·103	0·090	
	25	0·103–0·113	0·106	25	0·081–0·108	0·093	
	25	0·097–0·113	0·108	25	0·092–0·113	0·094	
	25	0·097–0·119	0·108	25	0·086–0·108	0·097	
	25	0·103–0·119	0·111	25	0·095–0·108	0·099	
Total	125			125			
Overall mean diameter (mm)		0·092–0·119	0·107 ± 0·0005		0·078–0·113	0·095 ± 0·0007	–0·012*s*

* s.e. = standard error of mean. *s* = significant, $P < 0{\cdot}05$.

(*b*) *Testicular tubules*

In order to investigate the reason for the small size of the testes of diploid drones in comparison with those of haploids, the outer membrane was removed from the testes of diploids and of normally reared haploids. Fig. 3 and Fig. 5 show that there were great differences between the testicular tubules of the two types.

From Table 4 it can be seen that the haploid drones had almost twice as many tubules as the diploids; Table 3 and Fig. 5 also show that the tubules of the diploids were only 42% as long as those of the haploids. The widths in the two groups differed less, although the mean for the diploids was significantly lower. Additional measurements of the diameters were made on transverse sections under higher magnification. The mean diameter in diploid drones was again significantly smaller, being 89% that of the haploids. The testes of diploid drones are, therefore, smaller mainly because of the smaller number and the shortness of the testicular tubules.

(*c*) *Vesiculae seminales*

The size of the vesiculae seminales was measured in three groups of drones which were the progeny of each of four queens: (1) normally reared haploids, (2) haploids reared in an incubator for the first two days of larval life, and (3) diploids (Table 5). The difference between the overall mean lengths in the two haploid groups (I-N) was significant, but the mean length of the vesiculae seminales of the normally reared drones produced by queen No. 212 was extremely low; this sample may have been a particularly low value one from drones with small vesiculae. The mean widths in these two groups showed no consistent differences. It is concluded that the partial rearing of the drones in an incubator did not influence the width of the vesiculae seminales, although the evidence presented here suggests that it may have increased the length.

The differences between the mean lengths of the vesiculae seminales in diploids and in the two groups of haploids (Table 5, D-N and D-I) were significant in 7 cases out of 8, but the diploid progeny of two queens had larger mean values than the haploids, while the opposite was true for the progenies of the other two queens. It appears that the significance of the overall mean differences depends largely on the very low values for the diploid progeny of queen no. 929, and it may therefore not be meaningful.

The mean widths of the vesiculae seminales of the diploids were, however, lower than in the corresponding haploids in all groups except one, and the overall mean of the diploids was significantly lower than that of either of the haploid groups.

(*d*) *Mucus glands*

Table 6 shows that the size of the mucus glands in haploid drones was not significantly reduced by partial rearing in an incubator. The glands of the diploids were significantly shorter than those of either group of haploids, and the widths were also reduced, though not significantly in the progeny of 2 queens out of 4. The overall mean length in the diploids was 88% of that of the haploids, and the width 86%.

(*e*) *Sclerotized plates of reproductive organs*

The mean lengths of the long plates of the endophallus of normally reared haploid drones (Table 7) were slightly greater than those of the diploids ($P<0{\cdot}05$).

The external plates of the reproductive organs of haploid and diploid drones were also compared (Table 8). No significant difference was found between the mean lengths of the penis valves, but the overall mean width was significantly larger in diploid drones than in haploids.

TABLE 5. Mean lengths and widths of vesiculae seminales of haploid drones reared in normal conditions (N), or for 2 days in an incubator (I), and of diploid drones (D).

		Haploid drones (N)		*Haploid drones (I)*		*Differences (I–N)*	*Diploid drones (D)*		*Differences*	
Queen No.	*Race***	*No. measured*	*Mean ± s.e.**	*No. measured*	*Mean ± s.e.**		*No. measured*	*Mean ± s.e.**	*D–N*	*D–I*
					Length (mm)					
63	L	54	3·64 ± 0·030	48	3·75 ± 0·047	0·11	54	3·86 ± 0·054	0·22*s*	0·11
91	L	46	3·52 ± 0·031	42	3·56 ± 0·034	0·04	42	3·72 ± 0·069	0·20*s*	0·16*s*
212	L	40	3·08 ± 0·035	30	3·48 ± 0·058	0·40*s*	22	2·93 ± 0·019	–0·15*s*	–0·55*s*
929	Ca	16	3·37 ± 0·077	14	3·58 ± 0·096	0·21	42	2·23 ± 0·033	–1·14*s*	–1·35*s*
Total		156		134			160			
Overall mean			3·44 ± 0·032		3·61 ± 0·026	0·17*s*		3·27 ± 0·060	–0·17*s*	0·34*s*
					Width (mm)					
63	L	54	0·65 ± 0·020	48	0·71 ± 0·017	0·06*s*	54	0·65 ± 0·035	0·00	–0·06
91	L	46	0·70 ± 0·011	42	0·69 ± 0·012	–0·01	42	0·63 ± 0·008	–0·07*s*	–0·06*s*
212	L	40	0·62 ± 0·007	30	0·61 ± 0·008	–0·01	22	0·47 ± 0·011	–0·15*s*	–0·14*s*
929	Ca	16	0·76 ± 0·027	14	0·67 ± 0·020	–0·09*s*	42	0·42 ± 0·009	–0·34*s*	–0·25*s*
Total		156		134			160			
Overall mean			0·67 ± 0·009		0·68 ± 0·008	0·01		0·57 ± 0·009	–0·10*s*	–0·11*s*

* s.e. = standard error of mean. *s* = significant, $P<0{\cdot}05$.
** Ca = *A.m. caucasica*; L = *A.m. ligustica*.

TABLE 6. Mean length and width of mucus glands of haploid drones, reared in normal conditions (N), or for 2 days in incubator (I), and of diploid drones (D).

		Haploid drones (N)		*Haploid drones (I)*		*Differences (I–N)*	*Diploid drones (D)*		*Differences*	
Queen No.	*Race***	*No. measured*	*Mean ± s.e.**	*No. measured*	*Mean ± s.e.**		*No. measured*	*Mean ± s.e.**	*D–N*	*D–I*
					Length (mm)					
63	L	54	3·81 ± 0·017	48	3·76 ± 0·046	–0·05	54	3·50 ± 0·024	–0·31*s*	–0·26*s*
91	L	46	4·00 ± 0·029	42	3·94 ± 0·033	–0·06	42	3·76 ± 0·050	–0·24*s*	–0·18*s*
212	L	40	3·91 ± 0·013	30	4·07 ± 0·031	0·16*s*	22	3·68 ± 0·043	–0·23*s*	–0·39*s*
929	Ca	16	3·71 ± 0·087	14	3·90 ± 0·059	0·19*s*	42	2·85 ± 0·035	–0·86*s*	–1·05*s*
Total		156		134			160			
Overall mean			3·88 ± 0·023		3·90 ± 0·030	0·02		3·42 ± 0·033	–0·46*s*	–0·48*s*
					Width (mm)					
63	L	54	1·12 ± 0·051	48	1·12 ± 0·045	0·00	54	1·08 ± 0·026	–0·04	–0·04
91	L	46	1·16 ± 0·013	42	1·15 ± 0·012	–0·01	42	1·15 ± 0·012	–0·01	0·00
212	L	40	1·22 ± 0·009	30	1·23 ± 0·013	0·01	22	0·92 ± 0·024	–0·30*s*	–0·31*s*
929	Ca	16	1·21 ± 0·082	14	1·21 ± 0·029	0·00	42	0·83 ± 0·017	–0·38*s*	–0·38*s*
Total		156		134			160			
Overall mean			1·17 ± 0·009		1·16 ± 0·009	–0·01		1·01 ± 0·014	–0·16*s*	–0·15*s*

* s.e. = standard error of mean. *s* = significant, $P<0{\cdot}05$.
** Ca = *A.m. caucasica*; L = *A.m. ligustica*.

TABLE 7. Mean lengths of the long plates of the endophallus in haploid and diploid drones.

		Haploids (H)			*Diploids (D)*			*Differences*
Queen No.	*Race***	*No. plates*	*Range*	*Mean ± s.e.**	*No. plates*	*Range*	*Mean ± s.e.**	*D–H*
141	A	25	2·10–2·34	2·24 ± 0·018	25	1·93–2·49	2·28 ± 0·030	0·04
144	L	25	2·04–2·46	2·23 ± 0·026	22	2·04–2·35	2·21 ± 0·019	–0·02
155	L	14	2·07–2·39	2·26 ± 0·021	16	1·90–2·30	2·21 ± 0·026	–0·05
167	L	25	1·97–2·39	2·21 ± 0·020	25	1·83–2·56	2·15 ± 0·032	–0·06
439	L	25	2·14–2·46	2·21 ± 0·015	25	1·87–2·39	2·16 ± 0·022	–0·05
Total		114			113			
Overall mean			1·97–2·46	2·23 ± 0·009		1·83–2·56	2·20 ± 0·011	–0·03*s*

* s.e. = standard error of mean. *s* = significant, $P<0·05$.
** L = *A.m. ligustica*; A = *A.m. adansonii*.

TABLE 8. Mean lengths and widths of penis valves of haploid and diploid drones.

Queen No.	Race**	*Haploids (H)*			*Diploids (D)*			*Difference D–H*
		No. plates	*Range*	*Mean ± s.e.**	*No. plates*	*Range*	*Mean ± s.e.**	
				Length (mm)				
141	A	25	1·11–1·34	1·19 ± 0·010	25	1·14–1·24	1·18 ± 0·005	–0·01
144	L	25	1·06–1·25	1·14 ± 0·011	21	1·03–1·34	1·16 ± 0·016	0·02
155	L	25	0·80–1·01	0·93 ± 0·011	19	0·84–0·96	0·91 ± 0·007	–0·02
167	L	24	0·86–1·01	0·95 ± 0·008	25	0·86–1·06	0·97 ± 0·011	0·02
439	L	25	1·17–1·51	1·29 ± 0·022	25	1·18–1·51	1·31 ± 0·018	0·02
Total		124			115			
Overall mean			0·80–1·51	1·10 ± 0·0059		0·84–1·51	1·11 ± 0·0056	0·01
				Width (mm)				
141	A	25	0·70–0·92	0·82 ± 0·011	25	0·80–1·07	0·91 ± 0·011	0·09*s*
144	L	25	0·72–0·93	0·81 ± 0·013	22	0·73–0·97	0·87 ± 0·017	0·06*s*
155	L	24	0·79–0·99	0·88 ± 0·011	18	0·73–0·94	0·87 ± 0·013	–0·01
167	L	24	0·82–0·94	0·87 ± 0·006	25	0·80–1·01	0·92 ± 0·010	0·05*s*
439	L	25	0·58–0·89	0·78 ± 0·013	25	0·72–0·97	0·86 ± 0·013	0·08*s*
Total		123			115			
Overall mean			0·58–0·99	0·83 ± 0·0049		0·72–1·07	0·89 ± 0·0056	0·06*s*

* s.e. = standard error of mean. *s* = significant, $P<0·05$.
** L = *A.m. ligustica*; A = *A.m. adansonii*.

TABLE 9. Mean dimensions (mm) of laminae paramerales of haploid and diploid drones (see Fig. 1).

		Haploids (H)			*Diploids (D)*			
Queen No.	*Race***	*No. plates*	*Range*	*Mean ± s.e.**	*No. plates*	*Range*	*Mean ± s.e.**	*Difference D–H*
				1st measurement (length)				
141	A	25	0·89–1·02	0·96 ± 0·008	25	0·90–1·03	0·96 ± 0·007	0·00
144	L	25	0·85–1·04	0·92 ± 0·009	21	0·83–0·93	0·87 ± 0·009	–0·05*s*
155	L	25	0·78–0·96	0·86 ± 0·010	19	0·59–0·92	0·82 ± 0·018	–0·04
167	L	24	0·79–0·96	0·86 ± 0·009	25	0·72–0·94	0·83 ± 0·008	–0·03*s*
439	L	25	0·87–1·17	0·94 ± 0·012	25	0·85–0·97	0·90 ± 0·007	–0·04*s*
Total		124			115			
Overall mean			0·78–1·17	0·91 ± 0·0043		0·59–1·03	0·88 ± 0·0044	–0·03*s*
				2nd measurement (diagonal)				
141	A	25	0·68–0·85	0·76 ± 0·008	25	0·76–0·83	0·79 ± 0·005	0·03*s*
144	L	25	0·68–0·86	0·76 ± 0·009	21	0·69–0·93	0·83 ± 0·011	0·07*s*
155	L	25	0·69–0·86	0·80 ± 0·010	19	0·66–0·86	0·78 ± 0·011	–0·02
167	L	24	0·72–0·87	0·78 ± 0·008	25	0·73–0·89	0·76 ± 0·007	–0·02
439	L	25	0·65–0·93	0·77 ± 0·011	25	0·66–0·80	0·74 ± 0·008	–0·03*s*
Total		124			115			
Overall mean			0·63–0·93	0·77 ± 0·0041		0·66–0·93	0·78 ± 0·0037	0·01
				3rd measurement (diagonal)				
141	A	25	0·72–0·93	0·83 ± 0·009	25	0·76–0·92	0·86 ± 0·006	0·03*s*
144	L	25	0·76–0·90	0·83 ± 0·009	21	0·86–1·02	0·94 ± 0·013	0·11*s*
155	L	24	0·82–1·02	0·93 ± 0·010	18	0·66–0·99	0·89 ± 0·020	–0·04
167	L	24	0·87–1·04	0·93 ± 0·010	25	0·75–0·94	0·87 ± 0·008	–0·06*s*
439	L	25	0·76–0·94	0·82 ± 0·008	24	0·73–0·83	0·78 ± 0·007	–0·04*s*
Total		123			113			
Overall mean			0·72–1·04	0·87 ± 0·0042		0·66–1·02	0·87 ± 0·048	0·00
				4th measurement (width)				
141	A	25	0·41–0·50	0·46 ± 0·006	25	0·48–0·53	0·50 ± 0·004	0·04*s*
144	L	25	0·32–0·46	0·41 ± 0·007	22	0·29–0·45	0·40 ± 0·010	–0.01
155	L	25	0·38–0·53	0·44 ± 0·007	19	0·36–0·46	0·43 ± 0·006	–0·01
167	L	24	0·38–0·45	0·41 ± 0·006	25	0·34–0·45	0·41 ± 0·006	0·00
439	L	25	0·29–0·52	0·46 ± 0·011	25	0·42–0·52	0·46 ± 0·005	0·00
Total		124			116			
Overall mean			0·29–0·53	0·44 ± 0·0034		0·29–0·53	0·44 ± 0·0028	0·00
				5th measurement (width)				
141	A	25	0·48–0·57	0·53 ± 0·007	25	0·49–0·59	0·55 ± 0·006	0·02*s*
144	L	25	0·39–0·50	0·45 ± 0·005	22	0·42–0·59	0·48 ± 0·007	0·03*s*
155	L	25	0·39–0·53	0·48 ± 0·007	19	0·42–0·52	0·48 ± 0·006	0·00
167	L	24	0·41–0·46	0·44 ± 0·004	25	0·41–0·52	0·47 ± 0·006	0·03*s*
439	L	25	0·46–0·57	0·51 ± 0·006	25	0·46–0·57	0·54 ± 0·008	0·03*s*
Total		124			116			
Overall mean			0·39–0·57	0·48 ± 0·0026		0·41–0·59	0·50 ± 0·0030	0·02*s*

* s.e. = standard error of mean. *s* = significant, $P<0{\cdot}05$.
** L = *A.m. ligustica*; A = *A.m. adansonii*.

TABLE 10. Mean dimensions of testes of diploid drones.

Queen No.	*Race***	*No. testes*	*Length (mm)*		*Width (mm)*		*Thickness (mm)*		*Volume (mm^3)*	
			Range	*Mean ± s.e.**	*Range*	*Mean ± s.e.**	*Range*	*Mean ± s.e.**	*Range*	*Mean ± s.e.**
203	Ca	30	1·0–3·2	1·89 ± 0·106	0·6–1·8	1·17 ± 0·051	0·4–1·1	0·78 ± 0·035	0·15–2·13	1·00 ± 0·110
63	L	74	0·7–2·7	1·81 ± 0·048	0·5–1·7	1·16 ± 0·021	0·5–1·2	0·91 ± 0·018	0·09–2·26	1·05 ± 0·061
91	L	42	1·5–2·6	2·07 ± 0·034	1·0–1·6	1·27 ± 0·028	0·8–1·3	1·07 ± 0·017	0·92–2·10	1·07 ± 0·017
885	L	10	1·7–2·5	1·99 ± 0·078	1·1–1·3	1·19 ± 0·008	0·7–1·1	0·90 ± 0·047	0·78–1·72	1·14 ± 0·107
177	L	80	1·4–3·3	2·32 ± 0·045	1·0–2·0	1·50 ± 0·032	0·4–1·4	0·72 ± 0·026	0·40–2·33	1·33 ± 0·055
194	Ca	52	1·4–3·8	2·99 ± 0·073	1·1–2·1	1·70 ± 0·033	0·4–1·1	0·71 ± 0·037	0·44–4·10	1·96 ± 0·108
273	L	50	2·0–4·1	3·26 ± 0·058	1·2–2·3	1·82 ± 0·046	0·4–1·2	0·71 ± 0·031	1·13–4·10	2·20 ± 0·101
173	L	49	1·6–4·1	2·83 ± 0·080	1·0–2·1	1·53 ± 0·033	0·7–1·2	0·98 ± 0·020	0·75–3·82	2·27 ± 0·110
175	L	6	2·6–4·0	3·58 ± 0·243	1·3–1·8	1·60 ± 0·078	0·6–1·0	0·82 ± 0·113	1·93–3·02	2·42 ± 0·178
914	CF	12	2·1–3·4	2·90 ± 0·121	1·4–1·9	1·67 ± 0·050	1·0–1·2	1·15 ± 0·023	1·88–4·17	2·96 ± 0·232
458	L	16	2·5–4·0	3·44 ± 0·125	1·5–2·4	2·01 ± 0·065	0·7–1·4	1·09 ± 0·055	1·62–6·41	4·16 ± 0·430

TABLE 12. Mean dimensions of vesiculae seminales and mucus glands of diploid drones (age 1 day) originating from various queens.

			Vesiculae seminales				*Mucus glands*			
		No.	*Length (mm)*		*Width (mm)*		*Length (mm)*		*Width (mm)*	
Queen No.	*Race*	*measured*	*Range*	*Mean ± s.e.**	*Range*	*Mean ± s.e.**	*Range*	*Mean ± s.e.**	*Range*	*Mean ± s.e.**
203	Ca	30	2·9–4·0	3·48 ± 0·042	0·4–0·8	0·60 ± 0·011	3·2–4·0	3·55 ± 0·038	0·7–1·2	0·98 ± 0·022
63	L	74	2·5–4·6	3·91 ± 0·041	0·6–0·9	0·64 ± 0·005	2·9–4·5	3·54 ± 0·023	0·8–1·5	1·10 ± 0·018
885	L	10	3·5–4·6	4·07 ± 0·128	0·6–0·7	0·73 ± 0·032	3·2–4·3	3·75 ± 0·108	1·0–1·3	1·16 ± 0·028
177	L	80	2·3–4·3	3·28 ± 0·068	0·4–0·7	0·55 ± 0·026	2·5–3·8	3·31 ± 0·026	0·8–1·5	1·14 ± 0·019
91	L	42	3·1–4·5	3·72 ± 0·069	0·5–0·7	0·63 ± 0·008	2·9–4·3	3·76 ± 0·050	0·9–1·3	1·15 ± 0·012
194	Ca	52	2·9–3·8	3·28 ± 0·046	0·4–0·8	0·53 ± 0·040	2·5–3·5	3·15 ± 0·044	0·8–1·6	1·16 ± 0·025
273	L	50	2·3–3·7	3·15 ± 0·038	0·4–0·7	0·53 ± 0·042	2·6–3·6	3·14 ± 0·031	1·0–1·5	1·30 ± 0·044
173	L	48	2·0–4·1	3·13 ± 0·065	0·4–0·9	0·64 ± 0·016	2·4–4·2	3·54 ± 0·062	0·6–1·2	0·98 ± 0·023
175	L	6	2·5–3·0	2·82 ± 0·091	0·4–0·8	0·58 ± 0·061	3·2–4·6	3·90 ± 0·222	0·6–1·2	0·97 ± 0·091
914	CF	12	2·8–4·7	3·24 ± 0·175	0·5–0·6	0·59 ± 0·009	3·4–3·7	3·54 ± 0·023	1·2–1·3	1·21 ± 0·009
458	L	16	2·5–3·5	3·03 ± 0·068	0·5–0·8	0·66 ± 0·025	2·6–3·6	3·11 ± 0·068	0·7–1·3	1·11 ± 0·050

* s.e. = standard error of mean.

** Ca = *A.m. caucasica*; L = *A.m. ligustica*; CF = *A.m. carnica* × *A.m. fasciata*.

The laminae paramerales have an irregular outline, and therefore 5 different measurements of each plate were made (Fig. 1). Table 9 shows that the laminae of diploid drones were rather shorter (1st measurement) and wider (5th measurement) than those of the haploids ($P<0{\cdot}05$). The other measurements showed no consistent differences.

3. Comparison between reproductive organs of diploid drones originating from different queens

(*a*) *Testes*

Table 10 shows the mean dimensions of testes of diploid drones originating from the 11 queens of different races and crosses. The results are arranged in order of increasing mean volume of testes (final column).

There was considerable variation in the size between testes from different individual drones. The volume of the largest testes (6·41 mm^3) was 71 times that of the smallest (0·09 mm^3). The largest and smallest mean values for drones of various queens did not differ by more than about 4 times. Means for groups of drones produced by different queens also showed variation, and the significances of the differences between these means were therefore calculated (Table 11). Differences between two successive mean volumes in Table 10 were usually not significant, but Table 11 shows that 43 of 55 calculated differences were significant. Tables showing the significance of differences between the means for length, width and thickness of testes were similar to Table 11. They are not presented here but are deposited at the Bee Research Association. Out of 55 differences between the means, 44 were significant for length, 45 for width, and 35 for thickness. Thus most of the mean dimensions of testes of groups of diploid drones produced by different queens differed significantly.

TABLE 11. Significance of differences between the means of the testes volume (*mtv*) for diploid drones originating from various queens. Significant differences ($P<0{\cdot}05$) are marked +, and non-significant differences ($P>0{\cdot}05$) are marked O.

			Queen no.										
			203	63	91	885	177	194	273	173	175	914	458
Queen no.	*Race***	*mtv*	*Mean testes volume (mtv)* 1·00	1·05	1·07	1·14	1·33	1·96	2·20	2·27	2·42	2·96	4·16
203	Ca	1·00	×										
63	L	1·05	O	×									
91	L	1·07	O	O	×								
885	L	1·14	O	O	O	×							
177	L	1·33	+	+	+	O	×						
194	Ca	1·96	+	+	+	+	+	×					
273	L	2·20	+	+	+	+	+	O	×				
173	L	2·27	+	+	+	+	+	+	O	×			
175	L	2·42	+	+	+	+	+	+	O	O	×		
914	CF	2·96	+	+	+	+	+	+	+	+	O	×	
458	L	4·16	+	+	+	+	+	+	+	+	+	+	×

** Ca = *A.m. caucasica*; L = *A.m. ligustica*; CF = *A.m. carnica* × *A.m. fasciata*.

(*b*) *Vesiculae seminales and mucus glands*

Table 12 shows that the mean length of the vesiculae seminales of diploid drones from different queens varied from 2·82 to 4·07 mm, and the width from 0·53 to

0·73 mm. The mean length of the mucus glands varied from 3·11–3.90 mm, and the width from 0·97–1·30 mm. Statistical comparisons between individual means showed that 37 were significant for the length and 27 for the width of the vesiculae seminales, and 36 for the length and 29 for the width of the mucus glands. Thus many of the differences between the dimensions of the vesiculae seminales and the mucus glands of groups of diploid drones originating from different queens were significant.

Discussion and Conclusions

Significant differences were found between the mean dimensions of various reproductive organs of haploid drones produced by different queens.

Comparison of reproductive organs of haploid and diploid drones originating from the same queen showed that different organs differed to an unequal extent. The greatest differences were found between testes, whose mean volume in the diploids was about 10% of that in the haploids. The vesiculae seminales and mucus glands, which are also of mesodermal origin, were only slightly smaller in the diploids. The sclerotized plates, which are of ectodermal origin, showed no clear pattern of difference between haploids and diploids, some measurements being larger in the haploids and some larger in the diploids.

In comparisons between the mean volumes of the testes of groups of drones (both haploid and diploid) produced by different queens, many of the differences were found to be significant. This suggests that the size of the testes may depend on polygenes, and that selection for this character could be carried out.

The results presented here also suggest that there may be greater variability between the mean volumes of testes of diploid drones produced by different queens, than between the mean volumes of testes of haploid drones produced by different queens. One queen (no. 458) produced diploid drones with a mean testes volume more than 4 times that for drones produced by another queen (no. 203), whereas the largest mean volume recorded for the haploid progeny of a single queen (no. 60) was only 40% more than that of the smallest recorded haploid mean (from queen no. 81).

The small size of the testes of diploid drones is one of the factors that make it difficult to collect semen from these drones. The present results suggest that selective breeding of queens for the production of diploid drones with larger testes would help to overcome this difficulty.

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