



VARIATION IN SCALE PATTERN OF THE ABDOMINAL TERGUM OF
AEDES AEGYPTI (L.)
Worldwide Survey of Populations with Particular
Reference to East Africa

by

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SYNOPSIS

Aedes aegypti, a vector of arboviruses of undiminished importance in the tropics, shows apparently correlated morphological and behavioural variation of epidemiological significance. Feral populations in Africa south of the Sahara have been separated as subspecies formosus from less dark-coloured strains occurring mainly in other regions, which are usually closely associated with man. Paler individuals of these strains have been termed var. queenslandensis.

A number of field and laboratory populations from 33 different countries were sampled and the range of variation of scale patterns on the abdominal tergum analysed using an arbitrary scale of pattern grades and values. It is concluded that use of the currently defined sub-specific and varietal terms allows inadequate characterization of natural populations, leads to an oversimplified view of natural variability and should be abandoned. It is further suggested that more rigorous definitions be adopted relating the ecological concepts of domesticity, habitat and population.

INTRODUCTION

The undiminished epidemicity of yellow fever in Africa, the emergence during the 1960s of haemorrhagic dengue as a major plague of the urban tropics and the retrograde state of attempts to eradicate Aedes aegypti in the Americas, emphasize the continued and perhaps increasing importance of this mosquito. Despite the great store of biological information on this species, data on genetics, behaviour and ecology are still far from adequate especially at the population level. Most of what is known has been well summarized recently (Craig & Hickey, 1967; McClelland, 1967; Mattingly, 1967) and will not be reviewed in detail.

The naturally occurring variation in colour and patterns of scales of A. aegypti is legend. This has been reflected to some degree by the plethora of synonyms for the species, and is certainly due in part to the distinctive black and white colour pattern in which small variations are easily noticed.

Much of the variation is now recognized as controlled by single Mendelian factors (Craig & Hickey, 1967).

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The first variation in A. aegypti associated with proximity of its breeding to human habitation was reported by Hill (1921) in Queensland, Australia, who observed that those A. aegypti breeding in scrub were darker than those occurring in the vicinity of houses.

In the coastal region of Kenya the frequency of pale forms of A. aegypti has been shown to be clearly higher in populations in and around human dwellings than in those of the nearby bush (van Someren et al., 1955, 1958; McClelland, 1960). The implied correlation between colour and behaviour differences was among the many problems which prompted Mattingly (1957, 1958) to make the reappraisal of the whole biology and taxonomy of A. aegypti which has come to mark the turn from old to modern studies in this species.

Mattingly (1957) recognized a subspecies formosus (Walker) of A. aegypti as a form restricted to sub-Saharan Africa "where it is the only form known to occur, except in coastal districts and in one or two areas of limited inland penetration". As well as the dark-scaled parts of the pattern being generally blacker, this form "never has any pale scales on the first abdominal tergite".

The type form was defined as either distinctly paler and browner (at least in the female) than ssp. formosus or with pale scaling on the first abdominal tergite or both. Extension of the pale scaling is, however, limited to the back of the head and to the first tergite. A detailed description of the neotype was given later (Mattingly, 1965).

The third form, var. queenslandensis, was clearly regarded by Mattingly to include all specimens with any extension of the pale scaling on the thorax, tergites beyond the first, and legs. The colour of the integument was not considered relevant. Mattingly (1965) however stressed that the last two forms were colloquial terms defining arbitrary sub-divisions in a continuous spectrum of colour variation.

A fourth form, ssp. mascarensis, was added later by Mattingly (1965) but as a special case it is not pertinent to the present discussion.

To quote Mayr (1963): "A subspecies is an aggregate of local populations of a species, inhabiting a geographic sub-division of the range of the species, and differing taxonomically from other populations of the species." Few workers would deny that the "gestalt" of an African bush strain differs markedly from that of urban strains on other continents, yet, if A. aegypti is a polytypic species, it is desirable that its infra-specific taxa are unequivocally defined. If, as has been suggested before (McClelland, 1967), the species is polymorphic and "weedy", it is essential to abandon labels which tend to generate rigid concepts and camouflage the true extent of variability.

To this end, it was decided, after a preliminary study (McClelland, 1960), to examine populations of A. aegypti from as many sources as practicable, and to employ a classification which allowed quantification of the almost continuous range of variation in the pattern of pale and dark scales on the tergites.

MATERIAL

The present work was based entirely on living material reared in the laboratory thus avoiding equivocal interpretation of shrunken, faded or battered specimens. The methods of analysis were initially established with a strain from Delhi, India, maintained at the National Institute for Medical Research, London. This was compared with strain GA collected from a locality in Kenya studied earlier (McClelland, 1960), strain DI/1 of Indonesian origin maintained in Amsterdam, and several of the strains maintained at the University of Notre Dame, Indiana, United States of America, by Dr G. B. Craig jr.

It was then decided to obtain strains directly from the country of origin. Over 50 separate consignments of eggs were received in response to requests to nearly 100 workers.

During a visit to Tanzania in 1968 as a consultant for the World Health Organization, the author sampled several further populations. While Project Leader at the WHO East Africa Aedes Research Unit in Dar es Salaam, he examined additional strains from Tanzania and Kenya in 1970. A total of 74 samples from 69 different populations were analysed. Forty-three of these populations were "field strains" that had not passed through more than two generations in the laboratory. The samples originated from 48 distinct localities (50 km or more separation) in 33 countries. The complete list of strains used, with details of their sources, is given in Table 1. Because of the long time span and variety of sources, it was not possible to standardize sample size and method of collection.

METHODS OF HANDLING LIVING MATERIAL

Eggs were hatched in deoxygenated water and the larvae reared in about 550 ml tapwater in covered bowls at temperatures between 25° and 28°C. Larvae were fed daily with small amounts of liver powder or a mixture of liver powder and wheat germ. Pupae were usually isolated on moist cotton-wool pads in 75 x 25 mm vials, but sometimes up to 25 were placed together in plastic cups and held at temperatures between 26° and 29°C. Adults were examined while lightly etherized at between x20 and x60 magnification with a stereoscopic microscope under high intensity but relatively cool illumination. Adults were discarded or returned to their individual vials after examination and held for possible use in single-pair breeding attempts.

METHOD OF SCORING VARIATION IN SCALE PATTERN ON TERGITES

McClelland (1960) and Senevet & Andarelli (1961) employed a classification involving 11 arbitrary grades of pattern of the abdominal tergites. The series ranged from a grade satisfying the definition of ssp. formosus (grade F) with no pale scales on the first tergite and none but those of the pale basal bands and lateral spots on the remaining tergites, to that with an unbroken median stripe of pale scales on all tergites (grade Q, for queenslandensis) or almost completely pale (grade R).

In the present work, it soon became apparent that 11 pattern grades were inadequate to describe the range of observed variation. The early system of classification did not discriminate a speckling of pale scales from a dark tergite. Only a contiguous stripe of pale scales was scored. The system was therefore expanded to cover 30 basic patterns by supplementing the F to Q letter grades with digits to indicate the number of tergites (except the first) speckled or brindled with pale scales.

Grade R of the early study (McClelland, 1960) was merged with Q, while the darker grades were further sub-divided by the use of (-) indicating minimal criteria and (ap) indicating pale scales along the apical borders of the tergites. The absence of a pale basal band on tergite 2 of some examples of grade F was observed but not scored (Fig. 1).

Certain other variation on the tergum, principally that due to the mutant spot (Craig & Vandehey, 1962) figured by McClelland (1960), was also noted and is discussed, but the pattern grade was assigned independently. The full range of basic pattern grades is given in Figs. 1 and 2, while photographs of some living examples are given in Figs. 3-5.

Because the 30 basic pattern grades could not easily be arranged in a linear sequence of increasing paleness, a numerical equivalent was defined so that population characteristics could be presented as frequency distributions. A tergite with no pale scales other than the basal band or lateral spot scored zero, a brindled or speckled tergite was given one point and a medially pale tergite with at least a contiguous line of pale scales joining the basal band to the apical margin scored two points. An additional one point was added in all cases to avoid the zero score that would result from pattern grade F and cause difficulties in data processing. The sum of this point and those scored for each of the seven tergites constitutes the Pattern Value (PV) which ranges from 1-15. For a sample, a Mean Pattern Value (MPV) is then easily calculated. The basic pattern grades and values are summarized as a matrix in

Table 2. In scoring, it is obvious that a subjective element was unavoidable since all types of intermediates occur. Such indetermination would not, however, have exceeded three pattern grades or resulted in an error of more than one PV unit.

RESULTS

Pattern values of males and females compared

The MPV of males has been plotted against that of females for each of the 74 samples as a scatter diagram in Fig. 6. A logarithmic scale has been used to avoid crowding the lower values. The MPV of males was greater than that of females in only two samples; in strain EK 8.6:8.3 for a total sample of 77, but the even greater difference in strain GR of 6.0:4.7 can be attributed to the small sample size of nine. The median ratio of MPV (male):MPV (female) was 0.80 with the ratios of 90% of samples lying between 0.62 and 0.95.

Because pattern values are arbitrary figures, further statistical treatment is unwarranted but the scatter diagram shows little more strain separation in two dimensions that can be obtained linearly from MPV of females alone. Thus there is probably little justification in scoring males as a routine.

Pattern grades and values of all strains compared

Frequency distributions of PV for both sexes are plotted graphically for 24 samples of field strains in Fig. 7. Only two, MM and VL, had reached two generations in the laboratory; seven were F₁ generation with one laboratory mating; while 15 were reared from eggs, laid by field-mated females, or from field-collected larvae. Strains with a sample size of less than 30 females were excluded with the exception of strain GA with 27 that was included for comparison with strain GS. These 24 strains cover the entire range of MPV and can be considered representative of the various types of PV distribution encountered.

The selected strains can be compared with the entire set of ranked samples in Fig. 8 in which MPV and range of pattern grades of females are shown in a manner which emphasizes the relative differences between populations and their variability. Where potential for selection is considered, the extreme tails of a distribution can be very important even though they appear insignificant on a frequency histogram.

Occurrence of "spot" phenotype

Phenotypes showing the replacement of the normally metallic-silver lateral spots on the tergites by varying numbers of non-reflective white scales, or related modifications, were found in 19 strains, and they were revealed by subsequent selection in a further six strains. The occurrence of spot phenotypes is summarized in Table 3 and examples are illustrated in Fig. 3A, B, C, D, F; Fig. 4A, B, E, F and Fig. 5E, H. Heterozygous forms are also illustrated. For further information see the second paper in this series (McClelland, in press). Strain KN merits comment in that the sample was derived, by chance, from a single presumably heterozygous female, so that the frequency of 22% probably reflects a Mendelian expectancy of 25% rather than a true population frequency.

DISCUSSION

Variation in relation to taxonomy

Mattingly (1957) based his description of infra-specific forms of A. aegypti on museum specimens, largely individuals from points scattered in time and space. The sequence of populations shown in Fig. 8 at least shadows the three entities he described. The males of strains KK and darker and the females of strains MO and darker have a majority referable to pattern grade F. The probability of individuals from such strains conforming unequivocally to

the description of ssp. formosus is high. Furthermore, strains KK and darker all originated from Africa south of the Sahara. Similarly the great bulk of individuals from strains MM and paler to BK in Fig. 8 is definitely referable to the type form. Only one field and two colonized strains out of these 15 samples are from the Ethiopian region. The 26 strains, PN paler to EO/2 and KD paler to VL, are more variable but have nevertheless a clear majority of individuals in pattern grade H. Of these 26 samples, eight field and five colonized strains are from the Ethiopian region but only four originated more than 100 km from the Coast. Of the remaining paler strains from CC to JD, some have a majority of individuals in pattern grade H but most individuals in the group as a whole would be unequivocally classed as var. queenslandensis. The only two African strains, GR and GA (both field), in the group are from the same coastal locality.

While the present data, from living populations, are thus not inconsistent with Mattingly's observations based on museum material they require different interpretation.

There is no question of the utility of the type form as designated and described by Mattingly (1957, 1965) at least in regard to the abdominal tergum. In the present study, pattern grade H outnumbered all other pattern grades in 41 out of the 74 samples and was the only pattern grade ever to occur exclusively in single samples (strains EO/1, PM, WL and PS). A majority of individual females in 49 out of the 74 samples and at least some in 71 were referable to the type form.

The only objection to the use of the arbitrary term var. queenslandensis is that in terms of the amount of variation it encompasses, it is called upon to do more work than any of the other names.

Subspecies formosus presents a different and difficult problem. If the diagnostic character of the absence of pale scaling on the first tergite is accepted, pure populations of ssp. formosus, if they exist at all, must be much rarer and more restricted geographically than suggested by Mattingly. Populations and laboratory colonies which most nearly approach the described ssp. formosus are often smaller and more active than those referable to the paler forms (Craig & Hickey, 1966). The morphological, ecological and ethological differences of these extreme populations compared with typical populations would be enough to justify sub-specific status were there not the evidence of mixed or intermediate populations. If the definitive amount of pale scaling on the first tergite is increased from zero to a necessarily arbitrary amount corresponding to some point in the G or H range of patterns (Fig. 1), one could state that populations with no paler individuals were typical of most inland localities in the Ethiopian region; however, the character overlap with populations outside this area would have increased. Thus attempts to define limits between one "subspecies" and the other, at least on the basis of abdominal scale pattern, seem to fail because of variability within populations and the lack of geographic discontinuity. If biological evidence for subspeciation becomes compelling, it is possible that taxonomic separation may be achieved with morphological characters other than those given by Mattingly.

As has been said before (McClelland, 1967), A. aegypti can at present be interpreted as a polymorphic rather than a polytypic species. The comparison of strains in the present study suggests clinal differences between populations with some, probably exposed to a more diverse environment, much more variable than others. This is more true of the paler strains and both paleness and variability have been associated with domesticity (Mattingly, 1957; Craig & Hickey, 1966).

Variation in relation to bionomics and zoogeography

Had the distinction between domestic, peridomestic, and so-called feral strains of A. aegypti been made on a sound ecological basis, it is possible that the distribution of the different populations in Africa would show a clearer pattern.

Unfortunately, the concept of "domesticity" in mosquitos is very anthropocentric because it is based on the proximity of their occurrence to man rather than on their biology; there is confusion between habitat and population. The same population of mosquitos regarded as "feral" when breeding in a forest becomes "peridomestic" if it persists after a human settlement replaces the forest, and if found breeding inside a house it is often regarded as "domestic". The important issue is its degree of dependence on, or preference for, the man-made habitat, and particularly its liberation from the seasonal cycle of rainfall and evaporation. However, there is no a priori reason to believe that discarded tires or other man-made containers, when exposed to rainfall, are in themselves more than substitutes for tree-holes or other natural breeding sites. On the other hand, populations which maintain a high level throughout the dry season inside a house must evolve behavioural adaptations to patterns of water storage and use that differ markedly from the natural cycle. Such populations can be termed truly domestic. In order to clarify future discussion, the following definitions are proposed.

Domestic population: a population that breeds continuously, independently of the natural rainfall cycle, in water stored by man in or around his dwellings.

Feral population: a population in which breeding is determined by the natural rainfall cycle, is not dependent on (though not necessarily uninfluenced by) human activities, and is not limited to the vicinity of human dwellings.

Domestic habitat: parts of human dwellings sheltered from rainfall and enclosed on at least three sides harbouring containers of water filled and emptied by man.

Peridomestic habitat: highly modified areas around human dwellings exposed to direct or indirect rainfall harbouring both natural containers of water and those provided or used by man.

Feral habitat: areas of natural or cultivated vegetation at any distance from human dwellings where the majority of containers are natural and where all containers are subject only to the natural cycle of rainfall and evaporation.

It is important to note that the peridomestic habitat, from which most collections listed in Table 1 were made, could support populations of either sort or be the interface between two and thus appear mixed.

In two localities in Kenya, it was possible to obtain samples from domestic populations dependent on stored water for comparison with those obtained outside houses, where breeding occurred in both natural and man-made containers. Strains GA, GI and GR from domestic habitats at Ganda were unequivocally paler than strains GB and GS from outdoor habitats in the same village. Nearly a decade later, several years of extensive antimalarial house-spraying had apparently eliminated the formerly abundant domestic populations. At this time, strain GM was collected inside an unsprayed mosque in a cistern supplied by piped water. Despite its habitat, strain GM was clearly homologous with the feral populations collected earlier (Fig. 8). Gongoni is in a drier area than Ganda with few natural breeding places. Strain GN from a truly domestic habitat was nevertheless paler than strain GV from man-made containers in the peridomestic habitat outside, even though strain GV is much paler than any other outdoor strain from Kenya or Tanzania. This probably is an example of an overflow from the domestic population inside the house meeting limited competition from, or admixture with, feral populations outside. Similar paired data are not available for strains RB and NM, but the situation in southern Tanzania (strain NM) is analysed in more detail in later papers (McClelland & Hartberg, in preparation; Hartberg & McClelland, in preparation).

Even small differences in pattern value may be significant. Thus of 11 field-collected strains from Tanzania (excluding the domestic strain NM), the palest three - KK, DM, BU - were also the only strains from within the limits of the large coastal city of Dar es Salaam where extensive surveys had failed to reveal any truly domestic populations. The MPV of strain KN

from inland Kenya should be interpreted as exceptional in view of the comment made earlier regarding the "spot" phenotype.

The average MPV of 21 Asian strains (Zone I in Fig. 8) is 5.04 while that of 11 New World strains (Zones C and S in Fig. 8) is 4.37. Five strains from Florida and Jamaica (KW, MA, MM, PN and JM), however, included females of pattern grade F, which occurred in no other strains outside Africa. The average MPV of these five strains is 3.00 while that of the remaining six New World strains is 5.50 - even greater than the figure for Asia. The reason for the occurrence of darker populations in the north-west Caribbean area is obscure. Strain MM, however, was derived from larvae found in the feral habitat of tree-holes which may indicate low domesticity. The transatlantic slave-trade would have offered many opportunities for the direct transport of A. aegypti from the humid parts of West Africa to comparable areas in the Caribbean, whereas the eastward spread of A. aegypti from Africa probably required intermediate stages of adaptation to the necessarily more domestic habitats in the intervening arid zones bordering the Arabian Sea. The data of the present study, gathered in a variety of ways over a long period of time, undeniably lack the quality to permit more detailed quantitative analysis.

CONCLUSIONS

The type form of A. aegypti as defined by Mattingly (1957) with a detailed description of the neotype (Mattingly, 1965) serves as a meaningful reference point for this very variable species.

Subspecies formosus as defined by Mattingly represents an extreme in the range of variation of A. aegypti which, although individually frequent in Africa south of the Sahara, is probably rare as a pure population. The feral behaviour attributed to this subspecies is, however, characteristic of populations with a wider range of morphological variation but it is clearly correlated with darker scale patterns. Subspecific status for the darker forms seems unjustified since they often occur variously mixed with paler forms, so that the necessary geographical discontinuity is absent.

The third form var. queenslandensis covers a disproportionate part of what is obviously a continuous range of variation in scale pattern of A. aegypti.

The use of the taxonomic labels formosus and queenslandensis tend to preserve an inflexible and oversimplified concept of the species A. aegypti which does not match the observed ecological and genetical plasticity. It is recommended that the use of these terms be dropped, unless they can be clearly defined in a biological sense. Until that is possible, individuals or populations should be simply characterized by use of an arbitrarily coded system such as is presented here or in terms of their resemblance to the type form.

If later evidence appears to indicate true genetic or geographical discontinuities within the species, suitable taxonomic terms should be redefined.

The concept of domesticity in populations should involve the degree of independence of breeding from the natural rain cycle as well as the degree of dependence of populations on human habitation. A clear distinction should be made between population and habitat characters, and the definitions proposed here should be adopted in future discussion.

On the basis of the present analysis populations in the north-west Caribbean area bear a greater affinity to African strains than do strains from Asia and elsewhere outside Africa.

SUMMARY

Aedes aegypti is currently considered to include a dark-coloured subspecies formosus which is restricted to Africa south of the Sahara and the type form. The latter is less dark, usually closely associated with man and found throughout the remaining range of the species as well as in coastal areas of Africa. Paler varieties of the type form have been termed var. queenslandensis.

Whereas individuals can be assigned to one of these taxonomic terms, the extent of variation in populations was not known.

Seventy-four samples of A. aegypti from 49 separate localities in 33 countries were reared in the laboratory and examined alive. The scale pattern on the abdominal tergum was classified according to an arbitrary scheme and given a numerical value which could be averaged for each sex within a sample.

Although populations from inland Africa south of the Sahara were darker than others, only variable proportions of the individuals could be classed as ssp. formosus. Similarly, individuals from samples outside the supposed range of ssp. formosus showed characteristics of that subspecies. Furthermore, the fact that many populations were mixtures of individuals resembling both subspecies in varying proportions indicated a lack of the necessary geographical separation for subspeciation.

It is suggested that A. aegypti be treated as a polymorphic rather than polytypic species unless biological evidence of genetic or geographic discontinuity forces a search for diagnostic morphological characters.

The description of the type form serves as a valid point of reference, but it is recommended that use of the terms ssp. formosus and var. queenslandensis be dropped and that variation of individuals or populations be expressed in arbitrary values in the manner of this study.

The ecology of the species would be better understood if a clear distinction were made between habitat and population and between the terms domestic, peridomestic, and feral. It is recommended that the definitions offered here be accepted.

TABLE 1. LIST OF ALL POPULATIONS OF *Aedes Aegypti* SAMPLED

Strain code	Name of strain Place and country of original field collection	Coordinates ^b		Month and year exam- ined	Generations/ Years in Lab.	Remarks	Habitat	Person responsible for collection or supply for this study	Sample size studied	
		Lat.	Long.						Males	Females
BK ^a	Bangkok Thailand	13°45'N	100°29'E	5-61	F1	parent larvae from field	P	C. Yamarat	7	9
BU	Buguruni Tanzania	6°49'S	39°15'E	9-68	-	reared from field larvae	P	Author	38	44
BV	Barquisimeto Venezuela	10°04'N	69°19'W	7-61	F1	parent larvae from field	P	M. Dorante	15	14
BW	Bwamba Uganda	0°42'N	30°04'E	9-68	F5	colony in Tanzania	P	G. Surtees	31	28
CC	Cucuta Colombia	7°54'N	72°31'W	10-60	2yr	colony in Indiana, USA	P	G. B. Craig jr	74	82
CO	Colombo Ceylon	6°56'N	79°51'E	9-61	F1	parent larvae from field	P	W. A. Samarawickrema	88	112
CR	Carriacou Island Grenadines	12°30'N	61°27'W	7-61	<1yr	colony in Trinidad	P	F. R. S. Kellett	88	87
CT	Calcutta India	22°35'N	88°21'E	8-61	F1	parent pupae from field	P	S. M. Ghosh	7	14
DB	Durban Rep. of South Africa	29°53'S	31°00'E	10-60	20Yr	colony in Johannesburg	P	J. Muspratt	27	21
DC	Dacca East Pakistan	23°43'N	90°25'E	4-62	<1yr	colony in city of origin	P	N. A. Kuraishy	81	74
DH/1	Delhi India	28°40'N	77°14'E	2-60	5yr	colony in city of origin	P	N. G. S. Rahgavan	52	70
DH/2	Delhi India	28°40'N	77°14'E	1-61	6yr	same colony as above	P	N. G. S. Rahgavan	131	79
DI/1	Djakarta Java, Indonesia	6°08'S	106°45'E	12-59	6yr	colony in Netherlands	P	J. Bonne-Wepster	24	22
DI/2	Djakarta Java, Indonesia	6°08'S	106°45'E	7-60	<1/2 yr	same colony as above	P	J. Belterman	17	24
DJ/1	Djakarta Java, Indonesia	6°08'S	106°45'E	9-61	7yr	colony in city of origin	P	R. M. Harris	73	80
DJ/2	Djakarta Java, Indonesia	6°08'S	106°45'E	8-68	1-1/2 yr	same colony as above	P	R. M. Harris	55	58
DM	Dar-es-Salaam Tanzania	6°48'S	39°17'E	9-61	-	reared from field larvae	P	Author	189	186
EK	Ernakulam Kerala, India	10°00'N	76°16'E	7-61	<1/2 yr	colony in city of origin	P	S. Pattanayak	26	51
EN	Entebbe Uganda	0°04'N	32°28'E	1-62	>5yr	colony in London, England	?	D. S. Bertram	90	58
EO/1	El Obeid Kordofan, Sudan	13°11'N	30°13'E	4-60	2yr	colony, Wad Medani, Sudan	P	M. Qutubuddin	17	19
EO/2	El Obeid Kordofan, Sudan	13°11'N	30°13'E	10-60	2-1/2 yr	as above + 1/2 yr in London	P	M. Qutubuddin	31	19
GA	Ganda Kenya	3°13'S	40°04'E	1-60	-	reared from field eggs	D	G. Oketch	34	27
GB	Ganda Kenya	3°13'S	40°04'E	11-60	-	reared from field eggs	D	G. Oketch	23	20
GI	Ganda Kenya	3°13'S	40°04'E	10-60	-	reared from field eggs	D	G. Oketch	12	19
GM	Ganda Kenya	3°13'S	40°04'E	7-70	-	reared from field larvae	D	Author	-	21
GN	Gongoni Kenya	3°02'S	40°08'E	7-70	-	reared from field larvae	D	Author	-	74
GR	Ganda Kenya	3°13'S	40°04'E	6-61	-	reared from field eggs	D	G. Oketch	2	7
GS	Ganda Kenya	3°13'S	40°04'E	4-61	-	reared from field eggs	D	G. Oketch	57	69
GV	Gongoni Kenya	3°02'S	40°08'E	7-70	-	reared from field larvae	P	Author	-	33
IL	Indonesia	--	--	5-61	?yr	colony in Netherlands	P	J. J. Laarman	45	33
IV/1	Isla Verde Puerto Rico	18°27'N	65°59'W	12-60	2yr	colony in Indiana, USA	P	G. B. Craig jr	72	81
IV/2	Isla Verde Puerto Rico	18°27'N	65°59'W	7-64	6yr	as above, 7yrs in Canada	P	A. W. A. Brown	248	95
JD	Jeddah Saudi Arabia	21°30'N	39°10'E	3-61	F1	parent larvae from field	P	S. Afifi	48	54
JM	Jamaica	--	--	2-62	<1/2 yr	colony in area of origin	P	P. Rice	110	137
KD	Kaduna Nigeria	10°28'N	7°25'E	3-61	2yr	colony in city of origin	P	M. W. Service	64	49
KJ	Kimbiiji Tanzania	6°59'S	39°32'E	9-68	-	reared from field larvae	P	Author	21	19

^a Strains are referenced in the text by a two-letter code

^b Where the place of original collection is not known exactly, the coordinates are those of the centre of the listed town

TABLE I. LIST OF ALL POPULATIONS OF AEDES AEGYPTI SAMPLES (continued)

Strain code	Name of strain Place and country of original field collection	Coordinates		Month and year exam- ined	Generations/ Years in Lab.	Remarks	Habitat	Person responsible for collection or supply for this study	Sample size studied	
		Lat.	Long.						Males	Females
KK	Kariakoo Tanzania	6°48'S	39°16'E	9-68	-	reared from field larvae	P	Author	18	15
KL	Kuala Lumpur Malaya	3°10'N	101°42'E	10-60	F1	parent adults from field	P	R. H. Wharton	145	97
KN	Karen Forest Nairobi, Kenya	1°20'S	36°44'E	5-61	F1	parent adult from field	P	E. C. C. van Someren	16	25
KR	Karachi West Pakistan	24°52'N	67°03'E	8-61	2yr	colony in city of origin	P	S. Ashrafi	46	57
KS	Karankasso Upper Volta	11°13'N	4°38'W	3-60	2yr	colony in London, England	P	J. Hamon	16	27
KT	Kaohsiung City Taiwan	22°38'N	120°17'E	7-61	3yr	colony in area of origin	P	J. C. Lien	34	25
KU	Kauriro, Tana River Kenya	0°08'S	38°12'E	5-62	F2	colony in Nairobi, Kenya	P	D. M. Minter	21	18
KW	Key West Florida, USA	24°34'N	81°48'W	10-60	<1yr	colony in Indiana, USA	P	G. B. Craig jr	96	117
MA	Miami Airport Florida, USA	25°46'N	80°17'W	5-61	F1	parent larvae from field	P	J. E. Porter	61	70
MF	Mafia Island Tanzania	7°50'S	39°50'E	7-70	F1	parent adult from field	P	R. Buxton	-	12
MG	Mbagala Tanzania	6°54'S	39°16'E	9-68	-	reared from field larvae	P	Author	25	18
MH	Milolii Kona Hawaii, USA	19°11'N	155°54'W	6-61	F1	parent larvae from field	P	P. Y. Nakagawa	40	69
MI	Mornington Isle Australia	16°33'S	139°24'E	11-60	?yr	colony, Sydney, Australia	P	A. R. Woodhill	25	52
MJ	Mboamaji Tanzania	6°52'S	39°25'E	9-68	-	reared from field larvae	P	Author	47	37
MK	Mkuranga Tanzania	7°07'S	39°12'E	8-68	-	reared from field larvae	P	Author	59	63
MM	Miami City Florida, USA	25°45'N	80°15'W	1-62	F2	colony in area of origin	P	J. E. Porter	331	284
MO	Morogoro Tanzania	6°49'S	37°40'E	11-60	-	reared from field eggs	P	D. F. Clyde	42	45
MP	Manila Philippines	14°36'N	120°59'E	1-61	?yr	colony in city of origin	P	F. E. Baisas	45	67
MU	Mikindu Tanzania	6°47'S	39°04'E	8-68	-	reared from field larvae	P	Author	58	72
MY	Mandalay Burma	22°00'N	96°05'E	3-62	F1	parent larvae from field	P	M. Tu	16	25
MZ	Manzessi Tanzania	6°47'S	39°13'E	9-68	-	reared from field larvae	P	Author	39	56
NM	Nambunga Tanzania	10°52'S	39°16'E	9-68	-	reared from field larvae	P	Author	116	196
NR	Nairobi Airport Kenya	1°19'S	36°56'E	6-60	F2	colony in city of origin	P	E. C. C. van Someren	11	21
PM	Paramaribo Surinam	5°52'N	55°14'W	3-61	F1	parent larvae from field	P	E. van de Kuyp	56	26
PN	Pensacola Florida, USA	30°26'N	87°12'W	5-61	F3	parent larvae from field	P	H. B. Morlan	56	65
PS	Pescadorees Isles Pescadorees Isles	23°30'N	119°30'E	3-61	3yr	colony in city of origin	P	J. C. Lien	65	23
RB	Rabai Kenya	3°57'S	39°36'E	7-61	-	reared from field eggs	D	M. Furlong	32	38
SG	Singapore City Singapore	1°20'N	103°50'E	2-61	F1	parent adults from field	P	A. Rudnick	49	28
SK	Salakope Ghana	5°47'N	0°35'E	11-61	F1	parent larvae from field	P	W. Z. Coker	123	116
SL	Salakope Ghana	Approximate only		9-61	F2	colony in Indiana, USA	P	G. B. Craig jr	103	60
SO	Sokode Etoe Ghana	6°35'N	0°25'E	11-61	F1	parent larvae from field	P	W. Z. Coker	95	127
SV	Suva Fiji	18°08'S	178°25'E	5-61	F1	parent larvae from field	P	W. H. McDonald	61	44
TR	Trinidad-Resistant Trinidad	--	--	3-60	4yr	colony in Indiana, USA	P	G. B. Craig jr	37	56
TS	Tiatiao Dakar, Senegal	14°45'N	16°36'W	2-61	F1	parent adults from field	P	E. Abbonen	137	99
TV	Townsville Australia	19°15'S	146°48'E	11-60	?yr	colony in Canberra, Austr.	P	D. H. Colless	58	47
WL	Waltair Andrah, India	17°45'N	83°25'E	5-61	F1	parent larvae from field	P	P. N. Ganapati	10	6
VL	Vellore India	12°56'N	79°09'E	4-61	F2	colony in city of origin	P	R. Reuben	95	99
YD	Yaoundé Cameroon	3°51'N	11°31'E	11-61	F1	parent larvae from field	P	H. Bailly-Choumara	51	47

TABLE 2. SCORE MATRIX FOR PATTERN GRADES OF ABDOMINAL TERGITES OF A. AEGYPTI

	Add score to base of one	Number of tergites brindled scores 1 x						
		0	1	2	3	4	5	6
Number of tergites medially pale scores 2 x	0	F ^a 1	G 2					
	1	H 3	J1 4	J2 5	J3 6	J4 7	J5 8	J6 9
	2	K0 5	K1 6	K2 7	K3 8	K4 9	K5 10	
	3	L0 7	L1 8	L2 9	L3 10	L4 11		
	4	M0 9	M1 10	M2 11	M3 12			
	5	N0 11	N1 12	N2 13				
	6	P0 13	P1 14					
	7	Q 15						

^a The figures at the bottom of each square are "colour values". These scores are obtained by adding twice the number of medially pale tergites and the number of remaining tergites that are brindled to a base of 1.

TABLE 3. FREQUENCY OF "SPOT" PHENOTYPES IN VARIOUS STRAINS

Strain	%	Strain	%
JD	78	MP	73
EK	55	DH/2	29
DH/1	22	KN	22
SL	17	KL	5
SK	5	CR	5
DJ/1	4	KT	3
GI	3	TS	3
CT	2	JM	2
MM	2	NM	1
VL	1	BV	^a +
GA	+	KD	+
KS	+	RB	+
SG	+		

^a Strains from which "spot" was subsequently isolated although absent phenotypically in the initial sample are recorded as (+). The presence of "spot" in other strains was not confirmed.

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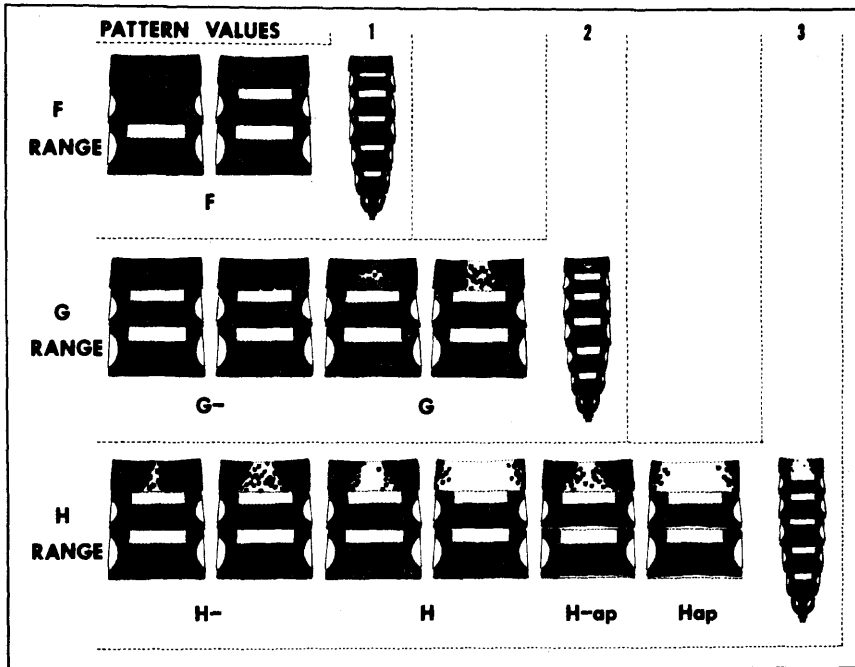


Fig. 1. Arbitrary pattern grades and pattern values corresponding to subspecies formosus and the type form of A. aegypti.

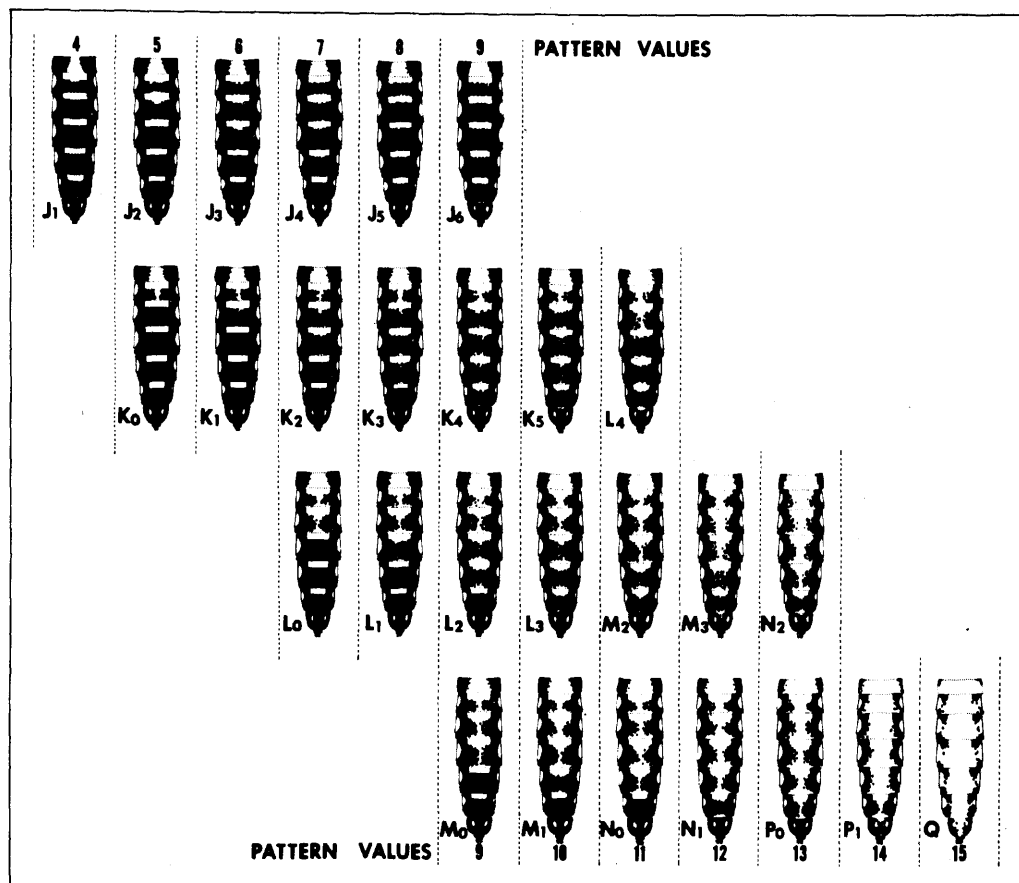


Fig. 2. Arbitrary pattern grades and pattern values corresponding to var. queenslandensis of A. aegypti.

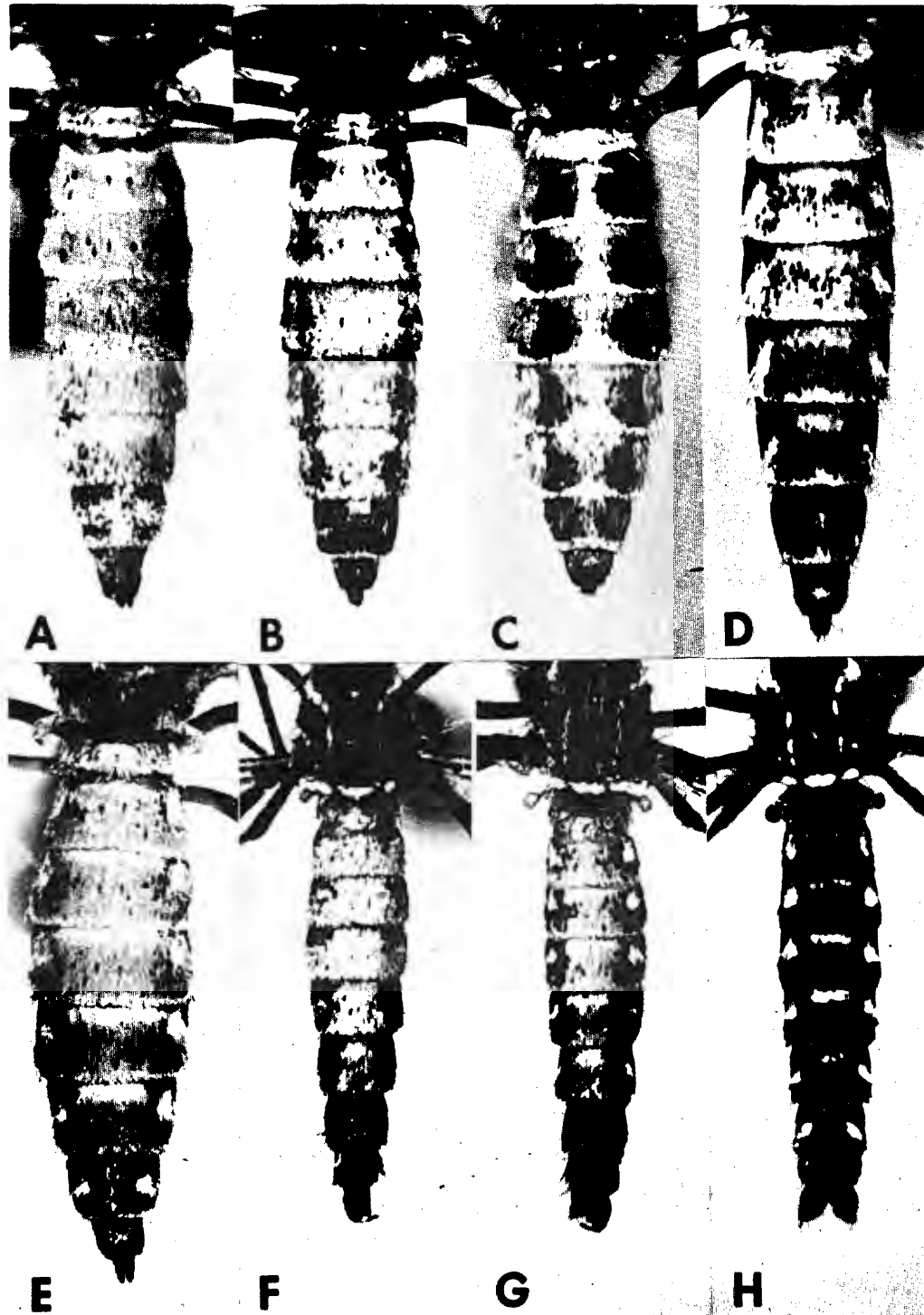


Fig. 3. Photographs of the abdominal dorsum of representative females and males of A. aegypti.

- A: strain JD, female, pattern grade Q, homozygous $\underline{S^g}$
B: strain MP, female, pattern grade P1, homozygous $\underline{S^g}$
C: strain SL, female, pattern grade Q, homozygous $\underline{S^g}$
D: strain KL, female, pattern grade M3, homozygous $\underline{S^w}$
E: strain JD, female, pattern grade Q, heterozygous $\underline{S^g}$
F: strain JD, male, pattern grade P0, homozygous $\underline{S^g}$
G: strain JD, male, pattern grade N2, heterozygous $\underline{S^g}$
H: strain MO, male, pattern grade F, homozygous $\underline{S^+}$

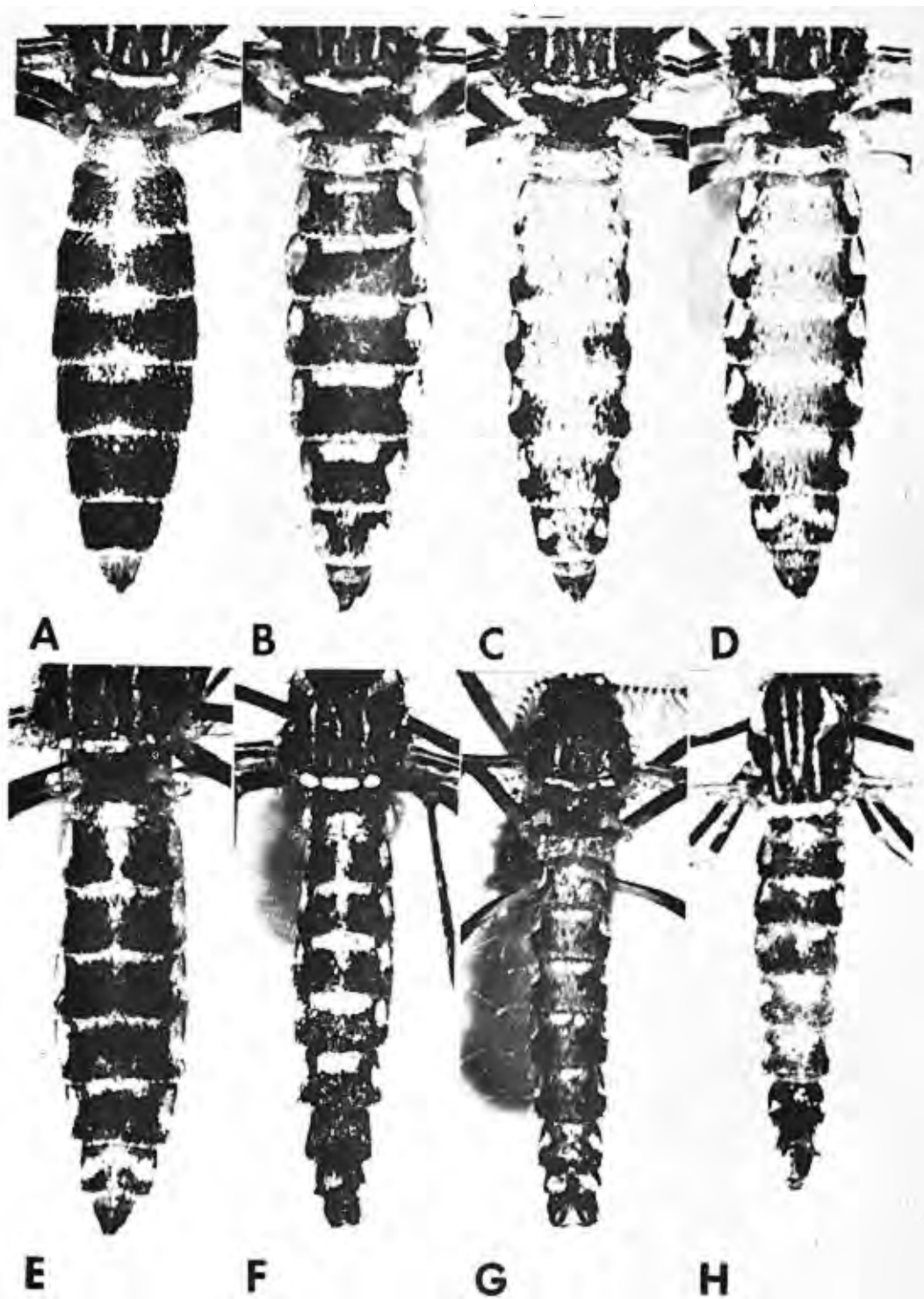


Fig. 4. Photographs of the abdominal dorsum of representative females and males of A. aegypti.

- A: strain GI, female, pattern grade K2, homozygous $\underline{S^1}$
- B: strain TS, female, pattern grade J1, homozygous $\underline{S^r}$
- C: strain GA, female, pattern grade Q, homozygous $\underline{S^+ pa}$
- D: strain IV/1, female, pattern grade Q, homozygous $\underline{S^+ pa}$
- E: strain KS, female, pattern grade K2, homozygous $\underline{S^p}$
- F: strain KS, male, pattern grade K2, homozygous $\underline{S^p}$
- G: strain GA, male, pattern grade N2, homozygous $\underline{S^+ pa}$
- H: strain IV/1, male, pattern grade J6, homozygous $\underline{S^+ pa}$

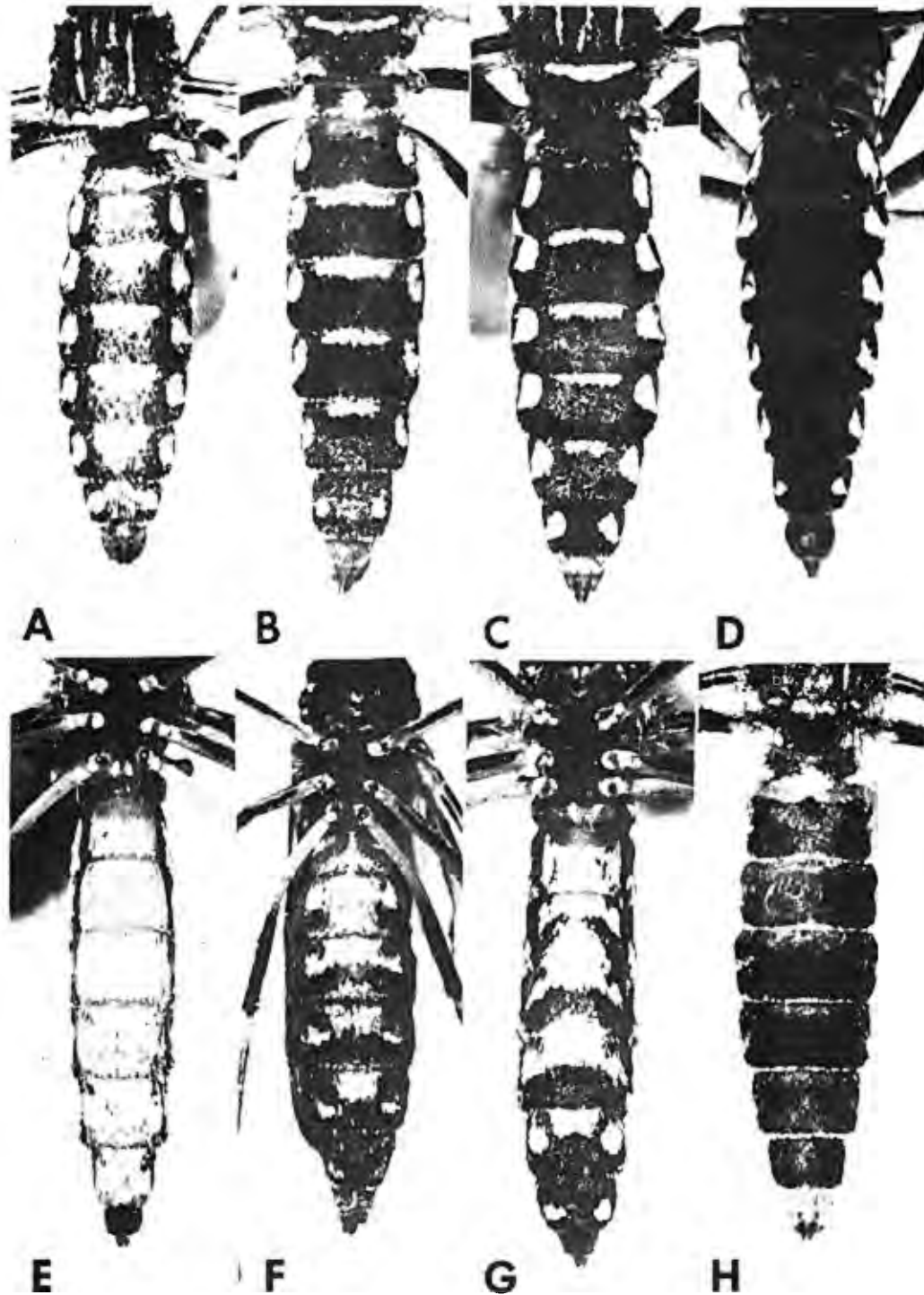


Fig. 5. Photographs of the abdominal dorsum and venter of representative females of A. aegypti.

- A: strain IV/1, female, pattern grade J6, homozygous $\overline{S^+}$ pa
 B: strain GA, female, pattern grade H ap, heterozygous $\overline{S^+}$
 C: strain YD, female, pattern grade F, homozygous $\overline{S^+}$
 D: strain SL, female, pattern grade F (without basal bands)
 E: strain TS, female (venter), pattern grade J1, homozygous $\overline{S^+}$
 F: strain IV/1, female (venter), pattern grade Q, homozygous $\overline{S^+}$ pa
 G: strain YD, female (venter), pattern grade F, homozygous $\overline{S^+}$
 H: strain GA, female, pattern grade H (without basal bands) homozygous $\overline{S^+}$

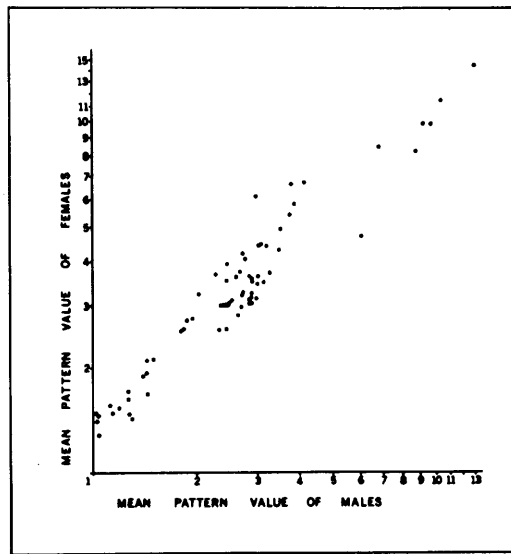


Fig. 6. Scatter diagram of Mean Pattern Value of males of *A. aegypti* plotted against the MPV of females in the same sample (double logarithmic axes).

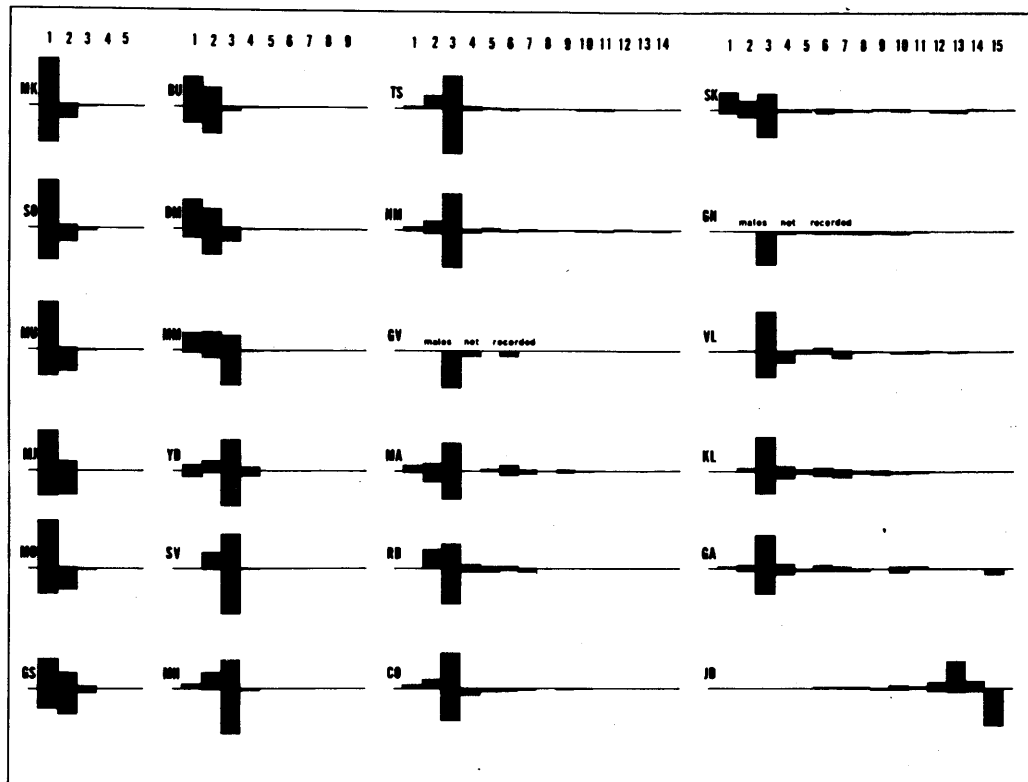


Fig. 7. Histograms showing frequency of males (plotted above baseline) and females (plotted below baseline) of given Pattern Value in each of 24 field strains of *A. aegypti*. Total bar area for each sex and strain is equal.

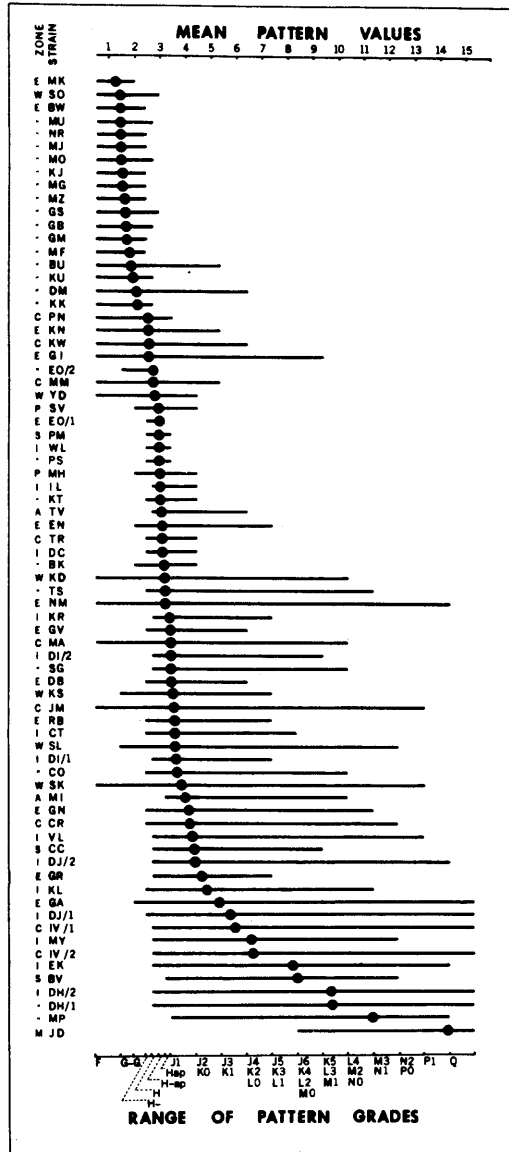


Fig. 8. Range of Pattern Grades (line) and Mean Pattern Value (solid circle) for females of 74 strains of *A. aegypti* arranged in sequence of increasing MPV. Zone code: E - East and South Africa; W - West Africa; C - Caribbean area (including coast of Florida, USA); P - Pacific Islands; S - South America; I - Indian sub-continent, E. and S.E. Asia; M - Middle East.