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EYE-STRIPES AND PIGMENTATION IN GRASSHOPPERS (ORTHOPTERA, ACRIDOIDEA): TYPES, BIOLOGICAL SIGNIFICANCE AND APPLIED IMPORTANCE

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(With 20 Text-figures and 1 Table)

INTRODUCTION

Eye-stripes and other pigment patterns in the compound eyes of grasshoppers (Orthoptera, Acridoidea) find casual mention in the older systematic literature, and it was not until more recent years, when attention was called to their physiological, biological and applied importance (Friza, 1929 ; Roonwal, 1936, 1947, 1949), that work was accelerated ; in some species, e.g., the Desert Locust, *Schistocerca gregaria*, eye-stripes are excellent indicators of polymorphism and population flux.

A limited study of eye-stripes was made by Volkonsky (1938a, b), Rao and Gupta (1939), Burnett (1951), Rao (1960), and Uvarov (1966). The histogy of acridoid eyes in relation to pigmentation and physiology of vision was studied by Friza (1929) and Roonwal (1947), while earlier studies are those of Leydig (1855, 1864), Exner (1891), Stefanowska (1892), Jörschke (1914), and Tümpel (1914). The chemistry of eye pigments has been investigated by Busnel and Drilhon (1942), Goodwin (1950, 1952), Goodwin and Srisukh (1951), and Linzen (1959) ; pigmentary movements by Pinamonti *et al.* (1973) ; and some aspects of eye physiology by Whittington (1951), Fernández-Moran (1958), Wallace (1958, 1959), Cosens (1966), Wolken (1971), Pinter (1972), and Rafi and Burtt (1974)

The present account is a comparative study of the distribution and characteristics of eye-stripes and other types of pigmentation in a considerable number of Acridoidea belonging to two principal families (the Pyrgomorphidae and the Acrididae) : 12 subfamilies, 47 genera, and 67 species and subspecies (48 for the first time) : The various types have been classified and their biological significance and applied importance discussed as regards phylogeny, taxonomy, polymorphism, geographical,

climatic and sexual variations, the number of moults, population flux, and the prediction of swarming.

Material and Methods

Most of the species and subspecies discussed here were examined either as fresh, living specimens or as dry museum examples ; in a few cases, accounts were taken from published sources. In dark, heavily pigmented eyes, examination in strong incident light (strong direct sunlight is handy) is necessary to discern the stripe and other patterns. The study of postembryonic development in some species (*Schistocerca gregaria* and *Nomadacris septemfasciata*, etc.) has shown that the stripes develop at the anterior eye-margin (the main region of growth) and travel to the posterior, so that the most posterior stripe is the first to develop, and the most anterior one the last ; the serial numbering of stripes should, accordingly, begin from the posterior end.

The taxonomic classification followed is that of Dirsh (1961) and Uvarov (1966) ; the monograph of Bei-Bienko and Mistchenko (1951a, b) and Tandon's (1976) Check-list were also helpful.

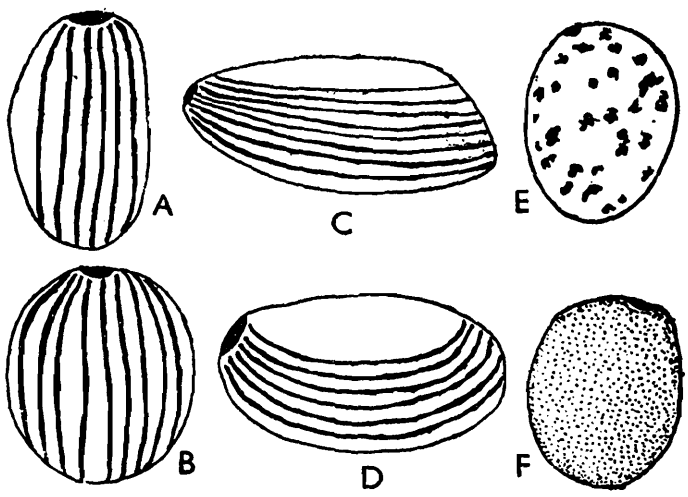
Types of Eye Pigmentation in the Acridoidea

On the basis of present knowledge (67 species and subspecies are discussed here), it is now possible to discern the basic types of patterns of eye pigmentation in the Acridoidea.

1. *The basic types of patterns* (Text-fig. 1)

The two eyes are elongate-oval to subround, and bulge out more or less from the head-surface. On the head they lie either vertically (most species) or obliquely to horizontally (in species with a forwardly projecting, snout-like head : *Atractomorpha*, *Acrida*, etc.). At the dorsal end in vertical eyes (and the front end in horizontal eyes) lies a small, sharply defined, dark, chocolate-coloured patch, the dorsal spot. In most cases it is spindle-shaped and abuts on the eye-margin, but in *Acrotylus* and *Trilophida* (Oedipodinae) it is hammer-shaped and a portion of it lies away from the margin. Below the dorsal spot lies a thin, pale line, the subdorsal streak (Roonwal 1936, 1947). Occasionally (*Aulacobothrus* sp.), another small dark patch, almost a 'second dorsal spot', lies below the subdorsal streak. The rest of the eye is pigmented in two principal patterns, viz., striped and unstriped. In the former case there are a number (about 4-10) of vertical (many species) or oblique to horizontal (*Atractomorpha*, *Acrida*, etc.), brown, olive or chocolate-coloured stripes running the entire length of the eye and alternating with similar but paler (often dirty white or cream coloured) lines, the inter-

stripes. The stripes may be either substraight and parallel or curved and subconcentric (being bent downward or anteriorward in some oblique or horizontal eyes). A type with 'curved and concentric' stripes has been mentioned by Rao and Gupta (1939), but this is doubtful (vide



Text-fig. 1. The principal types of eye-pigmentation in grasshoppers (Acridoidea). Type I. With stripes : (A) With vertical and parallel stripes in an elongate-oval eye. (B Same, in a rounded eye. (C) With horizontal and subparallel stripes. (D) With horizontal, curved and subconcentric stripes. Type II. Without stripes. (E) Mottled and marbled. (F) Plain (uniformly pigmented).

below). Occasionally, a wide, brownish band lies at the posterior end of the eye, and at the extreme posterior edge a narrow chocolate streak (almost in continuation with the dorsal spot), the posterior streak, is found (*Acrida, Trilophida*). Whether these two structures represent true stripes or are structures *sui generis* can only be elucidated by a study of postembryonic development. Unstriped eyes are mottled with irregular patches of colour.

The following types and subtypes may be distinguished :—

Type I. Eyes with stripes.

Category A. Stripes vertical.

Group 1. Stripes vertical, substraight and parallel.

(a) Stripes generally complete, not interrupted (Fig. 1A).

(b) Some stripes interrupted.

Group 2. Stripes vertical, curved and concentric (doubtful type).

Category B. Stripes oblique to horizoutal.

Group 1. Stripes oblique to horizontal, substraight and parallel.

(a) Stripes generally complete (Fig. 1C).

(b) Some stripes interrupted.

Group 2. Stripes oblique to horizontal, curved and subconcentric (Fig. 1D).

Type II. Eyes without stripes.

Category A, Eyes mottled.

Group 1. Mottling 'uniform' all over eye, sometimes interrupted by pale bands (Fig. 1E).

Group 2. Mottling not uniform ; one half of eye paler, the other (usually the lower half) much darker.

Category B. Eyes not mottled but uniformly coloured in one or more hues (brown, brownish black, grey, blue, yellow, etc.) (Fig. 1F).

2. *The distribution of various types*

The known distribution of the various types of pigment patterns in the different families and subfamilies is given below.

Type I. Eyes With Stripes

Category A. Stripes vertical

Group 1. Stripes vertical and parallel

(a) Stripes generally complete (not interrupted)

Pyrgomorphidae :

Chrotogonus cavus, *C. trachypterus trachypterus* (sometimes a few stripes interrupted, *see* below).

Acrididae :

Calliptaminae : *Acorypha glaucopsis*, *Calliptamus italicus*.

Cyrtacanthacridinae : *Anacridium aegyptium*, *A. melanorhodon*, *A. rubrispinum*, *Cyrtacanthacris tatarica*, *Nomadacris septemfasciata*, *Pachyacris vinosa*, *Patanga succincta*, *Schistocerca cancellata* (syn. *paranensis*), *S. gregaria*.

Dericorythinae : *Dericorys ramachandrai*.

Eyprepocnemidinae : *Eyprepocnemis alacris*, *E. polarans ornatipes*, *Heteracris littoralis asiaticus*, *H. l. littoralis*, *H. littoralis* ?subsp.

Gomphocerinae : *Ochrilidia* sp.

Hemiacridinae : *Spathosternum prasiniferum prasiniferum, Spathosternum* sp.

Oedipodinae : *Oedaleus abruptus, O. senegalensis, Oedaleus* sp.

Romaleinae : *Teratodes* sp.

(b) Some stripes interrupted

Pyrgomorphidae :

Chrotogonus trachypterus trachypterus (sometimes complete, *see* below).

Acrididae :

Acridinae : *Aulacobothrus* (=*Phorenula*) sp.

Catantopinae : *Catantops pinguis innotabilis, C. p. pinguis, Xenocatantops humilis humilis.*

Eyprepocnemidinae : *Choroedocus robustus.*

Hemiacridinae : *Hieroglyphus banian, H. nigrorepletus.*

Oxyinae : *Oxya hyla hyla, Oxya* sp.

Group 2. Stripes vertical, curved and concentric (doubtful type)

Of this type Rao and Gupta (1939) gave three examples from the Pyrgomorphidae (*Chrotogonus* sp., *Colemania sphenarioides* and *Pyrgomorpha* sp.). I have examined *Chrotogonus t. trachypterus* whose round eyes are greatly swollen (almost hemispherical) and have 6-10 vertical stripes which are subparallel (Fig. 7), not concentric. The eyes bulge out in all Acridoidea, but the excessive bulging in *Chrotogonus* may have induced Rao and Gupta to regard the stripes as "curved". I have no examples of *Colemania* and *Pyrgomorpha,* but the above considerations would suggest that here too the stripes may not be "curved and concentric".

Category B. Stripes oblique to horizontal

In some genera with long snouts (*Atractomorpha, Acrida*), the eye and its structures have undergone a forward turning of up to a right angle. As a result, in extreme cases the dorsal spot comes to lie at the front (anterior) end, the anterior margin becomes ventral, and the posterior margin dorsal ; the vertical stripes become horizontal or nearly so, but the mutual relationship of these parts remains unchanged. The stripes may be parallel (*Acrida*) or downwardly curved and subconcentric (*Atractomorpha*), but no truly concentric stripes have been recorded. In *Acrida* sp. a thin, chocolate-coloured streak (of the same colour as, and almost in continuation with, the dorsal spot) runs

along the dorsal (posterior) margin (Figs. 9B, C), and a brown band covers the posterior one-fifth. Whether these two structures are homologous with true stripes or are *sui generis* can only be determined by a study of postembryonic development.

Group 1. Stripes oblique to horizontal, substraight and parallel

(a) Stripes generally complete

Acrididae :

Acridinae : *Acrida* sp.

(b) Some stripes interrupted

Pyrgomorphidae :

Pyrgomorpha bispinosa deserti, *Pyrgomorpha* sp.

Acrididae :

Acridinae : *Acrida exaltata*.

Group 2. Stripes oblique to horizontal, curved and subconcentric

Pyrgomorphidae :

Atractomorpha crenulata, *Atractomorpha* sp.

Acrididae :

Acridinae : *Gonista* sp., *Orthoctha indica*.

Type II. Eyes Without Stripes

Eyes devoid of stripes ; either mottled with irregular patches or uniformly coloured without any mottling.

Category A. Eyes mottled

Eyes mottled with irregular patches of white, cream, yellow, brown or chocolate. Mottling may be uniform throughout the eye (though sometimes interrupted by one or more pale bands) ; or the eye is divided into two regions, a paler half and a much darker (usually lower) half, giving the false impression of a "double eye".

Group 1. Mottling uniform all over eye (sometimes interrupted by pale bands)

Acrididae :

Acridinae : *Chloebora crassa*, *C. marshalli*, *Phlaeoba infumata*, *P. panteli*, *Phlaeoba* sp.

Coptacridinae : *Eucoptacra praemorsa*.

Eyprepocnemidinae : *Choroedocus illustris*.

Gomphocerinae : *Dociostaurus* sp.

Oedipodinae : *Acrotylus humbertianus*, *Gastrimargus africanus orientalis*, *Locusta migratoria*, *Oedipoda coerulescens*, *Pyrgodera* sp., *Sphingonotus coerulans*, *Sphingonotus* sp.

Group 2. Mottling not uniform ; one half of eye darker than the other (usually the lower half much darker)

Acrididae :

Acridinae : *Dittopternis venusta.*

Oedipodinae : *Psophus stridulus, Trilophida annulata.*

Category B. Eyes not mottled but uniformly coloured in one or more hues

Pyrgomorphidae :

Aularches punctatus, Poekilocerus pictus.

Acrididae :

Eyprepocnemidinae : *Cataloipus indicus.*

Gomphocerinae : *Stenobothrus* sp.

BIOLOGICAL SIGNIFICANCE AND APPLIED IMPORTANCE

1. *Eye pigmentation in relation to phylogeny and taxonomy*

There are indications of a limited relationship between the types of eye pigmentation and phylogeny, but there are important exceptions. In the family Pyrgomorphidae eyes are striped in some genera *(Atractomorpha, Chrotogonus, Pyrgomorpha)*, and unstriped and uniformly pigmented in others *(Aulacrches, Poekilocerus)*. In Acrididae also eyes may be striped or unstriped. As far as known, some subfamilies show considerable uniformity of pattern (eyes are vertically striped in all Calliptaminae, Catantopinae and Cyrtacanthacridinae ; unstriped and mottled in most Oedipodinae ; and of several types in the Acridinae, Eyprepocnemidinae, Gomphocerinae, etc.). Generally, there is uniformity within a genus, but there are exceptions : In *Choroedocus* (Eyprepocnemidinae) the eyes are mottled in *C. illustris* and striped in *C. robustus* (Fig. 15).

Separation of species : To a certain extent differences in the pigment pattern of eyes have been used to differentiate species of a genus *(Melanoplus)* in a limited geographical area (Handford, 1946).

2. *Geographical variation in eye-stripes*

In *Anacridium aegyptium* (Volkonsky, 1938a, b ; and Roonwal, present account) there are fewer stripes in the northern latitudes (France, 5-7) than in the southern (North Africa and South Asia, 7-8). The same phenomenon is noticeable in *Calliptamus italicus* (Volkonsky, 1938a, b), which has 5-7 stripes, mostly 5 and 6, in the northern latitudes (Southern Europe) and 6-7 (in nearly equal numbers) in the southern (North Africa). In *Acrida exaltata* from South Asia, the more western examples (Baluchistan) have more stripes (6-10) than those from further southeast (Central India, 4-7).

3. *Eye-stripes in relation to season*

There are some early claims that in the Desert Locust, *Schistocerca gregaria*, the number of eye-stripes is related to season. Thus, Rao (1937, p. 41) observed that more 6-striped forms are produced in spring and summer (in coastal Baluchistan) and more 7-striped ones in the monsoon and winter (in the neighbouring Sind-Rajasthan desert). He further (1938, p. 18) stated that individuals with a reduced number of stripes, 5, were produced in the laboratory in September in 1936, and again in August-September next year. Due to paucity of data it is not possible to critically evaluate these relationships.

4. *Eye-stripes in relation to temperature*

The only suggestion that breeding temperature may affect eye-stripe number is by Husain and Ahmad (1936) who bred crowded hoppers of *Schistocerca gregaria* at various constant temperatures. At 24° C eyes are almost uniformly reddish brown, without any stripes, in all the five hopper stages ; at 33° C stages I and II are unstriped, III and IV have 3 reddish stripes each, and V has 5 stripes ; at 40° C the same occurs, except that in both III and IV stages 4 stripes are mentioned ; at 44° C, in conformity with the rest of the body, the eyes lose nearly all pigment and are whitish except that in stage IV 2, and in stage V 3, very fine light brown stripes are seen. Since in normal postembryonic development at ordinary temperatures, one stripe is usually added at each moult (Roonwal, 1947) the above results do not convey a very clear picture, and further work is necessary to eiucidate the effect of temperature.

5. *Eye-stripes in relation to sex* (Table 1)

In *Schistocerca gregaria* (Roonwal, 1936, 1941, 1945, 1954), in the *solitaria* phase, the proportion of females in a population increases with the number of eye-stripes, the ♂ : ♀ ratios being 60 : 40 in 6-striped, 35 : 66 in 7-striped, and 29 : 71 in 8-striped populations. In phase *gregaria*, where all individuals are 6-striped, the proportion is 50 : 50. According to Volkonsky (1938a, b), in *Anacridium aegyptium* males constitute 100% in 5-, 62.1% in 6-, 50.4% in 7-, and 30.7% in 8-eye-striped populations ; in *Calliptamus italicus* males constitute 100% in 5-, 62.7% in 6-, and 0% in 7-eye-striped populations.

From data in the present account it is seen that a similar trend is noticeable in a number of other species (Table 1).

On this basis, the following tentative rule may be given :—

Where sexual differencss in eye-stripes exist in a species, stripes

tend to be fewer in males than in females. (Put in another way, to characterise a mixed population, we may generalise thus : In a species population in an area the male ratio is higher in samples with fewer eye-stripes than in those with more numerous stripes.)

Table 1.—Variation in number of eye-stripes in relation to sex in some Acridoidea.

Species	Number of eye-stripes	
	Males	Females
Fam. Pyrgomorphidae		
1. *Chrotogonus t. trachypterus*	4-6 (mostly 5)	4-8 (mostly 5 and 6)
Fam. Acrididae		
2. *Acrida exaltata*	4-9	5-10
3. *Anacridium rubrispinum*	7-8 (mostly 7)	7-8 (mostly 8)
4. *Nomadacris septemfasciata*	7-9 (mostly 7 and 8)	7-9 (mostly 8)
5. *Oedaleus abruptus*	4-5 (mostly 4)	4-6 (mostly 5)

A satisfactory explanation of this sex-linkage is not forthcoming. Since generally one stripe is added at each moult, it could be that males undergo a moult or two less. While this does happen in some Acridoidea (vide Uvarov, 1966, p. 286), none of the species mentioned above (except *Anacridium aegyptium* occasionally) shows this difference. Some other explanation has, therefore, to be looked for, and genetic linkage is one possibility. Further work on this interesting phenomenon should be of interest.

6. *Eye-stripes in relation to moulting*

In *Schistocerca gregaria* Roonwal (1937, 1946, 1947) showed that while generally a stripe is added at each moult (beginning with one stripe in the first stage hopper, thus resulting in a 6-striped adult after 5 moults), 7-striped adults result in two ways (the majority, c. 75 %, by an extra moult leading to an additional stripe, and a few, c. 25 %, where an extra stripe is added in a hopper without an extra moult). Thus, both 'stripe-positive' and 'stripe neutral' moults occur (for details *see* Roonwal, 1947). Some workers have claimed an *absolute* correlation between the number of eye-stripes and the number of moults (Mukerji and Batra, 1938 ; Volkonsky, 1938a, b ; Rao and Gupta, 1939), but the correlation is only partial, as confirmed in *Nomadacris septemfasciata* by Burnett (1951) who

stated as follows :—"It will be seen that the number of eye stripes is not perfectly correlated with the number of instars passed through, in contrast with the report of Mukerji and Batra (1938) on *Schistocerca gregaria* (Forsk.), as has been noted already by Roonwal (1940, 1946)."

It is obvious that the adult number of eye-stripes cannot be reliably used to determine the number of moults in a species.

7. *Eye-stripes as indicators of phases and of population flux : Prediction of swarming*

Phases and population flux

In *Schistocerca gregaria* it has been established that eye-stripes are indicators of phase variations and of population flux (Roonwal, 1936, 1947, 1949, 1954, 1958), the swarming or *gregaria* phase individuals having 6-striped and deeply pigmented eyes, and the nonswarming or *solitaria* ones 5- to 8- striped (mostly 6-7) and weakly pigmented eyes. Laboratory breedings support these field results. Thus, Rao (1938) noted in India that hoppers bred crowded produced more 6-striped individuals, and Volkonsky (1938a, b) found the same feature in North Africa : hoppers produced 6-striped adults when bred crowded and both 6- and 7-striped ones when bred isolated.

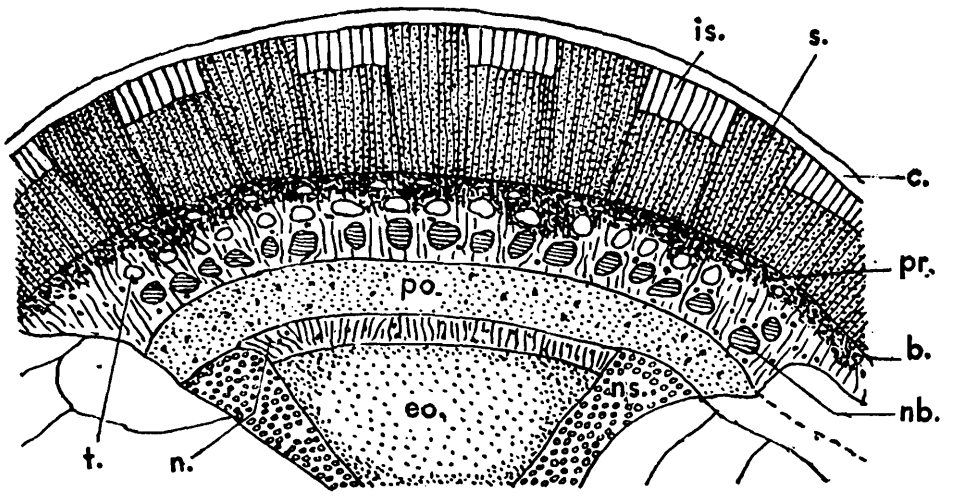
On these bases and on other correlated evidence, Roonwal (1954) has called attention to a new type of evolutionary effect, viz., the sharp increase of variation in low minimum populations and the decline and virtual extinction of it in high populations in *S. gregaria*. In the same paper he has correlated this feature with the shrinkage or spread of total world distribution of the species in plague and nonplague years (for world distribution, also *see* Waloff and Conners, 1964).

Prediction of swarming

Since the number of eye-stripes in some locusts has proved to be correlated with swarming (high populations and *gregaria* phase), they have been used for the practical task of predicting swarming. In the Desert Locust, *Schistocerca gregaria*, Roonwal (1945) gave a number of hypotheses, the first of which is as follows :—"If in a sufficiently large sample of a *solitaria* population, the proportion of 6-eye-striped individuals rises above about 80 per cent (maximum figure ; average 70.4 per cent), and tends towards 100 per cent, that population is rapidly on its way towards swarming...". Other hypotheses have been put forth by Nair (1952) and Roonwal and Misra (1952). These hypotheses are used in South Asia by locust warning organisations for assessing population trends. (Also see discussion by Bhanotar, 1975.)

8. *Eye-stripes and vision* (Text-figs. 2-4 ; 13)

The earliest studies on the structure of acridoid eyes, which paved the way for future detailed studies and an understanding of acridoid

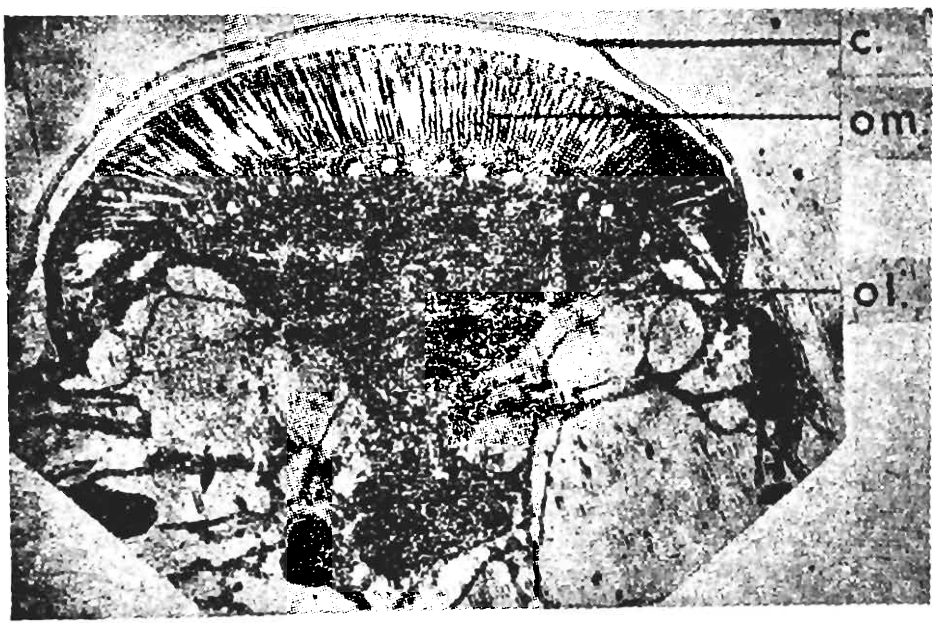


Text-fig. 2. *Schistocerca gregaria.* Longitudinal-vertical section through the striped eye of a phase *solitaria* fifth instar hopper, to show distribution of brown pigment in the stripe and interstripe regions, etc. Semidiagrammatic.

b., basement membrane ; *c.*, cornea ; *eo.*, epiopticon ; *is.*, interstripe region (pigment is absent in the secondary pigment cells) ; *n.*, layer of nerve cells ; *nb.*, bundle of nerve cells ; *ns.*, sheath of nerve cells ; *po.*, periopticon ; *pr.*, postretinular pigment layer ; *s.*, stripe region (pigment is present in the secondary pigment cells and is visible externally as a stripe); *t.*, trachea.

vision, are those of Lydig (1855, 1864), Exner (1891), Stefanowska (1892), Jörschke (1914) and Tümpel (1914).

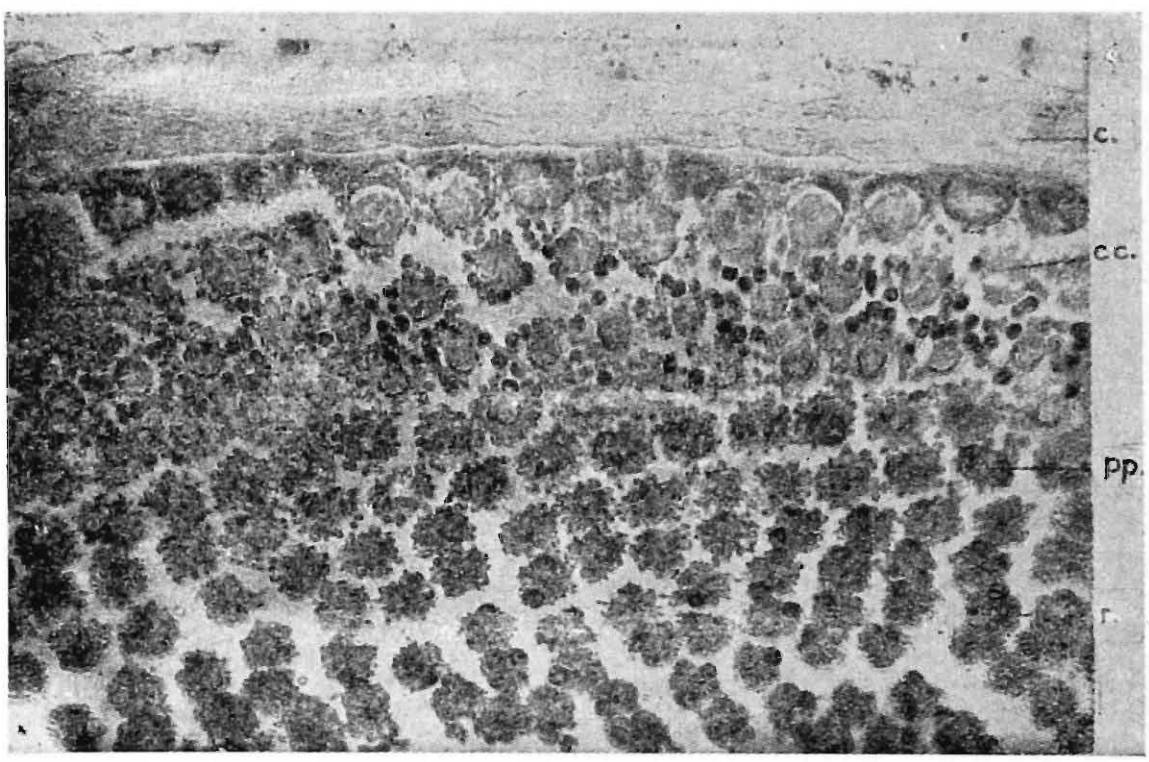
The significance of eye-stripes for vision has been discussed theore-



Text-fig. 3. *Schistocerca gregaria.* Photomicrograph of a vertical-longitudinal section (bleached and stained with Delafield's haematoxlin and eosin) of the eye of a 4th stage phase *gregaria* hopper.

c., cornea ; *ol.*, optic lobe ; *om.*, ommatidia.

tically. Chauvin (1941) thought that vision may help in the gregarisation of hoppers, but gave no details. Friza (1929) and Roonwal (1947) have shown in detail that differential distribution of pigment in striped and nonstriped eyes may cause differences in image formation (Figs. 2-4). Roonwal (l. c.) has correlated this feature with behavioral differences in the field in *solitaria* and *gregaria* phases in *Schistocera*



Text-fig. 4. *Schistocerca gregaria*. Photomicrograph of a section through the eye of a phase *solitaria* 5th stage hopper with transversely cut ommalidia at various levels. Bleached and stained with Delafield's haematoxylin and eosion.

c., cornea ; *cc.*, crystalline cone ; *pp.*, primary pigment cells ; *r.*, retinula.

gregaria ; the striped eyes of the former phase produce a diffuse image and locusts are unable to stand bright sunlight, while the 'nonstriped' eyes of phase *gregaria* produce a sharp image as well as cut out excessive light, thus enabling the locusts to go out boldly in bright sunlight. Roonwal (1958) has further shown that the sharp image in *gregaria* eyes assist in the maintenance of gregarisation. Wolken (1971), Pinter (1972) and Rafi and Burtt (1974) have discussed some aspects of image formation in the eyes of hoppers and adults in *Schistocerca gregaria*, but differences in pigment distribution in the two phases were apparently not kept in view.

9. *Ege-size in relation to phase and eye-stripe polymorphisms*

In the Desert Locust, *Schistocerca gregaria*, Roonwal and Bhanotar (1977) have found that in both length and width the eyes are significantly

smaller in phase *gregaria*. Within the *solitaria* phase, where 5- to 8-striped polymorphs occur (mostly with 6 and 7 stripes), eyes in 7-striped individuals are larger than in 6-striped ones by c. 3.1-7.4 per cent. The length and width are strongly correlated positively, the correlation coefficient being higher in females than in males. The ratio Width/Length varies within narrow limits (means 0.648-0.664) and shows no significant differences in respect of phase, sex and eye-stripe categories ; thus, irrespective of the size of eye, its shape remains nearly constant. In both length and width sexual dimorphism is lower in phase *gregaria* than in *solitaria* by c. 2.83-9.52 per cent ; no sexual dimorphism it evident in the ratio Width/Length. The presence of smaller eyes in phase *gregaria* as compared to *solitaria* is probably a device to reduce the amount of strong sunlight from entering the eyes, and seems to be correlated (along with other adaptations, such as the differences in the distribution of eye-pigment and the presence of an antihalation pigment layer, vide Roonwal, 1947) with differences in the flying and marching habits in the two phase —phase *gregaria* hoppers go out boldly into the sun and adults fly in the day, while *solitaria* phase hoppers avoid strong sunlight and hide inside bushes and adults fly mostly at night.

Eye-shape, while showing no phase polymorphic differences in adults, changes during postembryonic growth. In *Schistocerca gregaria* (Roonwal and Rao, 1977) the shape changes from elongate-oval to broadly oval, the mean ratio Width/Length gradually increasing in males from 0.4518 to 0.6274. A nearly similar change of shape occurs in the Red Locust, *Nomadacris septemfasciata* (Burnett, 1951).

10. *Eye-stripes and concealment*

The acridoid body is often cryptically coloured, but the bulging eyes could give the insect away were it not for the disruptive effect of eye-stripes and eye-mottling, which are common patterns among grass-hoppers. In contrast, some species with bright, warning colours (*Aularches* spp.) have apparently no use for the disruption device, and have almost uniformly coloured eyes. For the Desert Locust, *Schistocerca gregaria*, it is the common experienee of field workers that *solitaria* phase individuals (which have fawn or bluish-grey bodies and striped eyes) are almost invisible, and one can pass within a metre or two of a locust without spotting it unless it betrays its position by movement. Similarly, the green *solitaria* hoppers (also with striped eyes) are effectively concealed among the desert bushes. The stripes thus have an additional adaptive function.

Cott (1940, pp. 88-89) mentions the presence "ocular stripes" in several grasshoppers in conncealment, giving examples from widely separated areas, e.g., South America (*Diponthus bivittatus*, *Oxybleptella sagitta*, *Adimantus brachypterus*), Africa (*Oxya minor*, *Oraistes punctipennis)* and Australia *(Gesonia* [*Gesonula*] *mundata).* However, Cott evidently does not mean true eye-stripes in my sense, as in his Fig. 29 (*Oraistes punctipennis,* the only species he figures) the eye itself is unstriped but there is a horizontal stripe running on the head and body in the level of the eye and enclosing that organ in its sweep.

11. *Abnormalities in eye-stripes*

Volkonsky (1938a, b) noted that in a group of *Anacridium aegyptium*, whose development was slowed down from the fourth stage onward as a "result" of a sudden lowering of rearing temperature, all individuals had stripe nos. 2 and 3 relatively narrower and closer to each other ; in other groups, where development proceeded uniformly, this peculiarity was never observed. In a male, stripes 2, 3 and 4 in the right eye were fused into one ; this condition Volkonsky attributed to the removal of the right antenna during the course of the second moult, but with what justification it is difficult to assess. In other cases he noticed the fusion of stripes 2 and 3 in both the eyes ; the frequency of such anomalies was not more then 0.2 per cent. Asymmetry in the number of eye-stripes in the right and left eyes in *Schistocerca gregaria* has been reported by Bhanotar (1959) and Bhanotar and Mahto (1974).

Descriptions of Eyes in Various Species

Brief descriptions of eye pigmention in 67 acridoid species (10 Pyrgomorphidae and 57 Acrididae) are given below.

Family I. Pyrgomorphidae

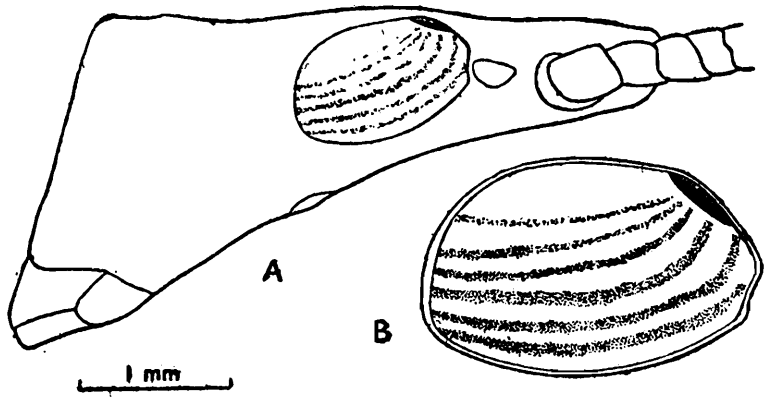
1. **Atractomorpha crenulata** (Fabricius)
(Text-fig. 5)

Material : India (Rajasthan, Uttar Pradesh and Madhya Pradesh), ♂ ♂, ♀ ♀, both living and dry examples.

Eyes elongate-oval (♂ ♂ 1.3 mm x 0·8 mm ; ♀ ♀ 1.8 mm x 1.5 mm), horizontal, with 4-7 horizontal, downwardly curved, subconcentric, olive green to dark brown stripes ; the upper (posterior) 2 or 3 stripes interrupted (sometimes all stripes interrupted by one or two oblique white bands). Interstripes dirty white ; dorsal spot chocolate-coloured ; dorsal streak thin, pale yellow.

Agrawal (1955) stated that the first stage hopper has yellowish eyes

with one curved, olive-green stripe, and thereafter a stripe is added at each of the five moults.



Text-fig. 5. *Atractomorpha crenulata* (Pyrgomorphidae), Varanasi, India. ♂. (A) Head, in side view. (B) Right eye, enlarged.

2. **Atractomorpha sp.**

Material : SOUTH ASIA (Baluchistan Coast : Pasni), ♀, a living example.

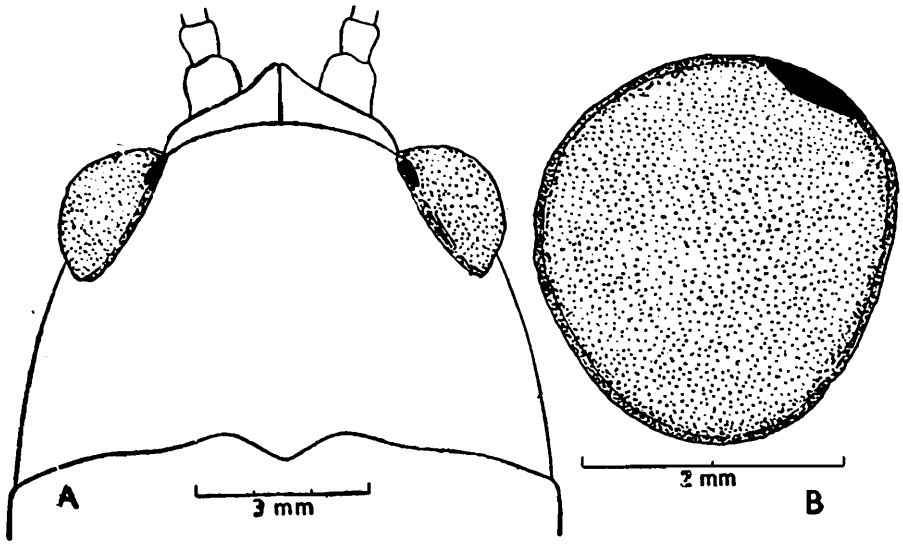
Eyes elongate-oval, horizontal, with 7 downwardly curved, subconcentric, dark brown stripes.

3. **Aularches punctatus** (Drury)

(Text-fig. 6)

[*A. militaris punctatus* of authors]

Material : INDIA (Dehra Dun, Uttar Pradesh), ♂♂, ♀♀, dry and alcohol-preserved examples.



Text-fig. 6. *Aularches punctatus* (Pyrgomorphidae). Dehra Dun, India. (A) Head, in dorsal view. (B) Right eye, enlarged.

Eyes round (*ca.* 3.0 mm x 2.8 mm), greatly bulging, almost hemispherical ; uniformly reddish-brownish-black, without stripes or mottling.

4. **Chrotogonus cavus** (Kirby)

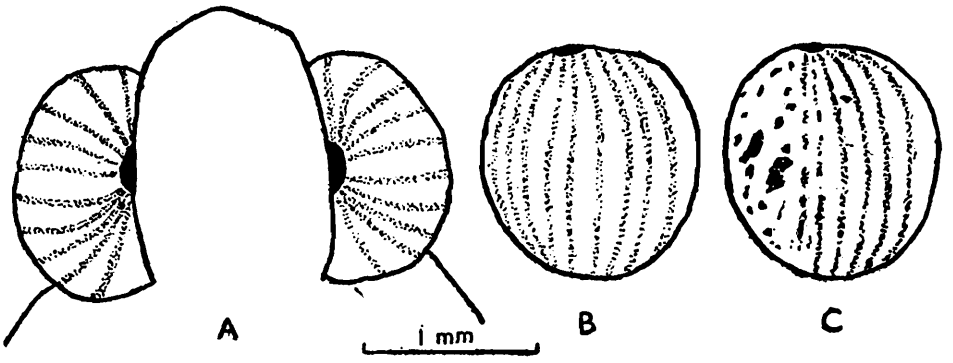
Material : INDIA (Dehra Dun, Uttar Pradesh).

Eyes with 5-6 vertical, parallel stripes (vide Katiyar 1955, Pl. XV, Fig. 12, his *Chrotogonus concavus* Kirby).

5. **Chrotogonus trachypterus trachypterus** (Blanchard)
(Text-fig. 7)

Material : INDIA (Rajasthan and Central India), ♂♂, ♀♀, both living and dry examples.

Eyes small, greatly swollen, almost hemispherical and subround (1.4 mm x 1.3 mm), with 3-10 dark brown to chocolate, vertical, subparallel stripes. Interstripes dirty white ; dorsal spot chocolate-coloured In examples with few stripes, the posterior ones often interrupted, and



Text-fig. 7. *Chrotogonus trachypterus trachypterus* (Pyrgomorphidae). Rajasthan, India. ♀. (A) Head, in dorsal view. (B) Right eye, with many stripes (all complete). (C) Same, with few stripes (some interrupted).

the posterior third of eye mottled with chocolate-brown patches. Sexual variation is evident in examples from Central India (Rewa district) : males tend to have fewer stripes (4-6, mostly 5) than females (4-8, mostly 5 and 6).

6. **Chrotogonus sp.**

Material : INDIA.

Eyes with curved and concentric brown stripes (number not stated, Rao and Gupta, 1939, see comments above).

7. **Colemania sphenarioides** I. Bolivar : Deccan or Jola Grasshopper

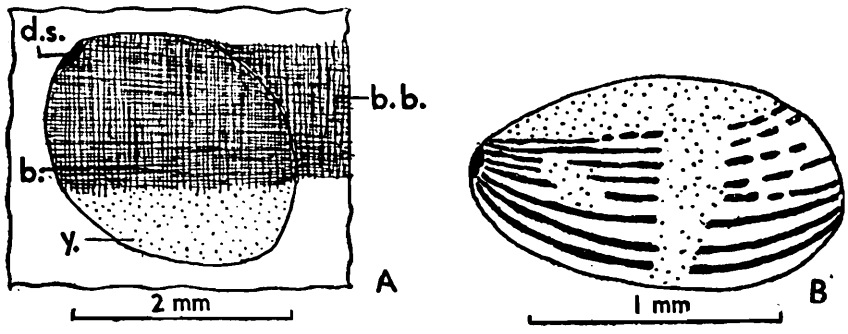
Material : INDIA.

Eyes with 6-7 circular and concentric brown stripes (Rao and Gupta, 1939, see comments above).

8. **Poekilocerus pictus** (Fabricius)
(Text-fig. 8A)

Material : INDIA (Palsana, Sikar District, Rajasthan), ♂♂, ♀♀, living examples,

Eyes roundish-oblong, unstriped ; the lower posterior part weakly projecting ; size : ♂ ♂ 2.2-2.8 mm x 1.4-2.4 mm ; ♀ ♀ 2.7-3.3 mm x 2.2-2.3 mm. Upper two-thirds to three-fourths dark blue (which is



Text-fig. 8. Eyes of two Pyrgomorphidae. (A) *Poekilocerus pictus*. Sikar District, Rajasthan, India. ♀, left eye with head-band (see text). (B) *Pyrgomorpha bispinosa deserti*. Jodhpur, India. ♀, right eye.

b., blue pigment of eye ; *b.b.*, blue band on head in continuation with eye pigment ; *d.s.*, dorsal spot ; *y.*, yellow pigment.

continued into a similar-coloured wide, horizontal band on head and pronotum) ; lower part dirty yellow. (In one ♂, the upper half of eye was chocolate brown mixed with blue.) Dorsal spot chocolate-brown.

9. **Pyrgomorpha bispinosa deserti** (Bei-Bienko)

(Text-fig. 8B)

Material : INDIA (Jodhpur, Rajasthan), ♂ ♂, ♀ ♀, living examples.

Eyes elongate-oval (♂ ♂ 1.2 mm x 0.8 mm, ♀ ♀ 1.2 mm x 1.0 mm), with 6-8 horizontal, subparallel stripes; often interrupted by withish patches. Differ somewhat in the two colour forms, as follows :—Brown form : Stripes dark chocolate-brown, interstripes dirty white ; dorsal spot dark chocolate ; a withish band running across stripes in middle of eye, and another in upper half, thus interrupting the stripes. Green form : Stripes dark chocolate, interstipes darkish brown (obscuring the former) ; rest as in brown form.

10. **Pyrgomorpha sp.**

Material : SOUTH ASIA (Baluchistan Coast).

Eyes striped, with curved and concentric brown stripes (number not stated, Rao and Gupta, 1939).

Family II. ACRIDIDAE

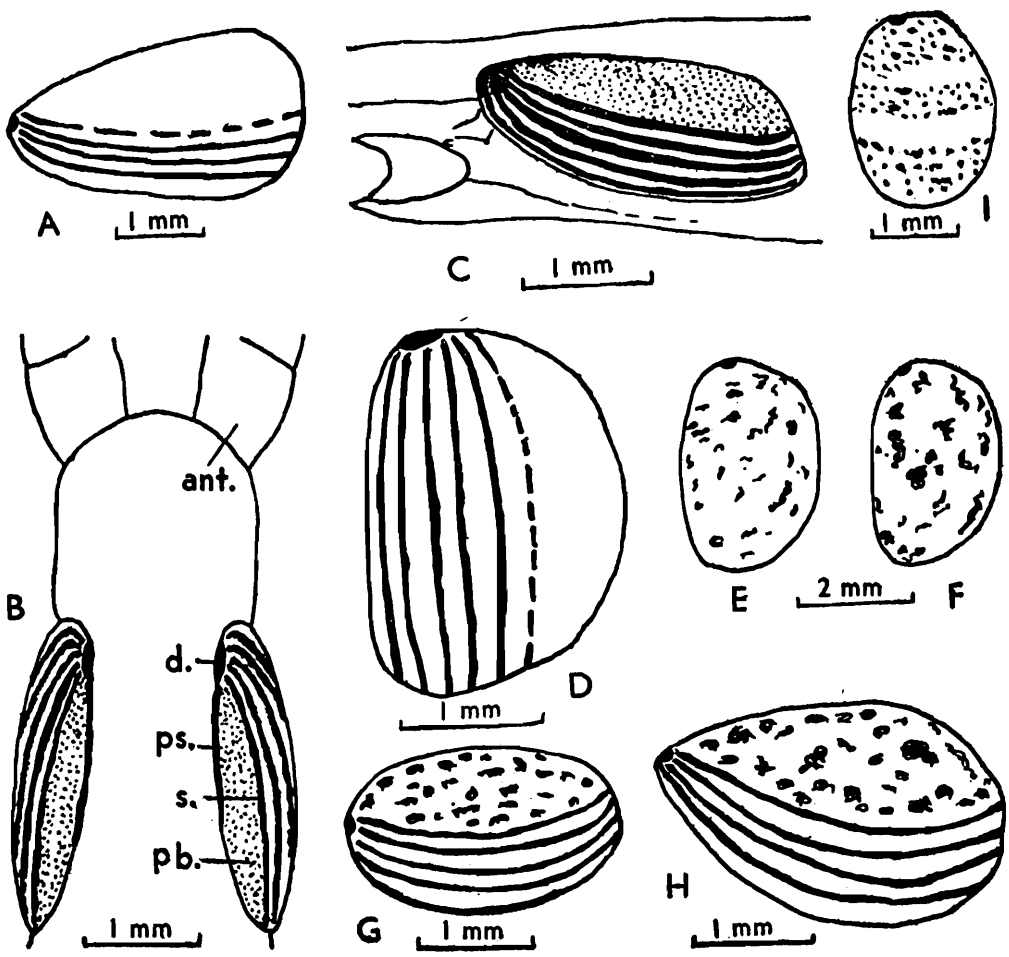
Subfamily (1) ACRIDINAE

11. **Acrida exaltata** (Walker)

(Text-fig. 9A)

Material : SOUTH ASIA : INDIA (Rajasthan and Central India) and BALUCHISTAN, ♂ ♂, ♀ ♀, both living and dty examples.

Eyes elongate-oval (♂ ♂ 3.0 mm x 1.5 mm, ♀ ♀ 3.6 mm x 2.0 mm), horizontal, with 3-10 dark brown, horizontal, subparallel stripes in the lower (anterior) half, the posterior one or two sometimes interrupted ;



Text-fig. 9. Eyes of some Acridinae from India. (A) *Acrida exaltata*. Udaipur. ♀, right eye. (B) *Acrida* sp. Varanasi. Head, in dorsal view. (C) Same, head, in side view. (D) *Aulacobothrus* sp. Udaipur. ♀, right eye. (E) *Chloebora crassa*. Udaipur. ♀, right eye. (F) *C. marshalli*. Udaipur. ♀, right eye. (G) *Gonista* sp. Udaipur. ♂, right eye. (H) *Orthoctha indica*. Udaipur, ♀, right eye. (I) *Phloeoba infumata*. Udaipur. ♀, right eye.

ant., antenna ; *d.*, dorsal spot of eye ; *pb.*, posterior pigment band ; *ps.*, posterior pigment streak ; *s.*, stripe.

rest of eye finely mottled with brown. Interstripes a dirty cream ; dorsal spot chocolate-brown, continued into a thin similar-coloured streak along the anterior margin of eye.

Some geographical and sexual variation is evident. Examples from Baluchistan tend to have more stripes (6-10, mostly 8 and 9) than those from Central India (4-7). Males tend to have fewer stripes than females (Baluchistan : ♂ ♂ 7-9, ♀ ♀ 6-10 ; Central India : ♂ ♂ 4-6, ♀ ♀ 5-7).

12. **Acrida sp.**

(Text-figs. 9B, C)

Material : INDIA (Varanasi, Uttar Pradesh), ♂ ♂, living examples. A small brachypterous species.

Eyes elongate and suboval (♂ ♂ 2.8 mm x 0.9 mm) ; anterior end narrowed, posterior end truncated ; with 5 horizontal, slightly downwardly curved, subparallel, earth-brown stripes in the lower (anterior) two-fifths of eye, and a wide, dirty brown band (pb.) covering the upper (posterior) one-fifth. Interstripes greenish white ; dorsal spot chocolate-brown ; subdorsal streak pale yellow. At the upper-inner (posterior) margin is present a thin chocolate-coloured streak, the posterior streak (ps.), which is almost continuous with the dorsal spot and runs down along three-fourths the length of eye-margin.

13. **Aulacobothrus sp.**

(Text-fig. 9D)

[*Phorenula* of authors]

Material : INDIA (Rajasthan and Madhya Pradesh), ♀ ♀ , both living and dry examples.

Eyes oval (2.5 mm x 2.0 mm), narrowed dorsally, with 6 vertical parallel brown stripes (interrupted at several places) in anterior two-thirds ; rest of eye mottled with fine brown spots. Interstripes pale cream ; dorsal spot chocolate ; dorsal streak thin, cream coloured. Below the dorsal streak lies a small chocolate patch similar to the dorsal spot, fading at the lower end into the general brown of eye. (Such a 'second dorsal spot' has not been recorded in other Acridoidea.)

14. **Chloebora crassa** (Walker)

(Text-fig. 9E)

Material : INDIA (Udaipur, Rajasthan), ♀ ♀ , dry examples.

Eyes suboval (3.8 mm x 2.6 mm), a little narrowed ventrally ; without stripes ; mottled with irregular dark brown patches. Dorsal spot small, chocolate-brown.

15. **Chloebora marshalli** (Henry)

(Text-fig. 9F)

Material : INDIA (Udaipur, Rajasthan), ♂ ♂ , dry examples.

Eyes suboval (♂ ♂ 3.5 mm x 2.5 mm), ventral end somewhat narrowed ; without stripes, and mottled with irregular brown patches. Dorsal spot small, chocolate-coloured.

16. **Dittopternis venusta** (Walker)

Material : INDIA (Madhya Pradesh), ♂ ♂ , ♀ ♀ , living examples.

Eyes oval, without stripes ; mottled brown against a cream coloured base, the lower half much darker than the upper ; with two pale transverse bands, one in middle, the other in upper half. Dorsal spot chocolate-coloured.

17. **Gonista sp.**

(Text-fig. 9G)

Material : INDIA (Udaipur, Rajasthan), ♂♂, ♀♀, dry examples.

Eyes oval (♂♂ 2.0 mm x 1.0 mm, ♀♀ 2.5 mm x 1.5 mm), oblique (due to forward prolongation of head), with 4 curved, subconcentric, brown stripes in the lower (anterior) half ; rest of eye mottled with brown patches.

18. **Orthoctha indica** Uvarov

(Text-fig. 9H)

Material : INDIA (Udaipur, Rajasthan), ♀♀, dry examples.

Eyes pear-shaped (♀♀ 3.0 mm x 2.0 mm), oblique, with 4 curved, subconcentric, brown stripes in lower (anterior) half ; rest of eye mottled with irregular brown patches.

19. **Phlaeoba infumata** Brunner

(Text-fig. 9 I)

Material : INDIA (Udaipur, Rajasthan), ♀♀, dry examples.

Eyes suboval (♀♀ 2.3 mm x 1.8 mm), without stripes ; finely mottled with dark brown patches, interrupted by two narrow, horizontal whitish bands. Dorsal spot small, chocolate-coloured.

20. **Phlaeoba panteli** I. Bolivar

Material : INDIA (Udaipur, Rajasthan), ♀♀, dry examples.

Eyes oval (2.8 mm x 2.0 mm), without stripes, mottled with irregular brown patches. Dorsal spot small, chocolate-coloured.

21. **Phlaeoba sp.**

Material : INDIA (Udaipur, Rajasthan), ♂, a dry example.

Eyes oval (♂ 2.0 mm x 1.5 mm), without stripes, finely mottled with dark brown patches.

Subfamily (2) CALLIPTAMINAE

22. **Acorypha glaucaupsis** (Walker)

[Genus *Caloptenopsis* of authors]

Material : SOUTH ASIA : Baluchistan Coast (Pasni), ♂♂, ♀♀, living examples.

Eyes striped, with 7 vertical, subparallel, dark brown stripes.

23. **Calliptamus italicus** (Linnaeus) : Italian Locust

Material : EUROPE.

Eyes with 5-7 vertical stripes (Volkonsky, 1938b). (The earlier contention of Friza, 1929, that the stripes are not continuous but

interrputed, was probably based on either exceptional or poorly perserved examples.) The number of stripes shows geographical and sexual variations ; it is smaller in the northern latitudes (South Europe, 5-7, mostly 5 and 6) than in the southern (North Africa, 6-7, in nearly equal number) (cf. *Anacridium aegyptium*). Males tend to have fewer stripes (5-6) than females (6-7). The histology of eyes has been studied by Jörschke (1913) and Friza (1929).

Subfamily (3) CATANTOPINAE

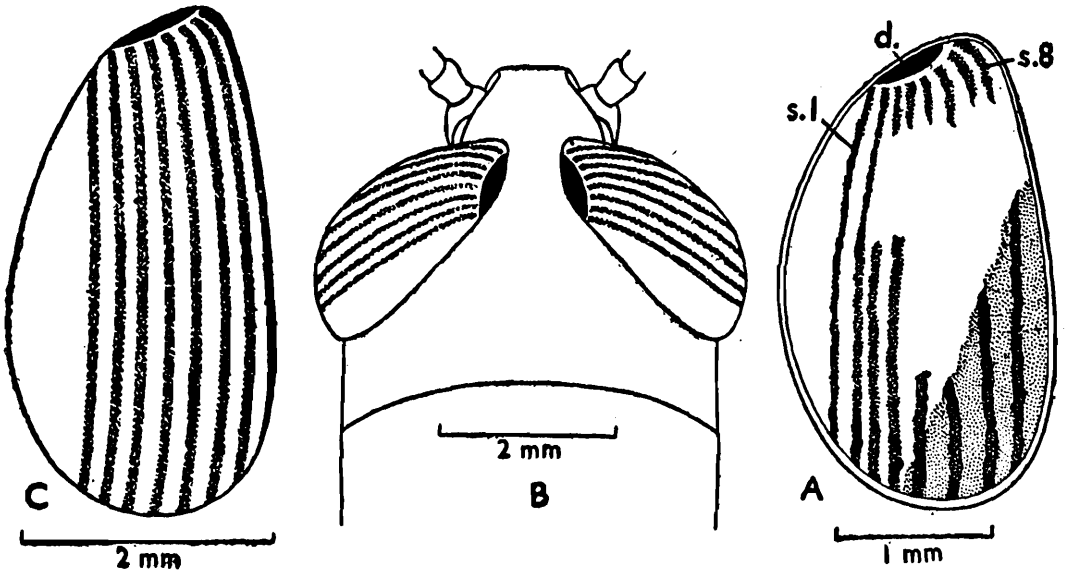
24. **Catantops pinguis innotabilis** (Walker)

(Text-fig. 10A)

[Syn. *Catantops indicus* I. Bolivar]

Material : INDIA (Varanasi, Uttar Pradesh), ♀ ♀ , living examples.

Eyes elongate-oval (♀ ♀ 3.0 mm x 1.7 mm), narrowed dorsally ; with 8 vertical, parallel, dark brown stripes, often interrupted. Part



Text-fig. 10. Eyes of Catantopinae. (A) *Catantops pinguis innotabilis*. India. ♀, right eye. (B) *Xenocatantops humilis humilis*. India. Head in dorsal view. (C) Same, right eye.

of the antero-ventral end blakish chocolate ; posterior half mottled cream-yellow, with brown patches ; upper anterior half irregularly mottled with brown. Dorsal spot dark chocolate ; subdorsal streak pale yellowish olive.

25. **Catantops pinguis pinguis** Stál.

Material : INDIA (Udaipur, Rajasthan), ♂ ♂, ♀ ♀, dry examples.

Eyes elongata-oval (♂ ♂ 3.3 mm x 2.1 mm ; ♀ ♀ 3.8 mm x 2.5 mm), the anterior margin substraight ; with 8 vertical, dark brown stripes, the anterior 3 interrupted by an oblique white band. Dorsal spot chocolate-coloured,

26. **Xenocatantops humilis humilis** (Serville)

(Text-figs. 10 B, C)

[*Catantops humilis* (Serville) of authors]

Material : INDIA, ♂ ♂, ♀ ♀ living examples.

Eyes suboval (3.2 mm x 1.7 mm), narrowed dorsally ; with 8 thin, vertical, parallel, brown to chocolate-coloured stripes. Dorsal spot dark brown to chocolate.

Subfamily (4) COPTACRIDINAE

27. **Eucoptacra praemorsa** Stäl

Material : INDIA (Udaipur, Rajasthan), ♀ ♀, dry examples.

Eyes elongate-oval (♀ ♀ 3.0 mm x 1.5 mm), with anterior margin substraight ; without stripes ; finely mottled with dark brown spots, the mottling being denser and darker at the anterior margin.

Subfamily (5) CYRTACANTHACRIDINAE

28. **Anacridium aegyptium** (Linnaeus)

Egyptian Grasshopper

Material : SOUTH ASIA (Baluchistan Coast), ♀ ♀, living examples.

Eyes elongate-oval (3.8 mm x 2.3 mm), with 7-8 vertical, parallel, brown stripes (Baluchistan examples only), in the proportion 67 (7) : 33 (8).

Earlier records from Southern Europe and North Africa (Volkonsky, 1938a, b) gave the number of stripes as 5-8, with a well marked geographical variation, there being fewer stripes in the northern latitudes (France, 5-7) than in the southern (North Africa, 7-8). There is also some indication of sexual differences, females tending to have more stripes than males.

29. **Anacridium melanorhodon** (Walker) : Northern Tree Locust

[*A. moestum melanorhodon* of authors]

Material : WEST AFRICA (Mauritiana).

Eyes with 7-8 vertical, parallel stripes (Volkonsky 1938a, b).

30. **Anacridium rubrispinum** Bei-Beinko

(Text-fig. 11 A)

[*A. aegyptium rubrispinum* of authors]

Material : INDIA (Kutch), ♂ ♂, ♀ ♀, livings examples.

Eyes, elongate-oval (5 mm x 3 mm), with 7-8 vertical, subparallel, chocolate-coloured stripes ; anterior stripe very thick ; 8 stripes appa-

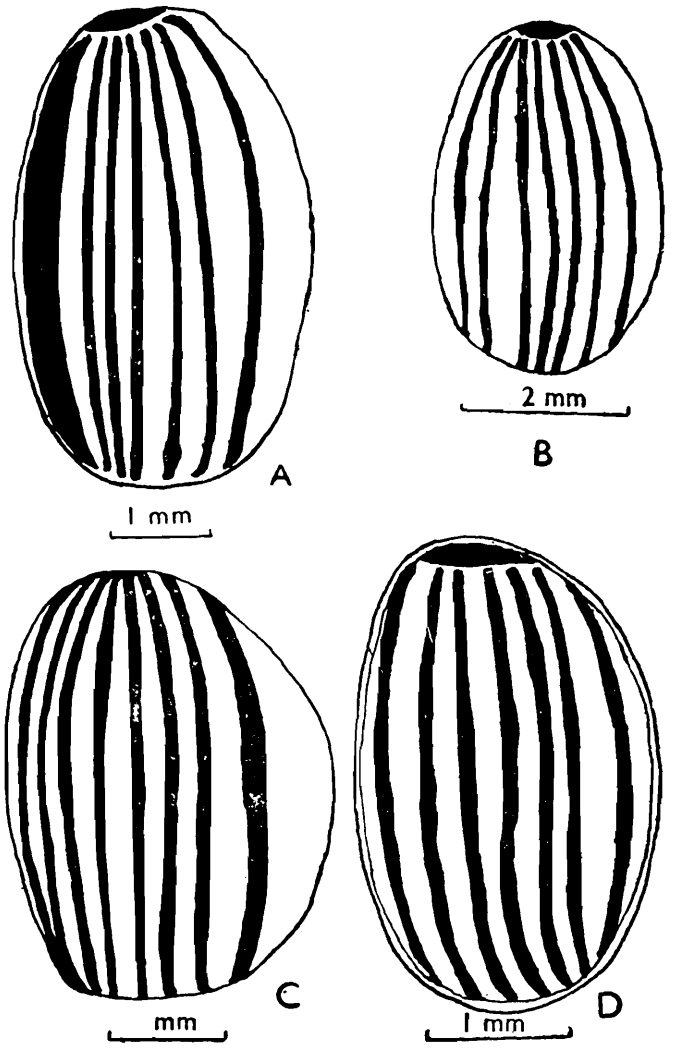
rently more common in females, 7 in males. Interstripes grey-white ; dorsal spot dark chocolate. (Also see Addendum.)

31. **Cyrtacanthacris tatarica** (Linnaeus)

(Text-fig. 11B)

Material : INDIA (Udaipur, Rajasthan), ♂ ♂, ♀ ♀, dry examples.

Eyes oval (3.5-5.0 mm x 2.7-3.2 mm), with 6-8 vertical, parallel, dark brown stripes. Interstripes cream coloured to dirty white, that between



Text-fig. 11. Eyes of some Cyrtacanthacridinae. (A) *Anacridium rubrispinum*. Kutch, India. ♀, left eye. (B) *Cyrtacanthacris tatarica*. Udaipur, India. ♀, right eye. (C) *Nomadacris septemfasciata*. South Africa. Right eye. ♀, phase *solitaria*, with 8 stripes. (D) *Schistocerca cancellata*. Argentine. ♀, left eye of phase *solitaria*.

the anterior stripe Nos. 2 and 3 wider than the rest. Dorsal spot chocolate-brown. (Present account ; also see Rao and Gupta, 1939, 6-7 stripes ; Uvarov, 1960, p. 412, Fig. 238, ♂, 6 stripes ; and Venkatesh and Harjai, 1976, 7-8 stripes.)

32. **Nomadacris septemfasciata** (Serville)

(Text-fig. 11 C) : Red Locust

Material : SOUTH AFRICA.

Eyes oval (3.7 mm 2.8 mm), with 7-9 vertical, parallel, dark brown

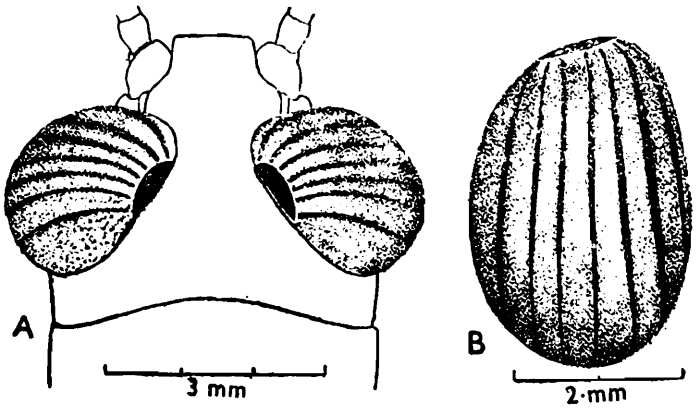
stripes (Burnett, 1951 ; Albrecht, 1955 ; also Rao and Gupta, 1939, 7 stripes).

According to Burnett (1951), who gave the number of stripes in phase *solitaria* as 7-9, there is some phase variation, and the number is "greater in the *solitaria* phase" (p. 489), but the actual number in the *gregaria* phase was not mentioned. He further stated that in the older hopper stages the eyes are so heavily pigmented in the *gregaria* and *transiens* phases that stripes are hardly distinguishable ; in the *solitaria* phase, on the other hand, the stripes are clear. The data of Burnett also suggest some sexual differences in the number of stripes, which is mostlv 8 (92%) in females, with very few 7 and 9 (6% and 2 % respectively) ; in males also the common number is 8 (72%), but 7 also occurs in substantial proportion (26%) and 9 is rare (2%).

33. **Pachyacris vinosa** (Walker)
(Text-fig. 12)

Material : INDIA (Udaipur Rajasthan), ♂ ♂ , dry examples.

Eyes elongate-oval (♂ ♂ 4.0 mm x 2.5-2.8 mm), slightly narrowed dorsally ; with 5-7 rather thin, vertical, parallel, brown stripes. Dorsal spot dark brown to chocolate.



Text-fig. 12. *Pachyacris vinosa*. Udaipur, India. ♂. (A) Head. in dorsal view. (B) Right eye, enlarged.

34. **Patanga succincta** (Linnaeus) : Bombay Locust

Material : INDIA.

Eyes vertically striped with 7-9 (mostly 8) dark brown stripes (Rao and Gupta, 1939).

35. **Schistocerca cancellata** (Serville)*
(Text-fig. 11) : South American Locust.

Material : ARGENTINA : ♂ ♂, ♀ ♀ , dry examples.

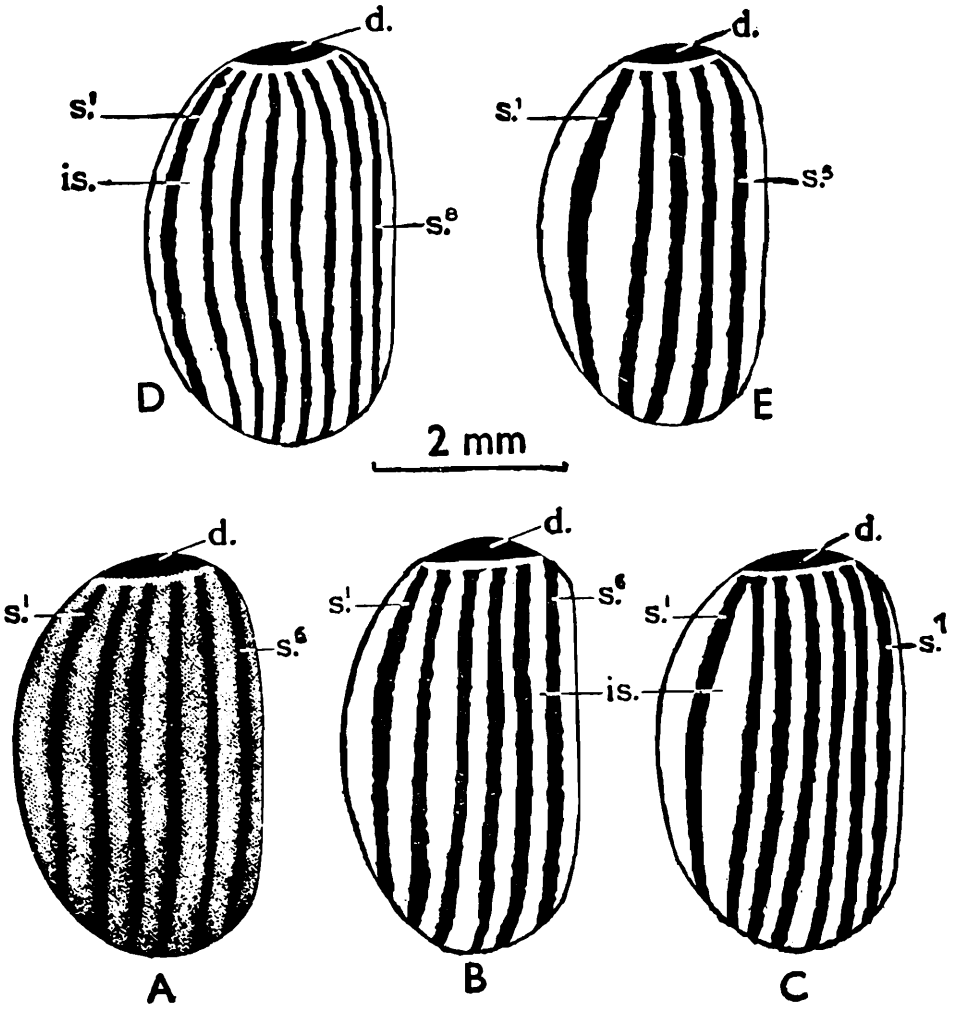
* Dirsh (1974) regards *S. cancellata* as a subspecies of *S. americana* (Drury). *S. paranensis* (Burmeister), formerly regarded as a synonym of *S. cancellata*, is regarded by Dirsh as a distinct subspecies of *S. americana*.

Eyes oval (3.0-4.0 mm x 2.0-2.5 mm). Eyes in females slightly longer than in males. In the ratio Length/Width (0.64-0.71) there is no significant difference between the sexes or the phases. In both *gregaria* and *solitaria* phases, there are only 7 vertical, parallel, dark brown stripes (Roonwal and Bhanotar, 1964).

36. **Schistocerca gregaria** (Forskal) †
(Text-fig. 13) : Desert Locust

Material : INDIA, PAKISTAN : ♂♂, ♀♀, living examples.

Eyes oval (♂♂ 3.4 – 4.0 mm × 2.2 – 2.5 mm ; ♀♀ 4.0-4.8 mm × 2.5 – 3.3 mm), with 4-8 (mostly 6 and 7) vertical, parallel, dark brown



Text-fig. 13. Right eyes of *Schistocerca gregaria*, showing phase and nonphase polymorphism. India. (A) Phase *gregaria*, with 6 eye-stripes. (B)- (E) Phase *solitaria*, with 6, 7, 8 and 5 eye-stripes respectively. (From Roonwal, 1954.)

d., dorsal spot of eye ; *is.*, interstripes ; $s^1 - s^8$, first to eighth stripes, counting from the posterior margin of eye.

stripes. Interstripes cream coloured in phase *solitaria* (Text-figs. 13B-E), and heavily invaded by brown (so as to almost obscure the stripes)

† Dirsh (1974) regards *S. gregaria* as a subspecies of *S. americana* (Drury), viz., *S. a. gregaria* (Forskäl). *S. flaviventris* (Burmeister), variously regarded as a junior synonym of *S. gregaria*, 'phase solitaria' of *S. gregaria*, and a subspecies of *S. gregaria*, is also now regarded by Dirsh (1974) a. a subspceies of *S. americana*.

in phase *gregaria* (Text-fig. 13A). Dorsal spot chocolate-coloured; subdorsal streak thin, white. (Also *see* Roonwal, 1936-1971 ; Rao, 1960 ; and others.)

Much work has been done in this species on phases and other aspects. In swarms (phase *gregaria*) only 6 stripes occur, a situation used for predicting swarming (Roonwal, 1945). The postembryonic development of stripes and eye histology have been studied by Roonwal (1936, 1937, 1947) ; also their relationship with population flux, sex ratio, etc. (Roonwal, 1941, 1945, 1949, 1954, 1958, 1962, 1971 ; Bhanotar and Srivastava, 1974 ; and Bhanotar and Mahto, 1977). According to Bernard (1937), the number of eye facets (mean values) increases from 2,470 in the 1st stage hopper to 9,400 in adults, and the length of ommatidia from 164 to 650 microns. The occasional occurrence of asymmetry in the number of eye-stripes has been mentioned by Bhanotar (1959) and Bhanotar and Mahto (1974).

Subfamily (6) DERICORYTHINAE

37. **Dericorys ramachandrai** Uvarov

Material : SOUTH ASIA (Baluchistan Coast : Pasni), ♀ ♀, living examples.

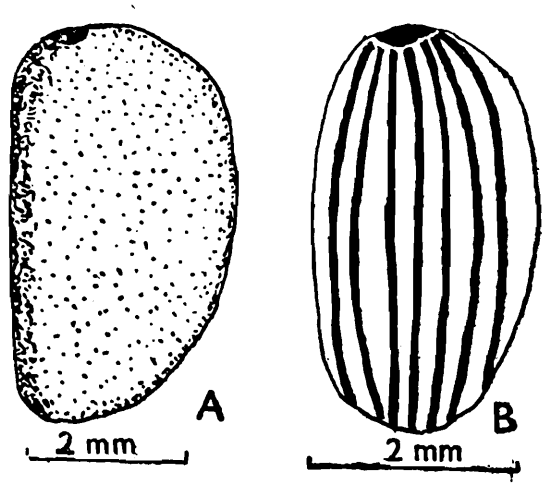
Eyes with 7 vertical, subparallel, dark brown stripes.

Subfamily (7) EYPREPOCNEMIDINAE

38. **Cataloipus indicus** Uvarov

(Text-fig. 14A)

Material : INDIA (Udaipur, Rajasthan), ♂ ♂, ♀ ♀, dry examples.



Text-fig. 14. Right eyes of two Eyprepocnemidinae. (A) *Cataloipus indicus*. Udaipur, India. ♀. (B) *Heteracris littorolis asiaticus*. India (Jaisalmer district, W. Rajasthan), ♀.

Eyes suboval (♂ ♂ 4.3 mm × 2.2 mm ; ♀ ♀ 5.0 mm × 2.8 mm), with anterior margin substraight ; without stripes or mottling ; apparently

uniformly pigmented which brown all over, except for a narrow strip at the anterior margin which is deeply pigmented chocolate-brown, and a simllar but narrower strip at the posterior margin. Dorsal spot chocolate.

39. **Choroedocus illustris** (Walker)

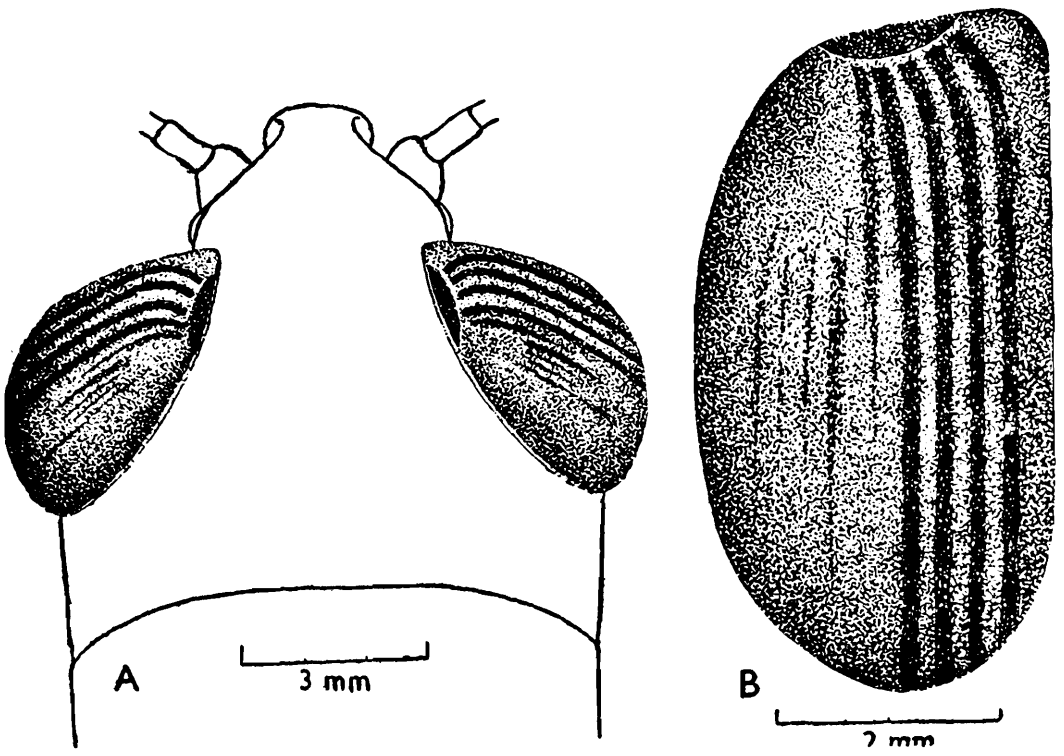
Material : INDIA (Udaipur, Rajastnan), ♂ ♂, ♀ ♀, dry examples.

Eyes elongate-oval (♂ ♂ 4.3 mm × 2.5 mm ; ♀ ♀ 5.0 mm × 3.0 mm), anterior margin substraight ; without stripes ; mottled brown (in some males apparently with 3 or 4 faint, interrupted stripes). Dorsal spot chocolate-brown.

40. **Choroedocus robustus** (Serville)
(Text-fig. 15)

Material : INDIA.

Eyes elongate-oval (6.7 mm × 3.3 mm) ; anterior margin almost straight and antero-lateral upper corner somewhat projected forward.



Text-fig. 15. *Choroedocus robustus* (Eyprepocnemidinae). India. (A) Head, in dorsal view. (B) Right eye, enlarged.

With 3-4 vertical, parallel brown stripes in the anterior half, and indications of 4 or 5 faintly visible, incomplete stripes in the posterior half (the latter masked by the general brown colour of interstripes).

41. **Eyprepocnemis alacris** (Serville)
(Text-fig. 16)

Material : INDIA (Udaipur, Rajasthan), ♂ ♂, ♀ ♀, dry examples.

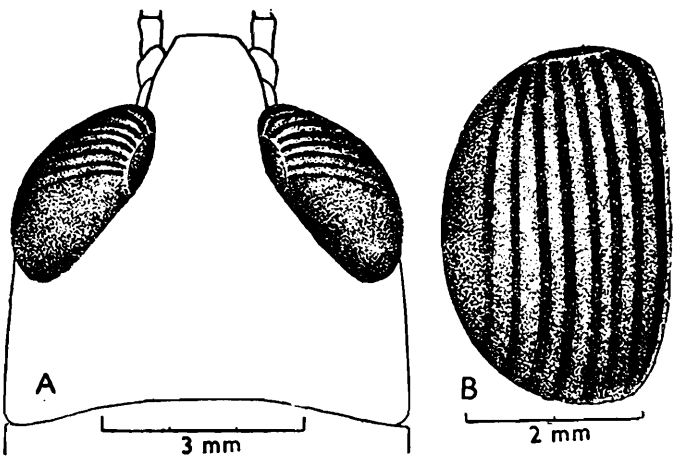
Eyes elongate-oval (3.0 – 4.0 mm × 2.2 – 2.5 mm), with 7-8 vertical,

parallel, chocolate-brown stripes. Interstripes pale brown ; dorsal spot chocolate-coloured. (Also see Addendum.)

42. **Eyprepocnemis polarans ornatipes** (Walker)

Material : EUROPE.

Eyes with 5 – 6 vertical, parallel stripes (vide Uvarov 1966, p. 412, Fig. 237).



Text-fig. 16. *Eyprepocnemis alacris* (Eyprepocnemidinae). India. (A) Head, in dorsal view. (B) Right eye, enlarged.

43. **Heteracris littoralis asiaticus** Uvarov
(Text-fig. 14B)

[Genus *Thisoicetrus* of authors]

Material : SOUTH ASIA : INDIA (Chandan, Jaisalmer district, Rajasthan) ; BALUCHISTAN COAST (Pasni) ; ♂ ♂ , ♀ ♀ , living examples.

Eyes oval (4.0 mm. × 2.0 mm), with 6 – 9 (usually 7 and 8) vertical, parallel, dark brown stripes ; occasionally, the posterior one or two stripes interrupted. Interstripes cream coloured to dirty white ; dorsal spot chocolate- coloured.

44. **Heteracris littoralis littoralis** (Rambur)

[Genus *Thisoicetrus* of authors]

Material : ? NORTH AFRICA.

According to Volkonsky (1938b), the eyes are vertically striped (number of stripes not mentioned).

45. **Heteracris littolaris ?subsp.**

Material : INDIA (Udaipur, Rajasthan), ♀ ♀ , dry examyles.

Eyes oval (4.0 mm × 2.6 mm), with 5-6 vertical, parallel, dark brown stripes (the posterior one or two stripes sometimes interrupted). Dorsal spot chocolate-brown.

Subfamily (8) GOMPHOCERINAE

46. **Dociostaurus sp.**

Eyes without stripes ; mottled with cream and brown patches (Rao and Gupta, 1939).

47. **Ochrilidia sp.**

[*Platyptera* of authors]

Material : SOUTH ASIA : Baluchistan Coast (Pasni), ♀ ; a living example.

Eyes striped, with vertical, subparallel, dark brown stripes (number not determined).

48. **Stenobothrus sp.**

Material : EUROPE.

Eyes uniformly pigmented without any stripes or mottling (Friza, 1929).

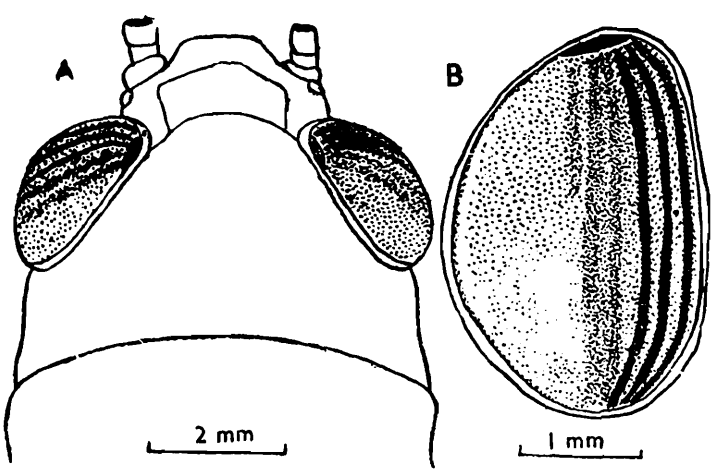
Family (9) HEMIACRIDINAE

49. **Hieroglyphus banian** (Fabricius) : Rice Grasshopper

Material : INDIA.

Eyes elongate-oval ; eye colour warm brown (no yellows), with 3 vertical, brown stripes in the anterior one-third (eye-stripes are clearer in hoppers than in adults). Dorsal spot chocolate-brown ; subdorsal streak narrow and pale yellow. (Also *see* Rao and Gupta, 1939.)

50. **Hieroglyphus nigrorepletus** I. Bolivar (Text-fig. 17) : Phadka Grasshopper



Text-fig. 17. *Hieroglyphus nigrorepletus*, brachypterus form (Hemiacridinae). India (Ajmer, Rajasthan), ♀ (A) Head, in dorsal view. (B) Right eye, enlarged.

Material : INDIA (Aimer, Rajasthan ; Varanasi, Uttar Pradesh), ♂ ♂ , ♀ ♀ , living examples ; barchypterous individuals.

Roonwal (1976) has described the eyes of the older hoppers and of adults and discussed the development of pigmentation pattern. Eyes

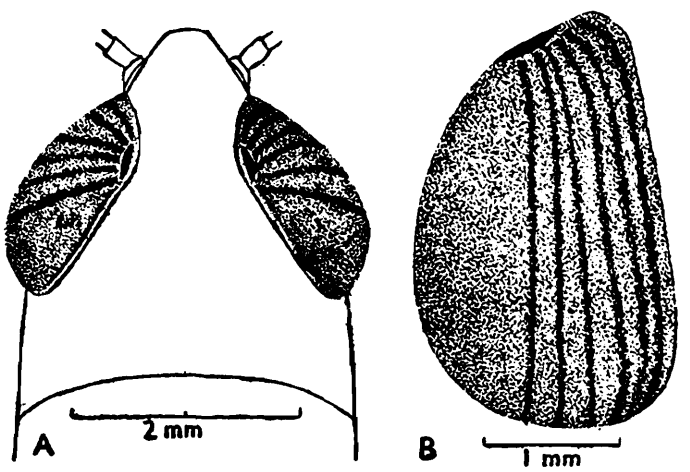
elongate-oval (3.3 mm × 2.0 mm), generally paler in males than in females. Dorsal spot dark brown to chocolate ; subdorsal streak dirty white. Pigmentation differs in green and brown morphs. Green morph : General colour of eyes yellow to brown (darker in posterior half, with a clear posterior edge) ; with 1-3 vertical parallel, brown stripes in anterior half, and 1 or 2 fainter ones in middle. Brown morph : General colour of eyes darker brown, almost dark smoky to black ; rest as in green morph.

51. **Spathosternum prasiniferum prasiniferum** (Walker)

(Text-fig. 18)

Material : INDIA (Rajasthan and Central India), ♂♂, ♀♀, both living and dry examples.

Eyes elongate-oval, subpyriform (2.5 – 3.1 mm × 1.5 – 1.9 mm), with a small rounded projection at the antero-lateral end ; with 4-6 vertical,



Text-fig. 18. *Spathosternum prasiniferum prasiniferum*. Rajasthan, India. ♀. (A) Head, in dorsal view. Right eye, enlarged.

parallel, dark brown stripes in anterior two-thirds ; posterior third of eye more or less uniformly dark brown. Interstripes pale olive ; dorsal spot chocoalate-coloured ; dorsal streak pale brown. (For life-history, *see* Iqbal and Aziz, 1974.)

52. **Spathosternum sp.**

Material : INDIA.

Eyes with 6-7 vertical, parallel stripes (Rao and Gupta, 1939).

Subfamily (10) OEDIPODINAE

53. **Acrotylus humbertianus** (Saussure)

(Text-figs. 19A, B)

Material : INDIA (Jodhpur, Rajasthan), ♂♂, ♀♀, dry examples.

Eyes small, subround (♂♂ 1.7 mm × 1.5 mm ; ♀♀ 2.0 mm × 1.8 mm), unstriped ; irregularly mottled with chocolate patches, with some-

times a horizontal, dirty white band running across the middle and a dark chocolate streak at the lower edge. Dorsal spot hammer-shaped and chocolate-coloured.

54. **Gastrimargus africanus orientalis** (Sjöstedt)

(Text-fig. 19C)

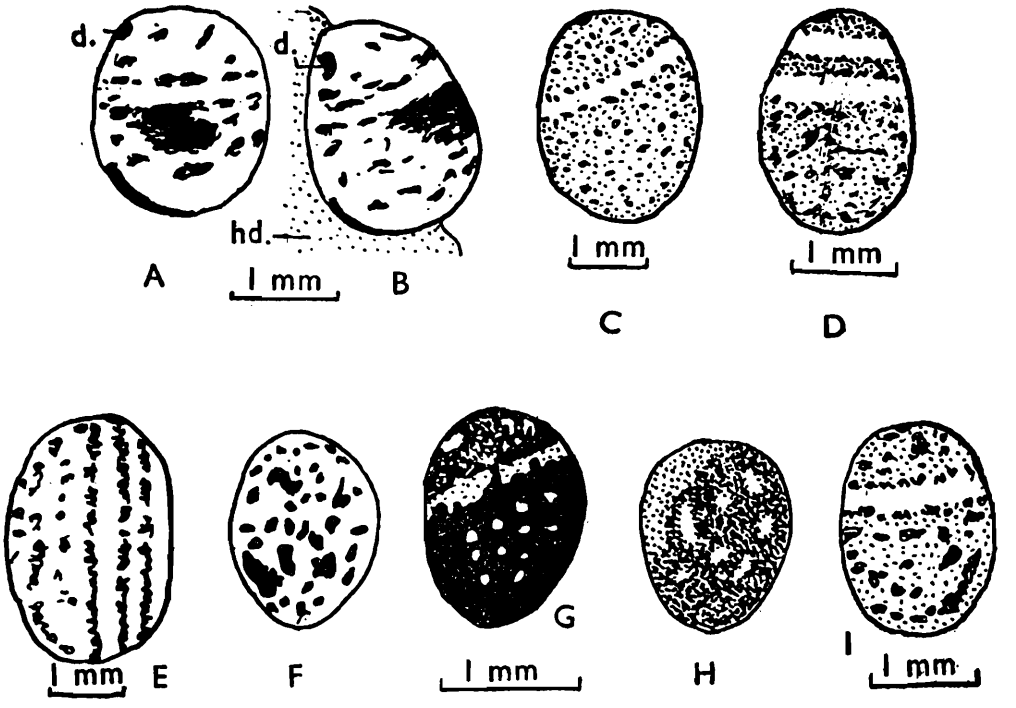
Material : INDIA (Udaipur, Rajasthan), ♂ ♂, ♀ ♀, dry examples.

Eyes elongate-oval (♂ ♂ 2.5 mm × 2.0 mm ; ♀ ♀ 3.0 mm × 2.6 mm), without stripes ; finely mottled with dark brown patches, which are interrupted by an obliquely horizontal whitish band.

55. **Locusta migratoria** (Linnaeus). Migratory Locust

Material : ?EUROPE.

Eyes without stripes ; irregularly mottled with cream and brown (Rao and Gupta, 1939).



Text-fig. 19. Eyes (all in side view, except B) of some Oedipodinae. (A) *Acrotylus humbertianus*, right eye. Jodhpur, India. (B) Same, in dorsal view, (C) *Gastrimargus africanus orientalis*, right eye, ♀. Udaipur, India. (D) *Oedaleus abruptus*, right eye India. (E) *Oedaleus senegalensis*, left eye, ♀, Udaipur, India. (F) *Oedipoda coerulescens*. Europe. (G) *Psophus stridulus*. Europe. (H) *Sphingonotus coerulans*. Europe. (I) *Trilophida annulata*. Udaipur, India. ♀ (F, G, H, adapted from Friza ; the rest original.)

d., dorsal spot ; *hd.*, head.

56. **Oedaleus abruptus** Thunberg

(Text-fig. 19D)

Material : INDIA (Rajasthan and Central India), ♂ ♂, ♀ ♀, both living and dry examples.

Eyes oval (2.0 mm × 1.5 mm), with 4-6 vertical, parallel, dark brown stripes (sometimes very faint) in anterior two-thirds, interrupted by one or two horizontal to oblique white bands ; rest of eye brownish. Interstripes pale brown ; dorsal spot chocolate-coloured ; dorsal streak thin, yellow. There is sexual variation in the number or stripes, which are fewer in males (4-6, mostly 4) than in females (4-6, mostly 5).

57. **Oedaleus senegalensis** (Krauss)
(Text-fig. 19E)

Material : INDIA (Udaipur, Rajasthan), ♀ ♀ , dry examples.

Eyes oval (3.5 mm × 2.3 mm), with 3-4 irregular, jagged, vertical, parallel, dark brown stripes in anterior two-thirds ; rest of eye mottled with irregular chocolate-brown patches.

58. **Oedaleus sp.**

Material : ? INDIA.

According to Rao and Gupta (1939), faint vertical eye-stripes are present (number not mentioned).

59. **Oedipoda coerulescens** (Linnaeus)
(Text-fig. 19F)

Material : EUROPE.

According to Friza (1929), eyes small, subround (1.4 mm × 1.1 mm), unstriped and mottled with grey-brown spots. Their histology has been studied by the same author.

60. **Psophus stridulus** (Linnaeus)
(Text-fig. 19G)

Materal : EUROPE.

Eyes small, rounded-oval (1.6 mm × 1.2 mm), without stripes ; irregularly mottled ; divided into an upper and lower half. Lower half blackish with numerous dots ; upper half pale grey with white dots ; in between is a narrow, horizontal, white streak (Exner, 1891, Jörschke, 1914, Friza, 1929). Histologically, the dark lower half contains a thick deposit of dark pigment in the secondary pigment cells ; this pigment is wanting in the pale half of eye (Friza, 1929). (Cf. *Schistocerca gregaria* above.)

61. **Pyrgodera sp.**

Material : INDIA.

Eyes without stripes ; mottled with cream and brown (Rao and Gupta, 1939).

62. **Sphingonotus coerulans** (Linnaeus) (Fig. 19H)

Material : EUROPE.

Eyes small, rounded-oval (1.4 mm × 1.1 mm), without stripes ; mottled with grey-brown flecks (Friza, 1929).

63. **Sphingonotus sp.**

Eyes without stripes ; mottled with cream and brown (Rao and Gupta, 1939).

64. **Trilophida annulata** (Thunberg)
(Text-fig. 19 I)

Material : INDIA (Udaipur, Rajasthan), ♀ ♀, dry examples.

Eyes oval (♀ ♀, 2.1 mm × 1.3 mm), without stripes ; mottled with dark chocolate-brown patches. A whitish horizontal band cutting the eye in two parts—a lower, much darker two-thirds and an upper, paler one-third. Dorsal spot small, chocolate-brown and hammer-shaped (not spindle-shaped as in most Acridoidea). (Banu and Kushwaha, 1976, have studied some aspects of its morphology, but not the eye-stripes.)

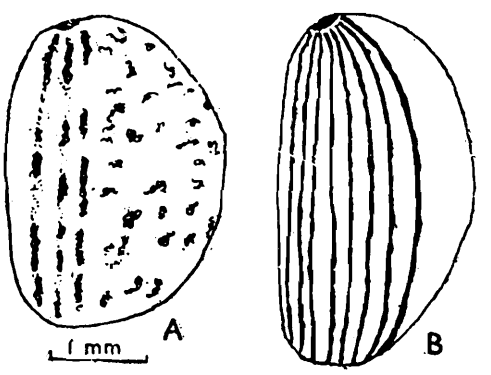
Subfamily (11) OXYINAE

65. **Oxya hyla hyla** Serville
(Text-fig. 20A)

[Syn. *Oxya ebneri* Willemse]

Material : INDIA (Udaipur, Rajasthan), ♂ ♂, ♀ ♀, dry museum examples.

Eyes oval (♂ ♂ 2.8 mm × 1.8 mm ; ♀ ♀ 3.2 mm × 2.3 mm), with 2 or 3 faint, brown, interrupted, vertical stripes in the anterior one-third



Text-fig. 20. Right eyes of : (A) *Oxya hyla hyla* (Oxyinae). Udaipur, India. ♂. (B) *Teratodes* sp. (Romaleinae), older (penultimate) stage hopper. Madhya Pradesh, India. ♂.

of eye ; in some cases the entire eye mottled with brown. Dorsal spot chocolate-coloured.

66. **Oxya sp.**

Material : INDIA.

Eyes with 2-3 vertical, parallel stripes in anterior half ; none in the posterior half where they are probably masked by brown pigment of the interstripes (Rao and Gupta, 1939).

Subfamily (12) ROMALEINAE

67. **Teratodes sp.**

(Text-fig. 20B)

Material : INDIA (Waidhan, Sidhi District, Madhya Pradesh), nymphs of both sexes, living examples.

In older nymphs (penultimate stage, with upturned elytra and wing-rudiments), the eyes are elongate-oval ; there are 8 vertical, parallel, olive-brown stripes in the anterior two-thirds of eye, the rest of the eye being irregularly mottled with brown spots. (Since a stripe is added at each moult, this would suggest 9 stripes in adults.) Interstripes cream-coloured ; dorsal spot brown.

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SUMMARY

1. A comparative study of various patterns of eye pigmentation (stripes, mottling, etc.) as occurring in grasshoppers (Orthoptera, Acridoidea) has been made in two principal families (the Pyrgomorphidae and the Acrididae) ; 47 genera and 67 species and subspecies were studied.

2. Pigmentary patterns have been classified into two principal types, e.g., striped and unstriped, with a number of subtypes, as follows :—

TYPE I. Eyes striped. *Category A.* Stripes vertical. Group 1. Stripes substraight and parallel : (a) Stripes complete ; (b) interrupted.

Gr. 2. Stripes curved and concentric (doubtful type). *Category B.* Stripes oblique to horizontal. Gr. 1. Stripes substraight and parallel. (a) Stripes complete ; (b) interrupted. Gr. 2. Stripes curved and subconcentric.

TYPE II. Eyes unstriped. *Category A.* Eyes mottled. Gr. 1. Mottling uniform. Gr. 2. Mottling not uniform (part of eye darker). *Category B.* Eyes not mottled ; uniformly coloured.

3. The known distribution of the various types among the Acridoidea is given.

4. Brief descriptions of pigmentary patterns in various species are provided.

5. The biological significance and applied importance of the eye patterns (especially the striped ones) are discussed with regard to phylogeny, taxonomy, polymorphism, geographical, climatic and sexual variations, the number of moults, population flux, the prediction of swarming, vision, concealment, etc.

6. There is some correlation of eye pigmenation with phylogeny and taxonomy, though there are important exceptions. In the Pyrgomorphidae eyes are striped in some genera and unstriped in others, and the same situation exists in the Acrididae. Subfamilies show greater, but by no means universal, uniformity. Eyes are vertically striped in all Calliptaminae, Catantopinae and Cyrtacanthacridinae ; unstriped and mottled in most Oedipodinae ; and of varying types in other acridid subfamilies. Generally, there is uniformity within a genus, but here too there can be exceptions (e.g., *Choroedocus*, Eyprepocnemidinae).

7. Some species exhibit geographical variation in the number of eye-stripes (e.g., *Anacridium aegyptium*, *Acrida exaltata*, etc.)

8. Some authors have claimed a correlation between the number of eye-stripes on the one hand, and season and temperature on the other. The data, however, are too inadequate to arrive at definite conclusions.

9. In some species the number of eye-stripes shows a relationship with sex, and the following tentative rule is given : Where sexual differences exist in a species, stripes tend to be fewer in males than in females. (Put in another way, to characterise a mixed population, we may generalise thus : In a species population in an area the male ratio is higher in samples with fewer eye-stripes than in those with more numerous stripes.)

10. During postembryonic development in a number of species a *partial* correlation between eye-stripes and moulting exists, one stripe

being generally added at each moult. There is, however, no *absolute* correlation as claimed by some authors, and the adult number of eye-stripes cannot be reliably used to determine the total number of moults in a species.

11. In some species the number of eye-stripes is correlated with phase variation and population flux (*Schistocerca gregaria*). On this basis, several hypotheses have been put forward by authors for the prediction of swarming.

12. Eye-stripes have been shown to play a significan trole in vision (i.e., the nature of image formed inside the eye), and in the behaviour of the individuals.

13. There is correlation between the size of eyes and phase and eye-stripe polymorphisms ; sex differences also exist in respect of eye-size.

14. Eye-stripes play an important role in concealment and thus have an additional adaptive function.

15. Abnormalities in eye-stripes are discussed.

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ADDENDUM

In *Anacridium rubrispinum*, Venkatesh et al. (1977) gave the number of eye-stripes as varying from 6—8. In 95 examples taken from the field, the majority of males (91.3%) had 7 stripes, with one having 6 and another 8. Among females also the majority (86.1%) had 7 stripes and the rest 8.

In *Eyprepocnemis alacris alacris* (Serville), Muralirangam and Ananthakrishnan (1977) gave the adult number of eye-stripes as 6 in both sexes. They further stated that the number increased from one in the first instar hopper to six in the adult, one stripe being added at each of the five months, and there was no extra moult. The occurrence of an extra moult is so common a feature in the Acridoidea that its 'absence' in *E. alacris* is no doubt due to an insufficency in the number of examples studied. If this is so, the number of adult eye-stripes may well vary from 6 to 8.

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