TAXONOMY AND BIOGEOGRAPHY OF THE GENERA OEDALEUS FIEBER AND GASTRIMARGUS SAUSSURE (ORTHOPTERA: ACRIDIDAE)

by

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ABSTRACT

The economically important grasshopper genus Oedaleus is revised. Twenty species and three subspecies are described, keyed, and illustrated. O. nadiae and O. plenus browni are described as new, and four species and five subspecies are synonymised. Two species are reduced to subspecies, one being transferred from Gastrimargus. All available primary types have been examined, and lectotypes and neotypes are designated where necessary. The biology and economic importance of the species are reviewed and their distributions mapped. The biogeography of the genus is discussed in the light of past and present geological, vegetational, and climatic factors. The fluctuations of the equatorial Brachystegia woodland zone in Africa during the Pleistocene are advanced as an explanation of the observed trans-equatorial speciation in Oedaleus and some other dry savannah organisms.

The closely related genus Gastrimargus is revised. G. miombo, G. insolens, G. obscurus, G. willemsei, and G. verticalis mpwapwae are described as new, and sixteen species and five subspecies are synonymised. Four species are reduced to subspecies, and two species and two subspecies are recalled from synonymy. Keys, diagnoses, figures, plates, and distribution maps are provided for the twenty three species recognised, and the biogeography of the genus is discussed.

CONTENTS

PAGE

ABSTRACT 2

CONTENTS 3

LIST OF TABLES 6

LIST OF PLATES 7

LIST OF FIGURES 8

PART ONE: TAXONOMIC, BIOGEOGRAPHICAL, AND BIOLOGICAL STUDIES OF THE GENUS OEDALEUS FIEBER. 11

1.1 TAXONOMY OF THE GENUS OEDALEUS

1.1.1 Introduction: taxonomic background and methods 12

1.1.1.1 Need for a revision of *Oedaleus* 12

1.1.1.2 History of the genus *Oedaleus* 13

1.1.1.3 Taxonomic affinities and diagnostic characters 15

1.1.1.4 Materials, methods, and terminology 17

1.1.1.5 Depositories 19

1.1.2 Generic synonymy 20

1.1.3 Description of the genus 20

1.1.4 Keys to the species of *Oedaleus* 22

1.1.4.1 Notes on the keys 22

1.1.4.2 Key to African species 26

1.1.4.3 Key to non-African species 34

1.1.5 Annotated species catalogue of the genus *Oedaleus*, with synonymy, descriptions, measurements, and biological notes 38

1.1.5.1 *O. senegalensis* (Krauss) 39

1.1.5.2 *O. nigrofasciatus* (De Geer) 45

1.1.5.3 *O. australis* Saussure 51

1.1.5.4 *O. abruptus* (Thunberg) 56

1.1.5.5 *O. virgula* (Snellan Van Vollenhoven) 62

1.1.5.6 *O. johnstoni* Uvarov 67

1.1.5.7 *O. nigeriensis* Uvarov 72

1.1.5.8 *O. carvalhoi* Bolivar 79

1.1.5.9 *O. plenus* (Walker) 84

1.1.5.10 *O. decorus* (Germar) 91

1.1.5.11 *O. infernalis* Saussure 102
1.1.5.12 *O. formosanus* (Shiraki) 112
1.1.5.13 *O. interruptus* (Kirby) 116
1.1.5.14 *O. instillatus* Burr 120
1.1.5.15 *O. obtusangulus* Uvarov 124
1.1.5.16 *O. rosescens* Uvarov 129
1.1.5.17 *O. miniatus* Uvarov 133
1.1.5.18 *O. nadiae* sp. n. 138
1.1.5.19 *O. inornatus* Schulthess-Schindler 142
1.1.5.20 *O. flavus* (Linnaeus) 145

1.2 BIOGEOGRAPHY OF THE GENUS *OEDALEUS* 152
1.2.1 Relationships within the genus 152
1.2.2 Geographical origin of the genus 153
1.2.3 The Pleistocene in Africa 154
1.2.4 The southern African *Oedaleus* fauna 155
1.2.5 The *Oedaleus* fauna of the Somali peninsula 164
1.2.6 The *Oedaleus* fauna of the subsaharan latitudinal belt 168
1.2.7 The non-African *Oedaleus* fauna 177
1.2.8 Problems of analysis of distribution patterns 183
1.2.9 East African origins of *Oedaleus* 183
1.2.10 The *Brachystegia* woodland barrier and 'trans-equatorial' speciation in *Oedaleus* 184
1.2.11 The woodland barrier and the 'arid corridor': biogeographical evidence from other groups 188
1.2.12 Conclusions 195

PART TWO: TAXONOMIC AND BIOGEOGRAPHICAL STUDIES OF THE GENUS *GASTRIMARGUS* SAUSSURE.

2.1 TAXONOMY OF THE GENUS *GASTRIMARGUS* 197
2.1.1 Introduction: taxonomic background and and methods 197
2.1.1.1 History of the genus and scope of revision 197
2.1.1.2 Economic importance of the genus *Gastrimargus* 198
2.1.1.3 Methods and terminology 198

2.1.1.4 Depositories 200

2.1.2 Generic synonymy 201

2.1.3 Description and Affinities of the genus 201

2.1.4 Keys to the species of *Gastrimargus* 204

2.1.4.1 Key to African species 204

2.1.4.2 Key to non-African species 210

2.1.4.3 Notes on the keys 212

2.1.5 Annotated species catalogue of the genus *Gastrimargus*, with synonymy, diagnoses, measurements, and biological notes 215

2.1.5.1 *G. africanus* (Saussure) 216

2.1.5.2 *G. nubilus* Uvarov 227

2.1.5.3 *G. lombokensis* Sjöstedt 230

2.1.5.4 *G. subfasciatus* (de Haan) 234

2.1.5.5 *G. musicus* (Fabricius) 237

2.1.5.6 *G. marmoratus* (Thunberg) 243

2.1.5.7 *G. immaculatus* (Chopard) 250

2.1.5.8 *G. hyla* Sjöstedt 252

2.1.5.9 *G. rothschildi* Bolivar 257

2.1.5.10 *G. verticalis* (Saussure) 262

2.1.5.11 *G. miombo* sp. n. 269

2.1.5.12 *G. determinatus* (Walker) 273

2.1.5.13 *G. crassicollis* (Saussure) 283

2.1.5.14 *G. drakensbergensis* sp. n. 287

2.1.5.15 *G. obscurus* sp. n. 290

2.1.5.16 *G. wahlbergii* (Stål) 293

2.1.5.17 *G. angolensis* Sjöstedt 298

2.1.5.18 *G. mirabilis* Uvarov 300

2.1.5.19 *G. insolens* sp. n. 305

2.1.5.20 *G. acutangulus* (Stål) 306

2.1.5.21 *G. ochraceus* Sjöstedt 311

2.1.5.22 *G. willemsei* sp. n. 315

2.1.5.23 *G. sarasini* (Saussure) 318

2.2 BIOGEOGRAPHY OF THE GENUS *GASTRIMARGUS* 322

2.2.1 The African Gastrimargus fauna 322

2.2.2 The *Gastrimargus* fauna of Asia 333

2.2.3 The *Gastrimargus* fauna of Malesia 333

2.2.4 The *Gastrimargus* fauna of Australasia 341

2.2.5 General discussion 342

SUMMARY		344
ACKNOWLEDGEMENTS		347
REFERENCES		348
APPENDICES		374
Appendix 1.	Taxonomy of Oedaleus: material examined	375
Appendix 2.	Taxonomy of Gastrimargus: material examined	379

LIST OF TABLES

[Legends have been abbreviated]

PART ONE

1-2	Oedaleus senegalensis, measurements	43
3	O. nigrofasciatus, measurements	49
4	O. australis, measurements	49
5-6	O. abruptus, measurements	60
7	O. virgula, measurements	66
8	O. johnstoni, measurements	66
9-12	O. nigeriensis, measurements	76, 77
13	O. carvalhoi, measurements	83
14-15	O. plenus, measurements	83, 88
16-20	O. decorus, measurements	88, 95-96
21	't' tests on measurements of O. decorus.	97
22-25	O. infernalis, measurements	97,106-107
26	O. formosanus, measurements	107
27	O. interruptus, measurements	119
28	O. instillatus, measurements	119
29-30	O. obtusangulus, measurements	127
31	O. rosescens, measurements	132
32	O. miniatus, measurements	132
33	O. nadiae, measurements	141
34	O. inornatus, measurements	141
35-36	O. flavus, measurements	150

PART TWO

1-5	Gastrimargus africanus, measurements	221, 223-224
6	G. nubilus, measurements	224

7	*G. lombokensis*, measurements	233
8	*G. subfasciatus*, measurements	233
9–11	*G. musicus*, measurements	240, 241
12–13	*G. marmoratus*, measurements	241, 248
14	*G. immaculatus*, measurements	248
15	*G. hyla*, measurements	256
16	*G. rothschildi*, measurements	256
17–18	*G. verticalis*, measurements	267
19	*G. miombo*, measurements	270
20–23	*G. determinatus*, measurements	270, 279, 281
24	*G. crassicollis*, measurements	281
25	*G. drakensbergensis*, measurements	288
26	*G. obscurus*, measurements	288
27	*G. wahlbergii*, measurements	296
28	*G. angolensis*, measurements	296
29	*G. mirabilis*, measurements	303
30	*G. insolens*, measurements	303
31–32	*G. acutangulus*, measurements	308
33	*G. ochraceus*, measurements	313
34	*G. willemsei*, measurements	313
35	*G. sarasini*, measurements	321

LIST OF PLATES

[Legends have been abbreviated]

PART TWO

1–2	*Gastrimargus africanus africanus* ♂, & *G. a. sulphureus* ♂	218
3–4	*G. nubilus* ♂, & *G. lombokensis* ♂	229
5–6	*G. subfasciatus* ♂, & *G. musicus* ♂	235
7–8	*G. marmoratus* ♂, & *G. immaculatus* ♂	246
9–10	*G. hyla* ♂ & ♀	254
11–12	*G. rothschildi* ♂ & ♀	259
13–14	*G. verticalis verticalis* ♂, & *G. v. mpwapwae* ♂	264
15–16	*G. ?verticalis* ♂, & *G. miombo* ♂	272
17–18	*G. determinatus determinatus* ♂ & ♀	275
19–20	*G. determinatus procerus* ♂, & *G. d. vitripennis* ♂	277
21–22	*G. crassicollis* ♂, & *G. drakensbergensis* ♂	286
23–24	*G. obscurus* ♂ & ♀	292

25-26 G. wahlbergii ♂, & G. angolensis ♂ 297
27-28 G. mirabilis ♂, & G. insolens ♀ 304
29-30 G. acutangulus acutangulus ♂, & G. ochraceus ♂ 310
31-32 G. willemsei ♂, & G. sarasini ♂ 317

LIST OF FIGURES

[Legends have been abbreviated]

PART ONE

1-17 Oedaleus species (males), wings 24, 25
18-38 Oedaleus species (females), heads & pronota, dorsal 30-33
39-59 Oedaleus species, ventral ovipositor valves, ventral 36-37
60-65 O. senegalensis, genitalia 41
66-70 O. nigrofasciatus, genitalia 47
71-74 O. australis, genitalia 53
75-78 O. abruptus, genitalia 57
79-82 O. virgula, genitalia 63
83-87 O. johnstoni, genitalia 68
88-91 O. nigeriensis, genitalia 73
92-95 O. carvalhoi, genitalia 80
96-99 O. plenus, genitalia 85
100-106 O. decorus, genitalia 92
107-110 O. infernalis, genitalia 103
111-114 O. formosanus, genitalia 113
115-118 O. interruptus, genitalia 117
119-123 O. instillatus, genitalia 121
124-127 O. obtusangulus, genitalia 125
128-133 O. miniatus, genitalia 134
134-137 O. rosescens, genitalia 130
138-141 O. nadiae, genitalia 139
142-146 O. inornatus, genitalia 143
147-150 O. flavus, genitalia 146
151 Vegetation maps of Africa during glacial & interglacial maxima (after Van Zinderen Bakker, 1976) 157
152 Distribution of Oedaleus species in Southern Africa 159
153 Distribution of O. plenus in southern Africa 160
154 Rainfall map of South Africa (after Adamson, 1938) 162
155 Distribution of Oedaleus species in Africa 163

156 Distribution of Oedaleus species in E Africa & SW Arabia 165
157 Vegetation of N region of the Somali Rep. (Hemming, 1966) & distribution of O. nadiae 167
158 Distribution of Oedaleus species in Asia 169
159 Distribution of O. decorus decorus 171
160 Late Pleistocene advance of the Sahara (after Hamilton, 1976). 173
161 Distribution of O. senegalensis in Africa & W Asia. 175
162 Distribution of O. nigeriensis in Africa 176
163 Distriburion of O. virgula in Madagascar 178
164 Distribution of Oedaleus species in E Asia 180
165 Distribution of O. australis in Australasia 181
166 Distribution of arid regions in Africa (after Balinsky, 1962) 190
167 The Somali Arid & SW Arid Districts & the past corridor between them (after Winterbotham, 1967) 191

PART TWO

1–7 Gastrimargus africanus, genitalia 217
8–11 G. nubilus, genitalia 228
12–15 G. lombokensis, genitalia 231
16–19 G. subfasciatus, genitalia 236
20–25 G. musicus, genitalia 238
26–32 G. marmoratus, genitalia 245
33–36 G. immaculatus, genitalia 251
37–40 G. hyla, genitalia 253
41–44 G. rothschildi, genitalia 258
45–51 G. verticalis, genitalia 265
52–56 G. miombo, genitalia 271
57–63 G. determinatus, genitalia 274
64–67 G. crassicollis, genitalia 285
68–71 G. drakensbergensis, genitalia 289
72–75 G. obscurus, genitalia 291
76–80 G. wahlbergii, genitalia 295
81–85 G. angolensis, genitalia 299
86–89 G. mirabilis, genitalia 302
90–97 G. acutangulus, genitalia 309
98–101 G. ochraceus, genitalia 314
102–106 G. willemsei, genitalia 316

107–110 G. *sarasini*, genitalia 320

111 Distribution of *Gastrimargus* species in Africa 323

112 Distribution of G. *crassicollis* & G. *drakensbergensis* 324

113 Distribution of G. *verticalis verticalis* & G. *v. mpwapwae* 325

114 Distribution of races of G. *rothschildi* in Ethiopia 328

115 Distribution of G. *determinatus* in Africa & Arabia 329

116 Distribution of *Gastrimargus* species in Africa, Arabia, & neighbouring islands 332

117 Distribution of *Gastrimargus* species & subspecies in Asia 334

118 Distribution of G. *lombokensis* in the Lesser Sunda Is. 337

119 Distribution of G. *marmoratus* in SE Asia 339

120 Distribution of *Gastrimargus* species in Australasia 340

PART ONE

TAXONOMIC, BIOGEOGRAPHICAL, AND BIOLOGICAL STUDIES OF THE GENUS *OEDALEUS* FIEBER

1.1 TAXONOMY OF THE GENUS OEDALEUS

1.1.1 Introduction: taxonomic background and methods

1.1.1.1 Need for a revision of Oedaleus

In recent years members of the genus Oedaleus have increasingly been designated as crop pests in Africa, India, and SE Asia. The most serious damage has been caused by Oedaleus senegalensis, a widespread and economically important species, reviewed by Batten (1969). The growing list of described species, and their possible economic importance, have highlighted the lack of any comparative taxonomic and biogeographical study and the need for accurate identification and a more certain knowledge of relationships within the genus. Descamps (1972), speaking at the International Study Conference on the Current and Future Problems of Acridology, included Oedaleus among a short-list of genera urgently in need of revision.

This study is intended to facilitate accurate identification of all Oedaleus species by agriculturists, ecologists, and entomologists involved in locust control and crop protection. To guarantee stable nomenclature, all available primary types have been examined, and neotypes have been designated to replace lost types. In cases where a holotype was not originally designated, lectotypes have been selected from the syntype series. Keys to, and descriptions of all the species and subspecies are included, with figures to illustrate the more important morphological characters. Accurate distribution maps have been compiled, based largely upon data from the labels of the many thousands of specimens examined which are listed for each species. Supplementary data have been obtained from correspondents and from reliable published sources. The biogeography of the genus is discussed in the light of known past and present geological, vegetational, and climatic features, and the available information on the life histories, biology, and economic importance is assembled.

1.1.1.2 History of the genus *Oedaleus*

The genus *Oedaleus* was erected as a subgenus of *Oedipoda* by Fieber (1853) to accommodate *Acrydium nigrofasciatum* De Geer 1773. Stål (1873) made *Oedaleus* a subgenus of *Pachytylus* Fieber 1853 and added to it three species now included in *Gastrimargus*, as well as *Gryllus Locusta flavus* Linnaeus 1758 and *Gryllus abruptus* Thunberg, 1815. He also synonymised *Gryllus arcuatus* Thunberg, 1824 with *Oedaleus nigrofasciatus* (De Geer, 1773), a fact overlooked by both Kirby (1910) and Johnston (1956).

Saussure (1884) gave *Oedaleus* full generic status and divided it into two subgenera, *Oedaleus* s. str., and the newly-erected *Gastrimargus*. He described *Oedaleus infernalis* and transferred *Pachytylus senegalensis* Krauss, 1877, but placed *Oedaleus flavus* (Linnaeus, 1758) in the genus *Humbella*. Unfortunately, he later (Saussure, 1888) described the same insect as *Oedaleus nigrofasciatus* var. *citrinus* and despite the use of the older name by Karsch (1887) and Kirby (1902), Saussure's name remained in common use as *Oedaleus citrinus* Saussure (Distant, 1902) until the synonymy was revealed by Dirsh (1961). Linnaeus (1758) assumed that his *Gryllus Locusta flavus* was identical with the "*Locusta capensis alis inferioribus luteis*" described by Petiver (1702) but in the absence of surviving material Petiver's figure cannot definitely be proved to represent this species. *Gryllus Locusta flavus* was wrongly identified with *Acrydium nigrofasciatum* De Geer, 1773, by De Geer himself and by several subsequent authors, although Kirby (1910) pointed out that the *Gryllus flavus* of Fabricius, 1775, a junior synonym of *Oedaleus nigrofasciatus*, should not be considered identical with the *G. L. flavus* of Linnaeus, known to Kirby as *Humbe flava*. He was also aware that the *G. L. flavus* of Stoll (1813) was not the same species as that of Linnaeus, and synonymised it (incorrectly) with *Oedaleus arcuatus* (Thunberg, 1824), which was itself a synonym of *Oedaleus nigrofasciatus* unbeknown to him.

This situation was further complicated by the fact that Oedaleus nigrofasciatus, a purely South African species, was always confused with the Mediterranean Oedaleus decorus (Germar, 1826), the older name being used indiscriminately until Uvarov (1923) finally demonstrated the separate identity of the two species. Since then some confusion of O. decorus and O. nigrofasciatus has continued (Hollande, 1926; Jovančić, 1953; Barbut, 1954; Rungs, 1962). Oedaleus australis Saussure, 1888, originally described as O. nigrofasciatus var. australis and given specific status by Kirby (1910), has also been the subject of some confusion. It was frequently identified as O. senegalensis (Krauss, 1877) (Froggatt, 1903, 1907, 1910; Sjöstedt, 1920, 1921; Zacher, 1925, 1949), although Uvarov (1930) gave reasons for believing the Australian species to be distinct from the African one.

Kirby (1910) synonymised Ctypohippus arenivolans Butler, 1881 and Pachytylus mlokoziewizteki Bolivar, 1887 with O. senegalensis. Distant (1892) transferred Epacromia plena Walker, 1870 to Oedalus [sic], and Uvarov (1925) synonymised O. nigrofasciatus var. caffer Saussure, 1888 with this species and transferred Chortoicetes interruptus Kirby, 1902 to Oedaleus. Throughout the last century numerous new species and subspecies have been described, notably by Uvarov (six species), but there has not been any revisionary treatment of the genus and nomenclatural changes have been limited to those outlined above.

At the commencement of the present study twenty four species and four subspecific taxa were recognised.

1.1.1.3 Taxonomic affinities and diagnostic characters

Oedaleus falls naturally within the subfamily Oedipodinae, recently reinstated by Dirsh (1975). It comprises a homogeneous group of species found widely in the Old World tropics and subtropics. It may be distinguished from related genera by a combination of the following characters: the presence of a wing band in most species, the form and markings of the pronotum, the hind femur having the upper marginal area not excised and lower marginal area not expanded, the tegmen lacking specialised stridulatory veinlets and by the short apical penis valves. It may be distinguished from the closely related genus *Gastrimargus* by the following key:

1. Pronotal x-marking with anterior and posterior arms continuous; posterior arms usually curved and with slightly convergent apices. Hind margin of pronotum rectangular to acutangular, never rounded ... ... *Gastrimargus*

-. Pronotal x-marking always with anterior and posterior arms separate; posterior arms straight, not converging. Hind margin of pronotum rounded to rectangular, never (except in *O. interruptus*, *O. miniatus*, and some *O. plenus*) acutangular ... *Oedaleus*

As indicated by the rather poor characters given above, there are no reliable objective criteria for separating the genera *Oedaleus* and *Gastrimargus* in their entirety one from the other. However all the species presently considered as members of either of these genera are more closely allied to their congeners than to any member of the other genus. Saussure (1884) separated out *Gastrimargus* as a subgenus of *Oedaleus* largely on the basis of an overall impression of stoutness in the former. *Gastrimargus* later rose to generic status without any reasoned defence of its elevation (Kirby, 1910).

Saussure himself and later authors have sometimes experienced difficulty in referring marginal species to one genus or the other.

It is probable (but not yet certain) that all or most species of Oedaleus possess a pronotal repugnatorial gland and that, by contrast, Gastrimargus species do not. This may in the future give a more certain separation between the two genera. At present the division is workable and convenient since it enables the separation of forty or so species into two almost equal groups of species with distinct ecological preferences. It appears that Oedaleus are basically characteristic of sub desert steppes and dry grasslands while Gastrimargus are found in more humid wooded savannahs and tall grass.

Despite the uniformity of morphology within the genus, useful characters for species identification can be obtained by close examination. These include the shape and patterning of the dorsal surface of the pronotum (Figs 18-38), the banding or lack of banding on the hind wing (Figs 1 - 17), and the colouration of the ventral surface of the hind femora. The male genitalia offer some useful supporting characters which may however be difficult to interpret. In the females some additional information can be gained by studying the ventral surface of the ovipositor valves (Figs 39 - 59). However the spermatheca is of little value for identification being variable within one species and rather uniform within the genus as a whole.

1.1.1.4 Materials, methods, and terminology

Measurements used in this study generally follow Dirsh (1953) except that total length is here defined as the distance from the frons to the apices of the folded tegmina, as used by Jago (1963), not to the end of the abdomen as used by Dirsh and several other authors; head width is here measured across the genae (Dirsh, 1953) or across the eyes (Jago, 1963), whichever is the larger. The forewing is referred to as the tegmen, not the elytron. All measurements were made with Mauser dial gauge vernier calipers graduated with 0.05 mm divisions.

The male genitalia figured in this study were removed and treated in the manner described by Dirsh (1956a). Female spermathecae were examined by removal of the posterior abdominal segments and maceration in 10% potassium hydroxide solution. The abdomen was then slit open along the lateral intersegmental membrane to display the spermatheca. After examination genitalia preparations were placed in 70% alcohol with a little glycerine, contained in a polythene vial with a silicone rubber stopper pinned to the appropriate insect specimen.

Abbreviations of terms used in the descriptions and figures of the male genitalia are as follows: A - ancorae of epiphallus; Ac - arch of cingulum; Ap - anterior projections of epiphallus; Apv - apical valves of penis; Apd - apodemes of cingulum; B - bridge of epiphallus; Bp - basal valves of penis; Cv - cingular valves; Dp - dorsal process of cingulum; Ejd - ejaculatory duct; E - ejaculatory sac; Gpr - gonopore process; L - lophi of epiphallus; Lp - lateral plate of epiphallus; Pp - posterior projections of epiphallus; Rm - rami of cingulum; Sps - spermatophore sac. These and most other morphological terms relating to acridids are described and illustrated by Dirsh (1965). Since the genitalia of all species are very similar only those of _O. senegalensis_ (Figs 60-64) have been labelled.

The nomenclature of the female spermatheca used in this study is that of Dirsh (1957). The term 'apical diverticulum' is thus understood to denote the bulbous blind-ending sac at the distal extremity of the spermathecal duct. In Oedaleus and other Acrididae this may be simple or it may possess a secondary diverticulum, which is usually much smaller. The apical diverticulum is always strongly recurved at its proximal end, and always continues in the direction of the coiling of the duct. The secondary or preapical diverticulum, on the other hand, when not reduced to a mere vestige, projects from the main duct at right angles on the outside of the coil. Since the secondary diverticulum is always smaller than the main seminal reservoir and is often absent, it is reasonable to refer to it as 'preapical' and to the larger diverticulum as 'apical'. However, Slifer (1939), a pioneer of the comparative study of the spermatheca, and other authors have used exactly the opposite designations, thus introducing some confusion. Recently Amedegnato (1976) has confirmed the nomenclature of Dirsh, used here, on the grounds that in the primitive condition there is only one diverticulum which should therefore be called apical.

The terminology of the venation used here is that of Ragge (1955). Except where otherwise stated, material examined is from the collections of the British Museum (Natural History), London, and dates of collection are of the twentieth century.

To save space the listing of material examined (Appendix 1) has been restricted to the label data of primary type specimens, and a statement of the number of other specimens of each species studied. The full list of material examined is deposited in the library of the Centre for Overseas Pest Research, and is available on request.

1.1.1.5 Depositories

ANIC Canberra - Australian National Insect Collection, Canberra

MHN Geneva - Muséum d'Histoire Naturelle, Geneva

MCSN Genoa - Muséo Civico di Storia Naturale, Genoa

RNH Leiden - Rijksmuseum van Natuurlijke Historie, Leiden.

ZI Leningrad - Zoological Institute, Academy of Sciences of the USSR, Leningrad

MLZA Lisbon - Museu e Laboratorio Zoologico e Antropologico, Universidade de Lisboa, Lisbon

BMNH - British Museum (Natural History), London

UM Oxford - Hope Department of Entomology, University Museum, Oxford

MNHN Paris - Muséum National d'Histoire Naturelle, Paris

DATS Pretoria - Department of Agricultural Technical Services, Pretoria

NR Stockholm - Naturhistoriska Rijksmuseum, Stockholm

ZIUU Uppsala - Zoologiska Institutionen, Uppsala Universitet, Uppsala

NM Vienna - Naturhistorisches Museum, Vienna

1.1.2 OEDALEUS Fieber, 1853

Oedipoda (Oedaleus) Fieber 1853: 126.

Pachytylus (Oedaleus) Stål 1873: 123.

Oedaleus (Oedaleus) Saussure 1884: 50.

Type-species: Acrydium nigrofasciatum Degeer, 1773 by monotypy.

1.1.3 Description of the genus

Medium size (20 - 44 mm male, 25 - 49 female). Integument rugose and pitted. Fastigium of vertex angular with truncate apex, flat or slightly concave, with obtuse lateral carinulae variable in emphasis, with or without median longitudinal carinula; fastigial foveolae obsolete. Antennae (except in O. miniatus) filiform, as long as, or longer than length of head and pronotum together. Frons in profile oblique, convex, straight, or concave; frontal ridge sulcate with marginal carinulae diverging ventrally, reaching or not reaching clypeus. Eyes elongate-oval to oval, long axis vertical. Pronotum from high tectiform to saddle shaped, constricted anterior to and at junction of prozona and metazona, wider and with distinct 'shoulders' in metazona; median carina linear, often intersected by posterior transverse sulcus; raised lateral carinae absent in most species, occasionally present in prozona underlying anterior arms of x-marking; metazona equal to or little longer than prozona, rarely (in O. interruptus) much longer, posterior margin rounded or angular; mesosternal interspace wider than long, widening posteriorly, usually wider than metasternal interspace. Tegmina and wings fully developed, or only slightly abbreviated; intercalary vein of medial area of tegmen well-developed and finely serrate, at least in males, continuing to distal apex of medial area; membrane of tegmen semi-transparent with variable reticulation in basal half. Hind femur slender or broad, exterior ventral knee lobe acutely rounded; hind tibia as long as femur, apical spurs not specialised; arolium of medium size or small. Male supraanal plate shield-shaped, rounded triangular; cercus conical, apically acutely rounded, of variable length; subgenital plate (except in O. miniatus) short, subconical with rounded apex; epiphallus bridge-shaped with well-developed ancorae and large, bilobate lophi; ectophallic membrane sclerotised and forming sheath below apical penis valves; cingulum with horseshoe-shaped arch bearing moderately long apodemes; cingular valves acute, less sclerotised than apical penis valves; basal penis valves with anterior lateral expansions, sometimes recurved, flexure narrow; apical penis valves short, acute, with serrated ventral subapical process. Female ovipositor short, valves robust, vertically excurved; spermatheca with sac-like apical diverticulum with or without a short preapical diverticulum.

General colouration variable, greenish or brownish with contrasting light and dark markings. Genae of head with oblique light and dark markings. Pronotum with variable dorsal light markings in the form of an X, lacking central intersection and divided into four arms by median carina and posterior transverse sulcus. Anterior arms of X often continued anteriorly onto head crossing or not crossing eyes as a pale longitudinal stripe. Lateral lobes of pronotum with distinct white oblique marking centrally, sometimes reaching hind margin. Tegmina and hind femora with corresponding transverse light and dark bands, variable, sometimes obscure. Hind wing weakly or strongly tinted with yellow, pink, or red, usually but not always bounded by a dark fascia; remainder of wing transparent, colourless, sometimes apically darkened. Interior surface of hind femur straw-coloured, red, or mauve; tibiae red, straw-coloured, or grey.

1.1.4 Keys to the species of Oedaleus

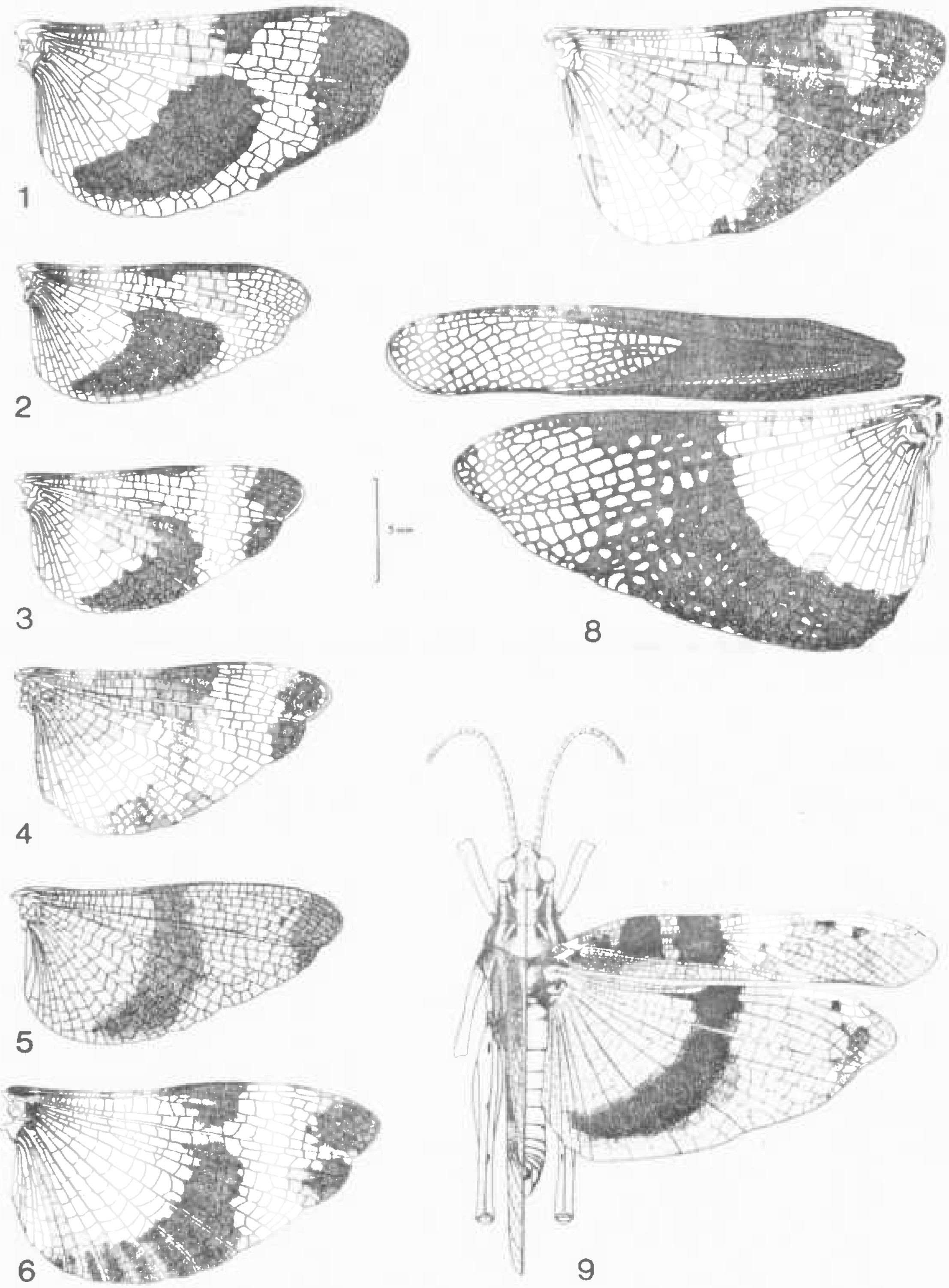
1.1.4.1 Notes on the keys

These are the first keys designed to facilitate the identification of all the known species of the genus Oedaleus. Keys to Oedaleus species occurring in eastern Asia were published by Chang (1939) and by Bei-Bienko and Mishchenko (1951a) but these are of little value since insufficient attention was paid to the examination of type material and assessment of the range of infra-subspecific variation. Succeeding students of the subject have uncritically adopted the erroneous judgements of earlier authors with the eventual result that the keys presently in use serve merely to distinguish imaginary taxa by the use of thoroughly unreliable characters. Thus the subspecies Oedaleus infernalis pendulus Steinmann (1965) was distinguished from other supposed subspecies largely on the basis of the proportions of the medial antennal segments. I am indebted to L.L. Mishchenko (pers. comm.), who has seen the type, for the information that it is in fact a junior synonym of Dociostaurus maroccanus (Thunberg).

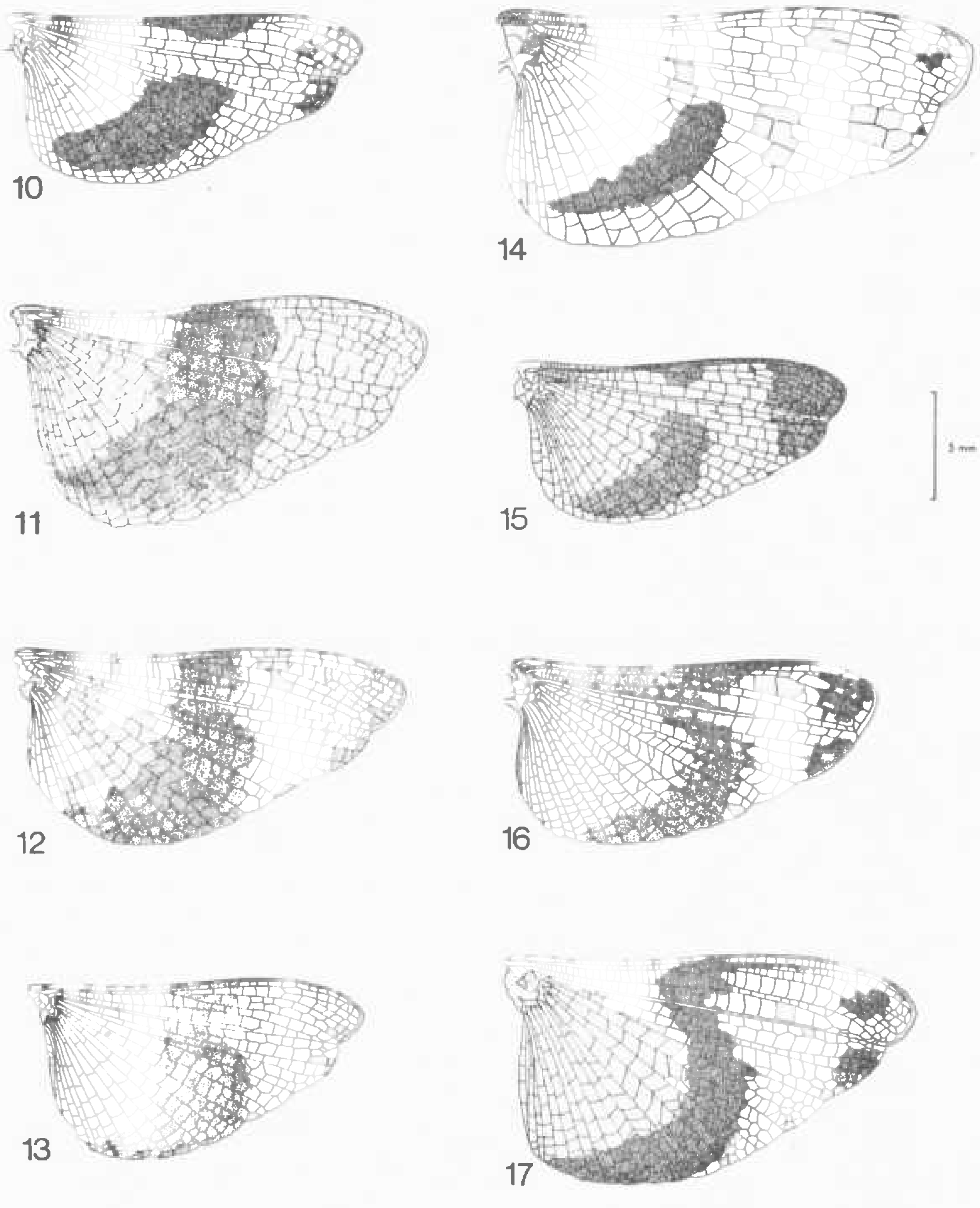
For brevity and ease of use, two keys are here provided, one covering Africa and its islands, Arabia and Madagascar, and the other dealing with the rest of the old world. In this way a specimen from Asia can be identified without needing to compare it to more than a dozen species which are known to be restricted to the Ethiopian Region. Some widespread species occur in both keys, and variable species are keyed out twice in the same key.

As in some other recent generic revisions in the Acrididae, for example that of Aiolopus by Hollis (1968), the male phallic complex has been found to display considerable uniformity. For this reason, although they are described and figured elsewhere in this study, genital characters have not been used to construct a separate key for males. Instead one key is given for both sexes with the main characters derived from the shape and markings of the pronotum, the form of the hind wing fascia, and the colour of the basal area of the hind wing and the interior surface of the hind femur. In addition, characters from the genitalia of either sex are used as subordinate evidence of identification where appropriate.

In these keys total length and head width have been used as subsidiary characters even if the known size-ranges of two taxa partially overlap.



Figs 1-9. *Oedaleus* species (males), wings. 1, *O. australis*; 2, *O. abruptus*; 3, *O. obtusangulus*; 4, *O. rosescens*; 5, *O. infernalis*; 6, *O. plenus plenus*; 7, *O. formosanus*; 8, *O. senegalensis* (melanic); 9, *O. senegalensis* (normal).



Figs 10-17. *Oedaleus* species (males), wings. 10, *O. nigeriensis*; 11, *O. decorus decorus*; 12, *O. instillatus*; 13, *O. interruptus*; 14, *O. johnstoni*; 15, *O. carvalhoi*; 16, *O. miniatus*; 17, *O. flavus*.

1.1.4.2 Key to African species of Oedaleus

1. Hind wing pink or red basally 2

-. Hind wing bright yellow or pale yellow basally 3

2.(1) Hind wing with basal area scarlet in male, salmon pink in female, bounded by distinct brown fascia (Fig. 16); antennae flattened, ensiform; male subgenital plate with medial dorso-posterior process (Figs 128, 129) (Somalia, E Kenya) ... ... Oedaleus miniatus Uvarov

-. Hind wing with basal area clear rose pink in both sexes, lacking fascia; antennae filiform; male subgenital plate normal (N. Somalia) ... ... Oedaleus nadiae sp. n.

3.(1) Hind wing fascia continuous to tip of wing; tegmen unicolourous brown, without pattern (Fig. 8) (Cape Verde Is.) ... ... melanic form of Oedaleus senegalensis (Krauss)

-. Hind wing fascia forming a distinct band, never continuous to wing tip; tegmen speckled or banded, never unicolourous brown 4

4.(3) Hind wing fascia complete, or narrowly interrupted at first anal vein (Figs 9,11) 5

-. Hind wing fascia broadly interrupted, indistinct, or absent 9

5.(4) Hind wing basally bright yellow; dorsal surface of pronotum with small light brown warts (Fig.34); hind femur internally mauve to deep violet (except E. African males) (S. and E. Africa) ... ... Oedaleus flavus (Linnaeus)

-. Hind wing basally pale yellow to colourless; dorsal surface of pronotum smooth; hind femur never mauve or violet internally 6

6.(5) Hind femora ventrally straw coloured; hind margin of pronotum rounded or parabolic 7

-. Hind femora ventrally red or reddish brown; hind margin of pronotum rectangular to obtusangular 8

7.(6) Hind margin of pronotum parabolic (Fig. 18); bridge of epiphallus with acutely curved interior surface (Figs 62, 63) (W. Africa to E. Africa N. of 8° S.) ... ... Oedaleus senegalensis (Krauss)

-. Hind margin of pronotum oval (Fig. 21); bridge of epiphallus with obtusely curved interior surface (Fig. 68) (Southern Africa S. of 17° S.) ... ... Oedaleus nigrofasciatus (Degeer)

8.(6) Small species, total length: 22-27.5 mm male, 30-37.5 mm female; general colouration mottled brown or grey; head, pronotum, and hind femora occasionally pale green suffused with brown, tegmina never tinged with green; white transverse bars on tegmen reduced, not reaching second cubital vein (E. Africa) ... ... Oedaleus instillatus Burr

-. Large species, total length: 29-45.5 mm male, 42-53 mm female; general colouration variable, green, straw, or brown, always broken up by bands of darker pigment; dorsal surface of folded tegmina suffused with green in green specimens; white transverse bars on tegmina always reaching to second cubital vein (N. Africa) ... ... Oedaleus decorus (Germar)

9.(4) Hind wing fascia absent or only faintly visible 10

-. Hind wing fascia distinctly visible but widely interrupted around first anal vein 12

10.(9) Large robust species, total length: 26.8-37.1 mm males, 33.5-48.5 mm females, head width: 4.3-5.4 mm males, 5.8-7.8 mm females (E. Africa) ... .. Oedaleus inornatus Schulthess

-. Small species, total length: 22.0-29.0 mm males, 29.0-40.0 mm females, head width: 3.0-4.0 mm males, 4.0-5.5 mm females 11

11.(10) Pronotal x-marking variable but never absent, posterior arms of x thick (Fig. 22); ventral surface of hind femora red, tegmina exceeding hind knees by one quarter of femur length or less; female posterior ventral basivalvular sclerite smooth, pale, unsclerotised, lightly pitted (Fig. 45) (Eastern S. Africa) ... ... extreme form of Oedaleus plenus browni subsp. n.

-. Pronotal x-marking thin, often indistinct, sometimes absent; ventral surface of hind femur brown, never red; tegmina exceeding hind knees by one third of femur length or more; female posterior ventral basivalvular sclerite dark, sclerotised, and with rugose warts (Fig. 42) (Madagascar) ... ... Oedaleus virgula (Snellan Van Vollenhoven)

12.(9) Large species, head width 4.5-5.2 mm male, 5.8-7.6 mm female; general colouration pale, uniform, mottled, usually sandy, occasionally suffused with pale green; pronotal x-marking indistinct, pronotal median carina weak, seldom raised, hind margin of pronotum evenly rounded, never angular (Mauretania to Ethiopia) ... ... Oedaleus johnstoni Uvarov

-. Smaller species, head width 3.5-4.6 mm male, 4.5-6.5 mm female; general colouration darker, with contrasting lighter markings on pronotum and tegmina; pronotal x-marking distinct, pronotal median carina strongly marked, slightly arcuate, hind margin of pronotum angular 13

13.(12) Tibiae and ventral surface of hind femora straw coloured, never red 14

-. Tibiae and ventral surface of hind femora red or orange red 15

14.(13) Pronotal hind margin forming an obtuse angle with concave sides (Fig. 23), pronotal x-marking very fine; hind wing fascia strongly marked (Fig. 15) (Southern Africa) ... ... Oedaleus carvalhoi Bolivar

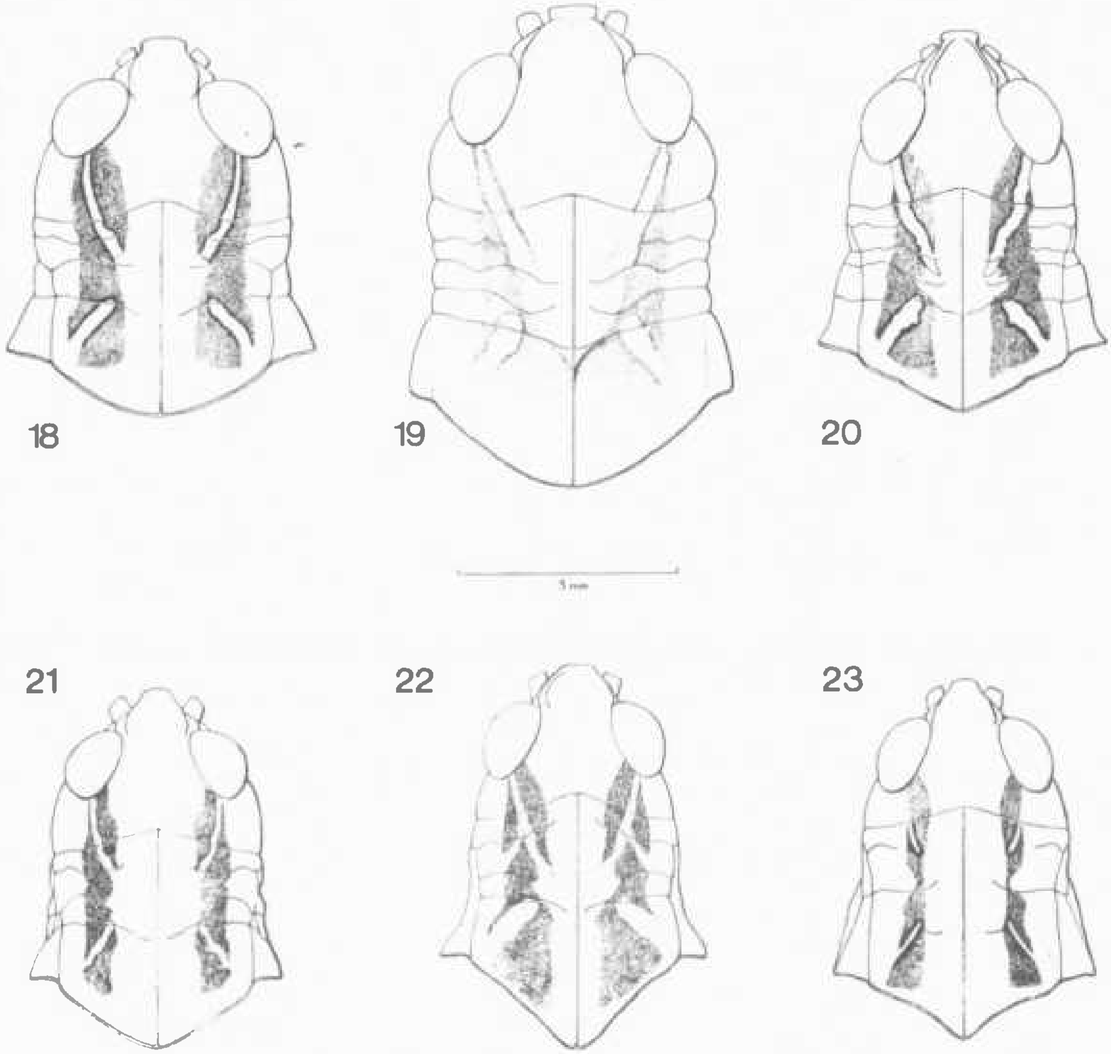
-. Pronotal hind margin forming a flat or convex-sided right angle (Fig. 35), pronotal x-marking thicker; hind wing fascia weakly marked (Fig. 3) (Aïr mts, Niger, and Arabia) ... ... <u>Oedaleus</u> <u>obtusangulus</u> Uvarov

15.(13) Hind margin of pronotum sharply acute, pronotal x-marking very thin; eyes seen from above small and close set, vertex narrow (Fig. 26); dark pattern of tegmina separated into rounded cells; hind wing fascia widely expanded and rounded anteriorly (Fig. 13) (Transvaal) ... ... <u>Oedaleus</u> <u>interruptus</u> (Kirby)

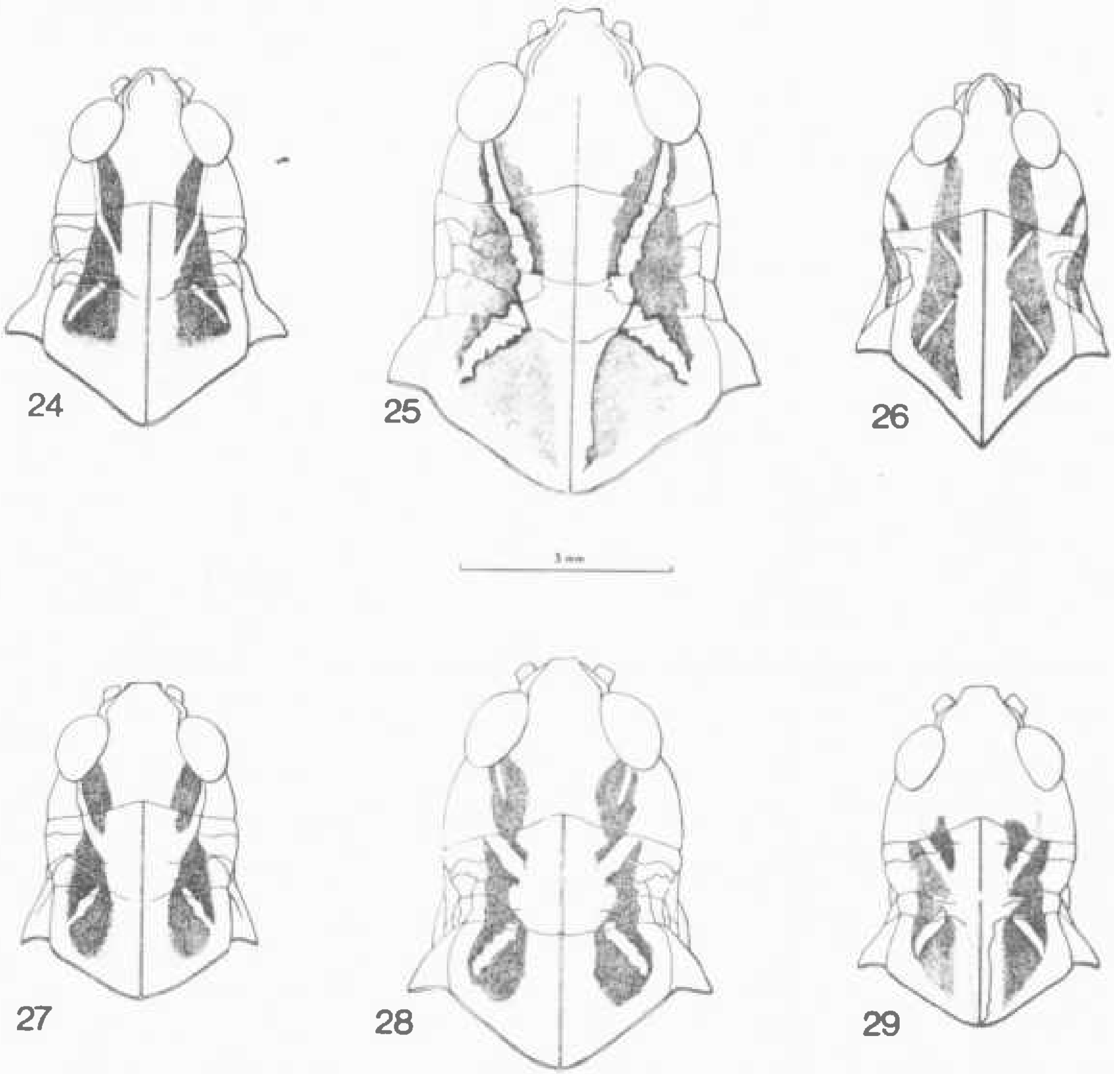
-. Hind margin of pronotum bluntly rectangular or obtusangular, pronotal x-marking variable but thicker; eyes normal, more widely set; vertex broader (Figs 20, 22); dark pattern of tegmina forming bands separated by narrow lighter areas; hind wing fascia narrowing or narrowly expanded anteriorly 16

16.(15) Hind margin of pronotum forming right angle or obtuse angle with concave sides (Fig. 22); hind wing fascia, when complete, not widening in anterior half (Fig. 6), often incomplete, failing to reach second anal vein, occasionally absent (Southern Africa and Tanzania) ... ... <u>Oedaleus</u> <u>plenus</u> (Walker)

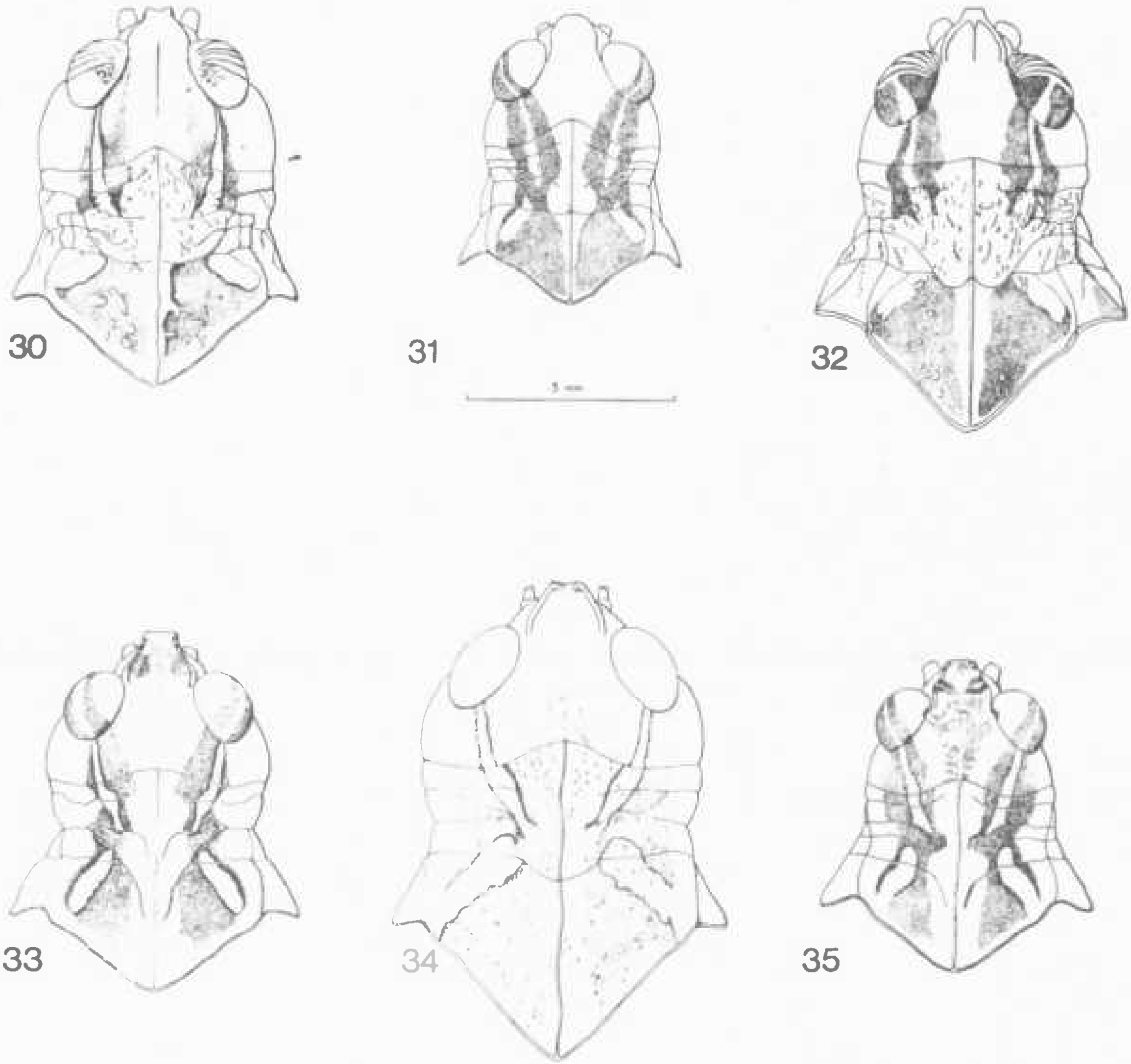
-. Hind margin of pronotum forming a flat or convex-sided angle (Fig. 20); hind wing fascia widening anteriorly, reaching to second anal vein (Fig. 10) (Senegal to Ethiopia and South to Tanzania) ... ... <u>Oedaleus</u> <u>nigeriensis</u> Uvarov



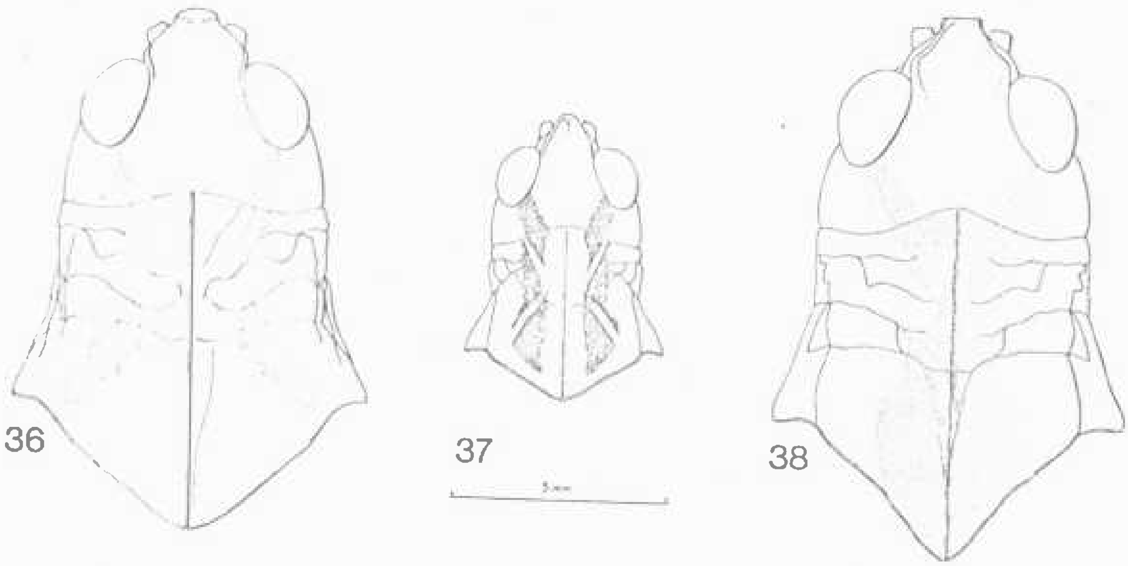
Figs 18-23. *Oedaleus* species (females), heads and pronota, dorsal. 18, *O. senegalensis*; 19, *O. johnstoni*; 20, *O. nigeriensis*; 21, *O. nigrofasciatus*; 22, *O. plenus* (brown form); 23, *O. carvalhoi* (green form).



Figs 24-29. *Oedaleus* species (females), heads and pronota, dorsal. 24, *O. virgula* (brown form); 25, *O. inornatus*; 26, *O. interruptus*; 27, *O. australis*; 28, *O. decorus decorus* (green form); 29, *O. decorus asiaticus* (brown form).



Figs 30-35. *Oedaleus* species (females), heads and pronota, dorsal. 30, *O. nadiae*; 31, *O. rosescens*; 32, *O. miniatus*; 33, *O. instillatus*; 34, *O. flavus*; 35, *O. obtusangulus*.



Figs 36-38. *Oedaleus* species (females), heads and pronota, dorsal. 36, *O. infernalis*; 37, *O. abruptus*; 38, *O. formosanus*.

1.1.4.3 Key to non-African species of Oedaleus

1. Hind wing fascia complete, or narrowly interrupted at first anal vein (Figs 9, 11) 2

-. Hind wing fascia broadly interrupted 6

2.(1) Hind wing basally pale pink (Fig. 4) (Pakistan, N.W. India) ... ... Oedaleus rosescens Uvarov

-. Hind wing basally pale yellow, or pale greenish yellow, in O. decorus tinged with pale blue at base of main veins 3

3.(2) Hind wing fascia continuous posteriorly with dark markings at wing tip (Fig. 7); pronotal x-marking indistinct, forming boundary to medial diamond-shaped dark area and merging laterally with lighter markings on sides of pronotum (Fig. 38); tegmen uniformly dark brown, light transverse bands absent or reduced to anterior edge of wing (Taiwan) ... ... Oedaleus formosanus (Shiraki)

-. Hind wing fascia not continuous posteriorly with dark markings at wing tip; pronotal x-marking variable, sometimes obscured, but not merging laterally with lighter markings on sides of pronotum; tegmen with two light transverse bands always present 4

4.(3) Hind margin of pronotum rounded, subarcuate (Fig. 18); ventral surface of hind femur never suffused with red (Arabia, Iran, Pakistan, W. India) ... Oedaleus senegalensis (Krauss)

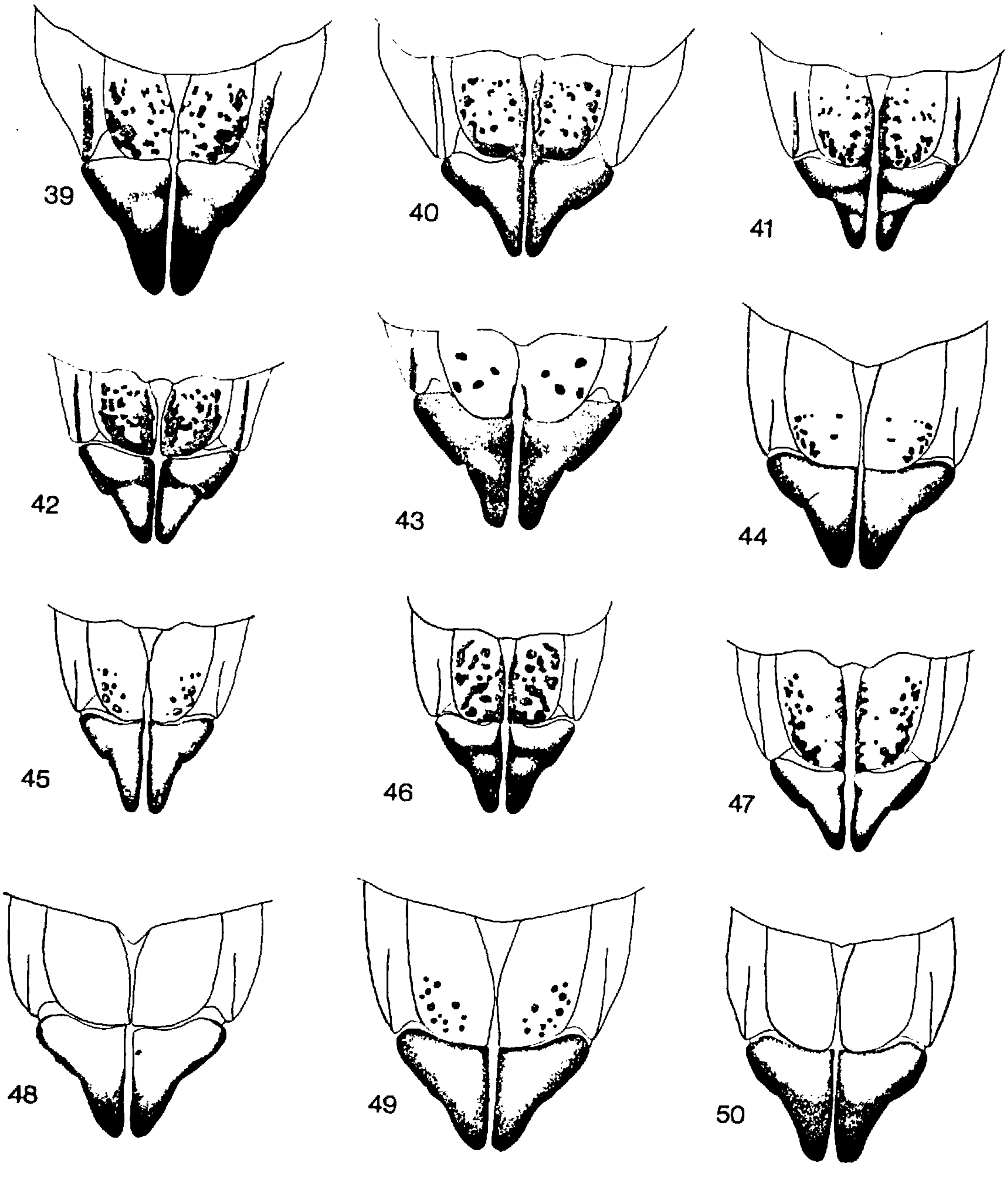
-. Hind margin of pronotum bluntly obtusangular; ventral surface of hind femora suffused with red 5

5.(4) Pronotal x-marking sharply outlined, anterior and posterior arms of equal width (Fig. 28); hind wing fascia always dark and well defined (S. Europe, Middle East, U.S.S.R., China, Mongolia) ... ... Oedaleus decorus (Germar)

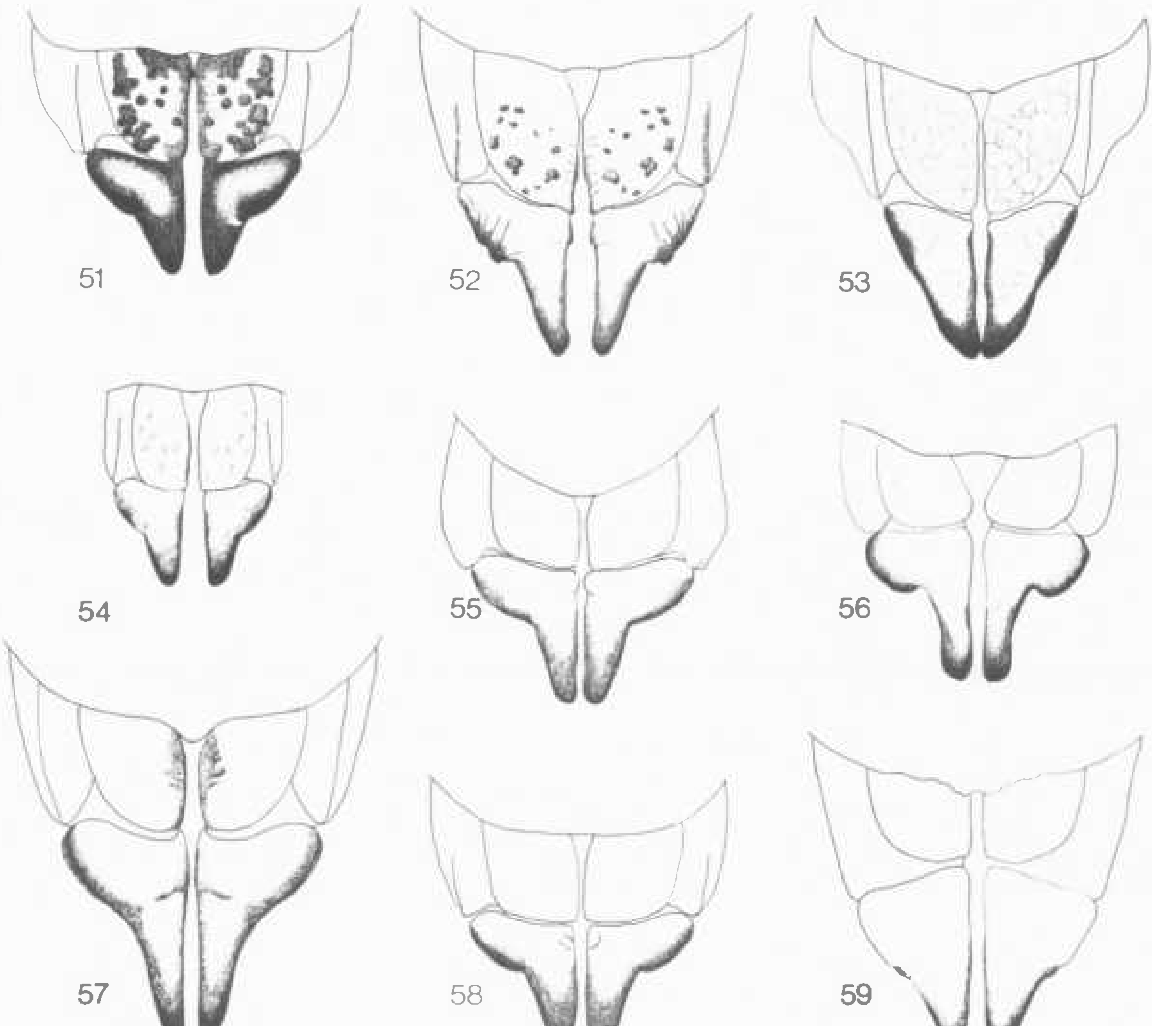
-. Pronotal x-marking often indistinct, sometimes absent, posterior arms thicker than anterior arms (Fig. 36); hind wing fascia variable, light brown, edges ill-defined (Fig. 5) (S.E. U.S.S.R., E. China, Japan) ... ... <u>Oedaleus</u> <u>infernalis</u> <u>Saussure</u>

6.(1) Anterior termination of hind wing fascia flattened, reaching or just surpassing second anal vein; fascia, particularly in male, often pale, posterior two thirds parallel to posterior edge of wing; wing narrow (Fig. 2); fastigium of vertex narrow, with lateral carinulae distinct, sharply converging (Fig. 37) (Pakistan, Nepal, India, Bangladesh, Indo-China, China) ... ... <u>Oedaleus</u> <u>abruptus</u> (Thunberg)

-. Anterior termination of hind wing fascia rounded, surpassing second anal vein, almost reaching first anal vein; fascia distinct, not parallel to edge of wing, wing tip in male heavily clouded; wing normal (Fig. 1); fastigium of vertex broader, carinulae less marked, less convergent (Fig. 27) (S.E. New Guinea, Australia, Tasmania) ... <u>Oedaleus</u> <u>australis</u> Saussure



Figs 39-50. Oedaleus species, ventral ovipositor valves, ventral. 39, O. nigeriensis; 40, O. senegalensis; 41, O. nigrofasciatus; 42, O. virgula; 43, O. johnstoni; 44, O. carvalhoi; 45, O. plenus; 46, O. interruptus; 47, O. australis; 48, O. abruptus; 49, O. flavus flavus; 50, O. flavus somaliensis.



Figs 51-59. *Oedaleus* species, ventral ovipositor valves, ventral. 51, *O. decorus*; 52, *O. infernalis*; 53, *O. formosanus*; 54, *O. rosescens*; 55, *O. obtusangulus*; 56, *O. instillatus*; 57, *O. inornatus*; 58, *O. nadiae*; 59, *O. miniatus*.

1.1.5. Annotated species catalogue of the genus *Oedaleus*, with synonymy, descriptions, measurements, and biological notes.

1.1.5.1 Oedaleus senegalensis (Krauss, 1877)

(Figs 8,9,18,40,60-65,161)

Pachytylus senegalensis Krauss, 1877: 56. Syntypes ♂♀, SENEGAL: St. Louis & Dagana, (F. Steindachner) (lost). NEOTYPE ♂, SENEGAL (BMNH), here designated [examined].

Ctypohippus arenivolans Butler, 1881: 85. Holotype ♀, CAPE VERDE IS. (BMNH) [synonymised by Kirby, 1910: 225] [examined].

Pachytylus mlokoziewiztcki Bolivar, 1884: 105. LECTOTYPE ♂, U.S.S.R.: Tiflis (MHN, Geneva), here designated [synonymised by Uvarov, 1921: 487] [examined].

Oedaleus mlokosiewitchi (sic) (Bolivar) Bolivar, 1887: 98; Jacobson & Bianchi 1902: 256.

Oedaleus (Oedaleus) mlokozievetsi (sic) (Bolivar) Saussure, 1888: 40.

Oedaleus (Oedaleus) mlokozievetzi (sic) (Bolivar) Saussure, 1888: 42.

Oedaleus (Oedaleus) senegalensis var. c. Saussure, 1888: 42; Uvarov, 1921: 487.

Oedaleus mlokosiewiczi (sic) (Bolivar) Jacobson & Bianchi, 1902: 188.

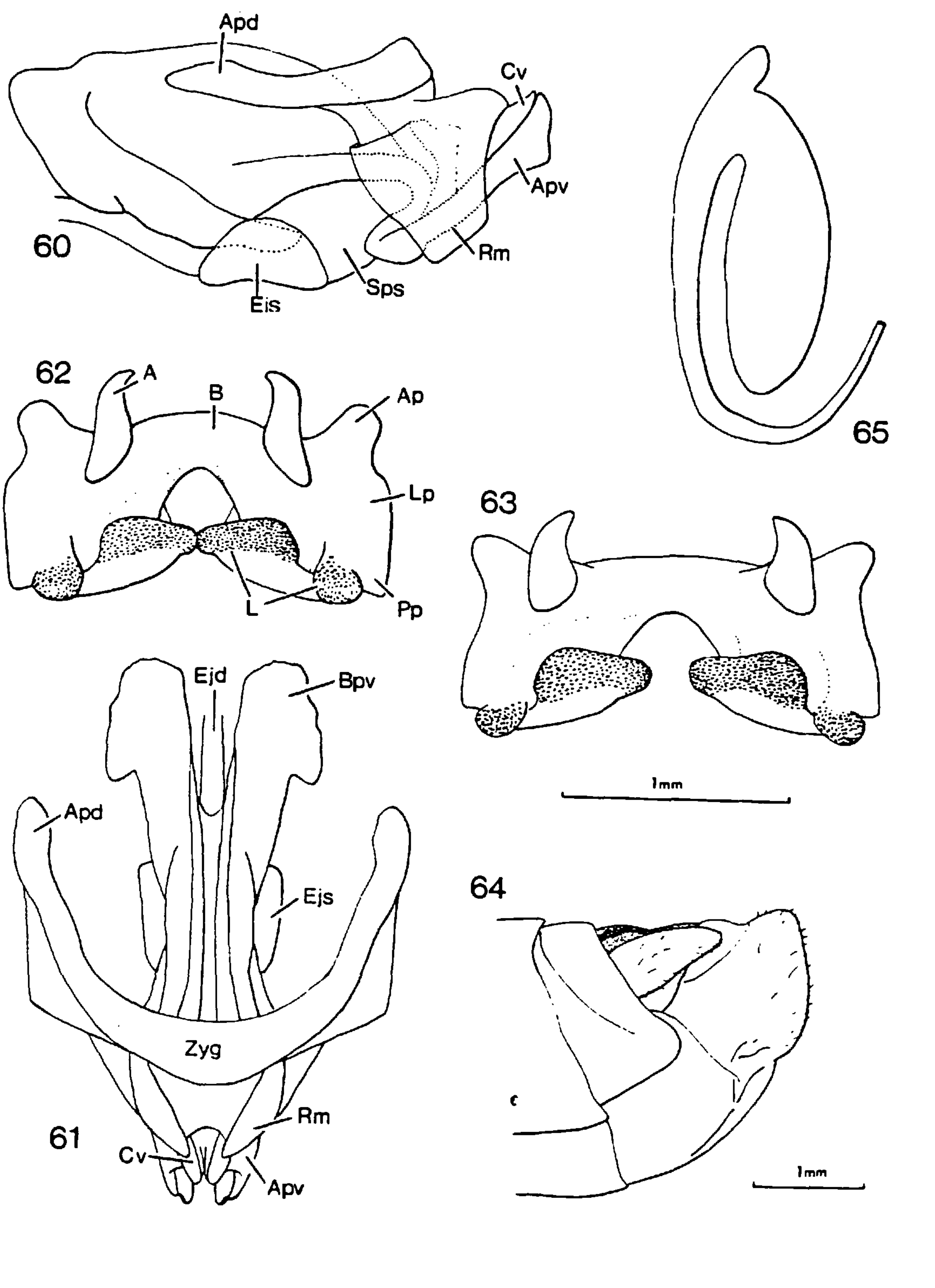
Oedaleus senegalensis (Krauss) I. Bolivar, 1889: 104.

Oedaleus senegalensis var. dimidiatus Bolivar, 1889: 105. Holotype ♀, CAPE VERDE IS. (MLZA, Lisbon) [examined]. **Syn. n.**

Redescription. ♂. Integument finely rugulose and pitted. Antennae up to twice as long as head and pronotum together, flagellum with 24-26 segments. Fastigium little longer than wide, concave, narrowing to little less than half of maximum width anteriorly, margins raised; frons in profile, slightly convex; frontal ridge barely constricted ventral to median ocellus. Eyes little less than one and a half times as deep as wide. Pronotum low tectiform; median carina arcuate, not or barely intersected by posterior sulcus; hind margin subarcuate. Tegmen surpassing folded hind knees by one third to one half length of hind femur. Hind tibia with 13 inner and 12-13 outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment twice claw length; arolium half claw length. Cerci one and three quarter times as long as basal width. Genitalia (Figs. 60 - 64): cingular apodemes moderate length and thickness; rami fully developed, with exposed portion of cingular and apical penis valves short, subapical ventral process rounded; epiphallus rectangular with narrow bridge; inner lobes of lophi more than twice as wide as outer; anterior projections large, rounded; posterior projections rectangular.

General colouration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum, and dorsal surface of folded tegmina and hind femora. Tegmen infuscate brown in basal two fifths with strong transverse pale band reaching first anal vein one third along from base; indistinct pale transverse band sometimes visible one sixth along from base; apical two fifths of tegmen clear with occasional infumate cells bordered by darkened veins. Hind wing fascia (Fig. 9) complete, sometimes narrowly interrupted between second cubitus and first anal vein, not reaching hind margin of wing; basal area pale yellow, apex very slightly speckled with infumate cells. Hind femora with three indistinct oblique transverse dark bands on outer upper marginal and medial areas extending onto inner surface; ventral surface pale straw-coloured; hind knee dark brown; hind tibia with dark basal ring, subbasal pale straw area then straw shaded with brown and distally pinkish.

♀. Larger and more robust. Ventral ovipositor valves (Fig. 40) short, well sclerotised. Spermatheca (Fig. 65) with apical diverticulum elongate with short, blunt subapical diverticulum.



Figs 60-65. O. senegalensis, genitalia. 60, endophallus and cingulum, lateral; 61, same, dorsal; 62, 63, variation in epiphallus shape; 64, apex of ♂ abdomen, lateral; 65, ♀ spermatheca.

Affinities. _O. senegalensis_ is most closely allied to _O. nigrofasciatus_ from southern Africa. They may be distinguished with difficulty on grounds of size, pronotal shape (Figs 18, 21), and the shorter anal cerci of male _senegalensis_ (Fig. 64). Both species belong to a close-knit group of species characterised by an epiphallus having lophi with large, transverse, inner lobes much larger than the outer lobes.

Material examined. Appendix 1, p. 375.

Measurements. Tables 1,2

Distribution (Fig. 161, and Biogeography section, p. 174). From the Canary Is in the west, across north and subsaharan Africa and Arabia, into the western U.S.S.R. in the north east and western India in the south east.

Biology. The available data on the life history, distribution, ecology, and economic importance of this species were reviewed by Batten (1969). More recently Lecoq (1978) has investigated the life cycle in relation to migration in Upper Volta, and Launois (1977) has advanced a theoretical model of the annual cycle consisting of three generations with latitudinal movements governed by the Intertropical Convergence Zone. Launois-Luong (1976) has made estimates of fecundity by a detailed study of the ovaries and Cheke, Fishpool, & Ritchie (in press) have studied the distribution and predation of egg pods, giving descriptions of the pod, the eggs, and oviposition behaviour. The influence of rainfall in terminating egg diapause has been investigated by Venkatesh et al. (1971). The occurrence of large numbers of _O. senegalensis_ out at sea off the West African coast has been documented by Ritchie (1978). The thoracic

Table 1
Measurements (Niger Republic, Danga, (J.M. Ritchie), at light, 7.viii.74):
Oedaleus senegalensis (Krauss)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	27.35	3.87	3.64	4.44	20.79	12.57	2.73	4.61	5.71
Range	23.5 - 30.35	3.4 - 4.45	3.15 - 3.42	3.85 - 5.3	17.35- 23.4	11.15- 14.35	2.35- 3.1	4.29- 5.04	4.96- 6.16
S.D.	2.127	0.236	0.278	0.358	1.783	0.932	0.175	0.197	0.266
No.	24	29	29	29	24	28	28	28	24
♀ Mean	35.38	5.04	4.55	5.57	26.97	15.61	3.3	4.74	5.96
Range	30.35- 39.0	4.45- 5.5	3.65 - 5.25	4.6 - 6.45	23.2 - 29.95	13.3 - 17.65	2.95- 3.8	4.11- 5.14	5.27- 6.64
S.D.	1.726	0.222	0.33	0.44	1.493	0.807	0.201	0.216	0.317
No.	42	45	45	44	42	45	45	45	42

Table 2
Measurements contd. (Niger Republic, Danga, (J. M. Ritchie), at light, 12.ix.74):
Oedaleus senegalensis (Krauss)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	32.64	4.60	4.56	5.47	24.56	15.53	3.39	4.59	5.44
Range	31.25- 34.8	4.25- 5.0	4.1 - 5.1	4.85- 6.25	22.7 - 26.65	13.25- 17.1	3.05- 3.65	4.21- 4.75	4.78- 5.87
S.D.	1.15	0.231	0.295	0.293	1.042	0.879	0.156	0.139	0.499
No.	18	19	19	19	18	20	20	20	18
♀ Mean	42.39	6.12	5.77	7.08	32.16	19.6	4.28	4.58	5.59
Range	40.4 - 46.85	5.75- 6.45	5.15- 6.5	6.75- 7.7	30.7 - 35.2	17.75- 21.25	3.95- 4.55	4.21- 5.0	4.94- 6.04
S.D.	1.551	0.204	0.382	0.264	1.095	0.938	0.199	0.189	0.295
No.	20	20	20	20	20	20	20	20	20

repugnatorial gland has been described by Vosseler (1902b), and the causes of colour change by Abushama and El Khider (1973). Several birds are known to prey on this species including the Carmine bee-eater, Merops nubicus (Nickerson, 1958), the Abyssinian roller, Coracias abyssinicus (Roy, 1970), and the Cattle egret, Ardeola ibis (personal observation). Since 1973 there have been several unpublished reports describing crop damage and aspects of the biology of O. senegalensis (Popov, 1974; McAleer, 1977; Page, 1977).

Discussion. The variety dimidiatus I. Bolivar from the Cape Verde Islands is here synonymised on the grounds that it is sympatric with the normal form of O. senegalensis and almost certainly constitutes a melanic variant rather than a good subspecies. A fuller treatment of this subject with measurements of the two forms has been given elsewhere (Ritchie, 1978). The measurements given above for this species form part of a study of the morphometric changes in this species during the 1974 rainy season in north-western Niger Republic (Tables 1,2)(Ritchie, in prep.). They illustrate the considerable size differences which may be encountered in this species within a small geographical area over a short period of time.

1.1.5.2 Oedaleus nigrofasciatus (Degeer, 1773)

(Figs 21,41,66-70,152)

Acrydium nigrofasciatum Degeer, 1773: 493. Holotype ♀, SOUTH AFRICA (NR, Stockholm) [examined].

Gryllus arcuatus Thunberg, 1824: 409. LECTOTYPE ♂, no data (ZIUU, Uppsala) here designated [synonymised by Stål, 1873: 126] [examined].

Pachytylus nigrofasciatus (Degeer) Schaum, 1853: 776 [partly confused with Oedaleus decorus (Germar)].

Pachytylus (Oedaleus) nigro-fasciatus (Degeer) Stål, 1873: 126 [partial confusion with Oedaleus decorus (Germar)].

Oedaleus (Oedaleus) nigro-fasciatus (Degeer) Saussure, 1884: 116.

Oedaleus (Oedaleus nigro-fasciatus var. gracilis Saussure, 1884: 116. LECTOTYPE ♀, SOUTH AFRICA: Cape of Good Hope (MHN, Geneva), here designated [partly confused with Oedaleus decorus (Germar)] [synonymised by Uvarov, 1923: 69] [examined].

Oedalus [sic] nigrofasciatus (Degeer) Distant, 1892: 260.

Oedaleus nigrofasciatus var. gracilis Saussure; Saussure, 1893: 581.

Oedaleus nigrofasciatus (Degeer) Brancsik, 1900: 182.

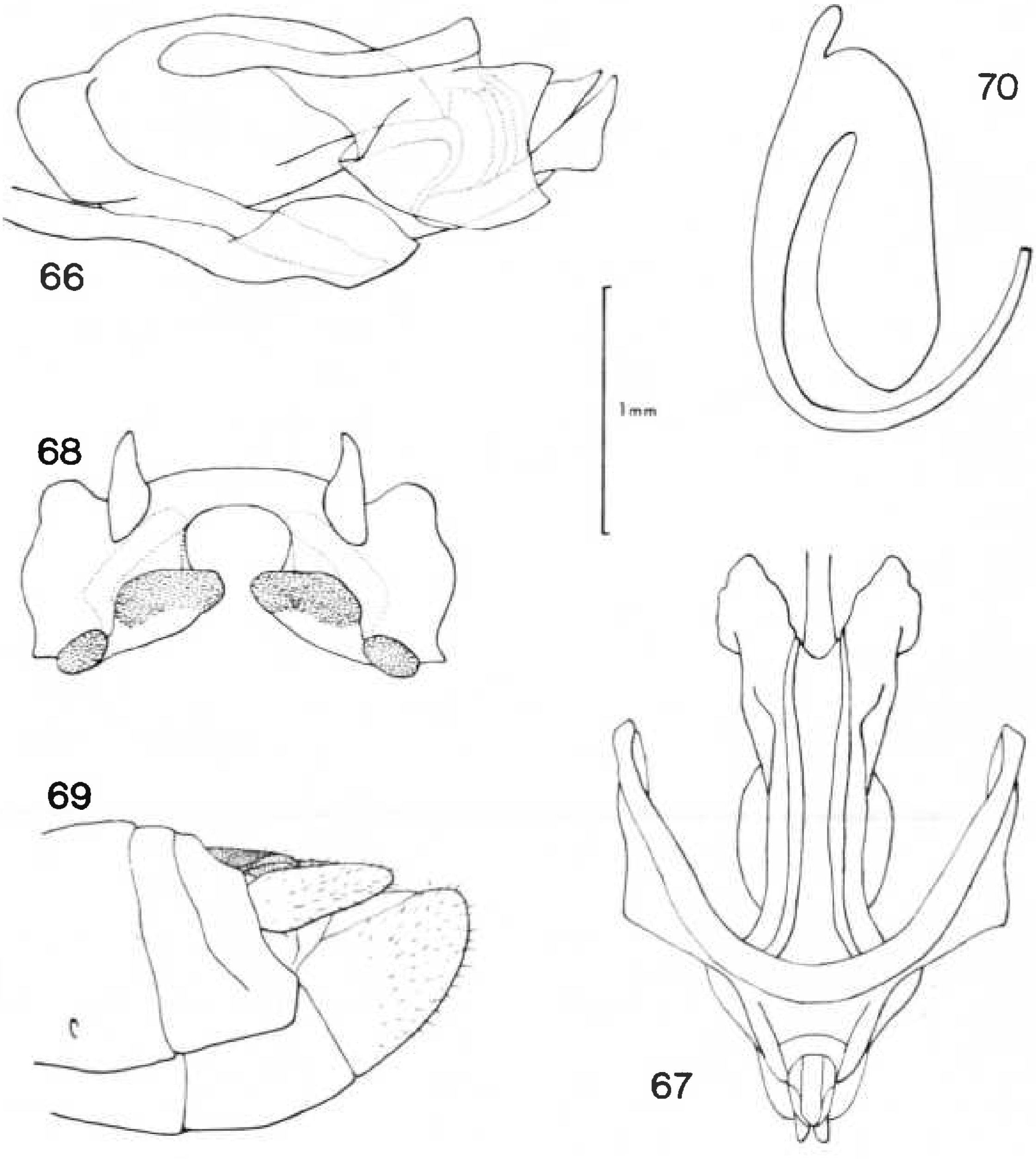
Oedaleus nigrofasciatus (Degeer) Kirby, 1910: 224. [partial confusion with Oedaleus decorus (Germar)].

Oedaleus gracilis (Saussure) Uvarov, 1922: 102 [synonymised by Uvarov, 1923: 69].

Redescription. ♂. Integument finely rugulose and punctate. Antennae one and a half times as long as head and pronotum together; flagellum with 23 segments. Fastigium longer than wide concave with lateral margins distinct and convergent posteriorly, narrowing to two fifths of maximum width anteriorly; frons in profile slightly convex; frontal ridge slightly expanded at median ocellus becoming obsolete ventrally. Eyes about one and a half times as deep as wide. Pronotum low tectiform; median carina arcuate, often finely intersected by posterior sulcus; hind margin rounded obtusangular. Tegmen surpassing folded hind knees by one third to one half of hind femur length. Hind tibia with 12 inner and 11 outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and a quarter times claw length; arolium three fifths of claw length. Cerci twice as long as basal width. Genitalia (Figs. 66 - 69): cingular apodemes thin, moderately long and curved; rami elongate dorsally; exposed portion of cingular and apical penis valves short; subapical ventral process angular; epiphallus rectangular with narrow bridge, inner lobes of lophi twice as wide as outer lobes; anterior projections large and rounded, posterior projections small and acute.

General colouration variable, brown, with lighter brown, ochraceous, or green markings on frons, vertex, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infuscate brown in basal half with three irregular pale transverse bands at intervals of one sixth, one third, and one half, along from base, basal band often obsolete; apical half clear with small variable brown patches. Hind wing fascia as in O. senegalensis, continuous, not touching hind margin; wing tip with irregular pattern of brown cells; basal area pale yellow. Hind femur with three dark brown variable oblique transverse bands on external medial, upper marginal, and interior upper marginal areas, obsolescent on interior medial area; ventral surface mid brown, hind knees dark brown to black; hind tibiae with dark basal ring, subbasal pale area, otherwise fawn.

♀. Larger and more robust. Ventral ovipositor valves (Fig. 41) short, moderately sclerotised, slightly incurved on external lateral surface. Spermatheca (Fig. 70) with finger-like subapical diverticulum.



Figs 66–70. *O. nigrofasciatus*, genitalia. 66, endophallus & cingulum, lateral; 67, same dorsal; 68, epiphallus; 69, apex of ♂ abdomen, lateral; 70, ♀ spermatheca.

Affinities. _O. nigrofasciatus_ is most closely allied to _O. senegalensis_ under which species heading the principal similarities are described (p. 42).

Material examined. Appendix 1, p. 375.

Measurements. Table 3

Distribution (Fig. 152, and Biogeography section, p. 158). Widely distributed and common throughout southern Africa south of the _Brachystegia_ woodland.

Biology. _O. nigrofasciatus_ has been studied in the Karroo where Reyneke (1941) noted that the species has similar habitat preferences to the brown locust _Locustana pardalina_. It was found in open sandy or pebbly patches with short grass and scattered shrubs at an average density of 5 insects per square metre. Nymphs were seen from the end of September until November. In the Cape peninsula Key (1930) found adults from November to June and observed oviposition from January to June. Egg pods were 21 - 24 mm long with 15 - 19 eggs, and were usually curved and medially constricted. In Johannesburg Chesler (1938) found somewhat larger pods, about 29 mm x 5 mm with 20 - 25 eggs in rows of four. Chesler described the five nymphal instars which occupied an average of 80 days for their completion. She postulated a two-generation cycle with eggs hatching in September to produce adults November - December whose eggs hatched in January to give a second generation of adults in April. These adults then lay eggs which remain in the soil until the next rains in September. Nolte (1939) compared the biology of _O. nigrofasciatus_ with six other common species of grasshopper including _O. carvalhoi_.

Table 3
Measurements (Cape Province, various localities):
Oedaleus nigrofasciatus (De Geer)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	26.52	3.47	3.89	4.47	20.17	12.44	2.85	4.38	5.20
Range	23.35-30.2	3.15-3.9	3.1 - 4.75	4.1 - 5.0	17.55-23.5	10.85-13.75	2.45-3.15	4.05-4.63	4.61-5.85
S.D.	1.557	0.190	0.383	0.211	1.295	0.766	0.182	0.164	0.299
No.	27	26	27	27	27	27	27	27	27
♀ Mean	32.99	4.58	4.97	5.85	25.15	15.67	3.48	4.50	5.07
Range	29.85-35.6	4.25-4.9	4.35-5.55	5.4 - 6.5	22.75-27.0	13.8 - 17.15	3.05-3.75	4.25-4.79	4.70-5.65
S.D.	1.755	0.208	0.375	0.280	1.375	0.964	0.202	0.189	0.255
No.	13	13	13	12	13	13	13	13	13

Table 4
Measurements (all available material):
Oedaleus australis Saussure

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	24.13	3.71	3.73	4.36	17.59	12.5	3.05	4.11	4.74
Range	20.0 - 27.75	3.1 - 4.1	2.85-4.2	3.9 - 4.95	14.25-20.9	10.55-14.25	2.6 - 3.45	3.7 - 4.98	3.84-5.62
S.D.	2.371	0.299	0.377	0.339	2.034	1.085	0.223	0.347	0.539
No.	11	12	12	10	12	12	12	12	12
♀ Mean	31.09	4.93	4.99	5.86	23.02	15.3	3.8	4.03	4.63
Range	28.65-34.45	4.25-5.55	3.75-6.05	5.25-6.9	20.0 - 26.15	13.65-16.6	3.35-4.15	3.83-4.24	4.19-5.33
S.D.	1.712	0.305	0.479	0.464	1.562	0.84	0.222	0.113	0.328
No.	18	22	21	[illegible]	21	21	21	21	21

He reported that adult females of O. nigrofasciatus have 15 ovarioles per ovary. Both Oedaleus species were found to have a karyotype of 2N = 22. There is one record of damage to tobacco seedlings in Rhodesia (Bünzli & Buttiker, 1956).

1.1.5.3 <u>Oedaleus</u> <u>australis</u> Saussure, 1888

(Figs 1,27,47,71-74,165)

<u>Oedaleus</u> (<u>Oedaleus</u>) <u>senegalensis</u> var. <u>d</u>. Saussure, 1884: 117; Uvarov, 1930d: 599.

<u>Oedaleus</u> (<u>Oedaleus</u>) <u>nigro-fasciatus</u> var. australis Saussure, 1888: 41. LECTOTYPE ♀, AUSTRALIA (MHN, Geneva), here designated [examined].

[<u>Oedaleus</u> <u>senegalensis</u> var. Froggatt, 1903: 1105. Misidentification; Uvarov, 1930d: 599.]

[<u>Oedaleus</u> <u>senegalensis</u> Krauss; Froggatt, 1907: 539; 1910: 7. Misidentifications; Uvarov, 1930d: 599.]

<u>Oedaleus</u> <u>australis</u> Saussure; Kirby, 1910: 225.

[<u>Oedaleus</u> <u>senegalensis</u> Krauss; Sjöstedt, 1920: 11. Misidentification; Uvarov, 1930d: 599.]

[<u>Oedaleus</u> <u>senegalensis</u> Krauss; Sjöstedt, 1921: 53. Misidentification.]

[<u>Oedaleus</u> <u>senegalensis</u> Krauss; Zacher, 1925: 204; 1949: 298. Misidentifications; Batten, 1969: 29.]

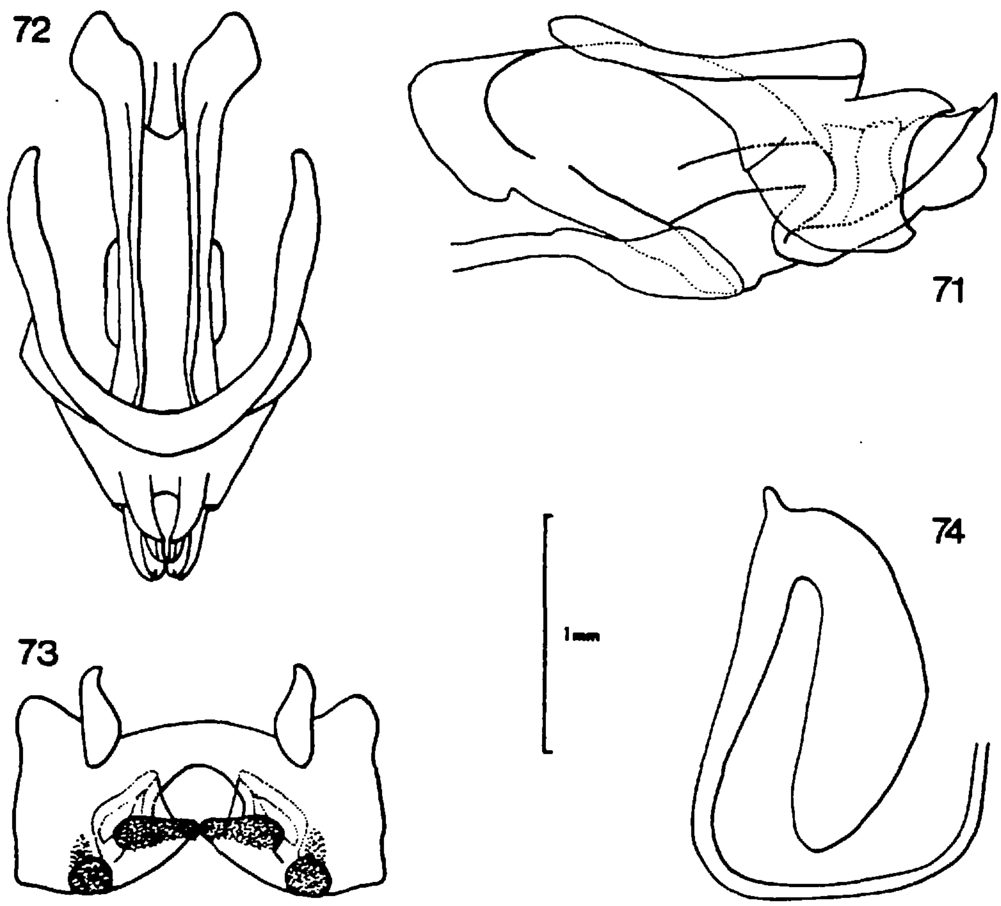
<u>Oedaleus</u> <u>australis</u> var. <u>plana</u> Sjöstedt, 1931: 2. Holotype ♀, AUSTRALIA, A.C.T., Canberra, 20.ii.29, (Fuller) (ANIC, Canberra). **Syn. n.**

Redescription. ♂. Integument finely rugulose and pitted. Antennae about one and a third times as long as head and pronotum together; flagellum with 22 segments. Fastigium longer than wide, concave, narrowing to less than one third of maximum width anteriorly, with well defined lateral carinae; frons in profile slightly convex; frontal ridge slightly expanded at median ocellus. Eyes about one and a third times as deep as wide. Pronotum low tectiform; median carina arcuate, narrowly intersected by posterior sulcus; hind margin of pronotum rounded obtusangular. Tegmen surpassing folded hind knees by one quarter to one half of hind femur length. Hind tibia with 11 inner and outer spines; inner apical spurs twice as long as outer;

apical tarsal segment three times length of claw; arolium one third length of claw. Cerci little more than twice as long as basal width. Genitalia (Figs. 71-73) with cingular apodemes long, thin, strongly curved; rami fully developed, with exposed portion of cingular and apical penis valves short; subapical ventral process small; epiphallus rectangular with narrow bridge; inner lobes of lophi nearly twice as wide as outer; anterior projections large, rounded acutangular; posterior projections rectangular.

General colouration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infuscate brown in basal half with irregular pale transverse band extending from costal margin to second anal vein posteriorly, situated one third along from base; indistinct secondary band sometimes visible one sixth along from base; apical half of tegmen clear with variable brown patches. Hind wing fascia (Fig. 1) narrowly interrupted at first anal vein, not reaching hind margin of wing; wing tip infuscate brown, basal area of wing pale yellow. Hind femora with three indistinct dark, variable, oblique transverse bands on outer and inner upper marginal and medial areas; ventral surface of hind femur straw coloured; hind knees blackish; hind tibiae with dark basal ring, subbasal pale area, otherwise light brown.

♀. Larger and more robust. Frons in profile convex. Ventral ovipositor valves (Fig. 47) short, strongly sclerotised, with strongly curved apices. Spermatheca (Fig. 74) with apical diverticulum acutely rounded distally and finger-like subapical diverticulum.



Figs 71-74. O. australis, genitalia. 71, endophallus & cingulum, lateral; 72, same, dorsal; 73, epiphallus; 74, ♀ spermatheca.

Affinities. _O. australis_ is most closely allied to _O. senegalensis_ and _O. nigrofasciatus_ which it very closely resembles in most respects, and with which it was originally confused. It may be distinguished by its smaller size, the interrupted band of the hind wing (Fig. 1), and the relatively short tegmen and correspondingly low TL / PL ratio.

Material examined. Appendix 1, p. 375.

Measurements. Table 4

Distribution (Fig. 165, and Biogeography section, p. 179). Common throughout the eastern half of Australia, and Tasmania. The species is newly recorded here from New Guinea. Additional data for the distribution map have kindly been provided by Dr K.H.L. Key, from specimens in the Australian National Insect Collection, Canberra.

Biology. Little is known of the biology of _O. australis_. There are probably at least two generations with eggs surviving the dry season April - September, since adults and nymphs have mainly been recorded September - March. Adults do however occur in all months in suitable localities (ANIC specimens). Large swarms were recorded damaging pasture at Singleton, N.S.W., in 1906-7 (Froggatt, 1907). There was a heavy incidence of an unspecified dipterous parasite. Eggs were laid in well-defined egg beds. In a later account (Groggatt, 1910) egg pods were said to be laid about 1.25 inches deep in hard clay soil on open grassy ridges with 30-50 eggs per pod. _O. australis_ has been recorded among the stomach contents of the straw-necked ibis, _Threskiornis spinicollis_ (Jameson) and the white ibis, _T. molucca_ (Cuvier) (Carrick, 1959). It seems that this species rarely achieves swarm densities.

Discussion. The type of O. australis var. plana was generally supposed to be at Stockholm. However I am indebted to Dr. Key for the following recent information:

"There is indeed in Stockholm a specimen determined as plana by Sjöstedt and bearing his "Typus" label. But it came from Colosseum, Qld., whereas the only locality given for plana in the brief original description of 1931 (under "Oedaleus senegalensis") mentions only one locality, namely "Canberra". Thus the Stockholm "type" is not even a syntype. However the ANIC does have a single female bearing the capture data essentially as cited by Sjöstedt, namely "Canberra F.C.T. 20 Feb. 1929 M. Fuller". It bears also the following labels; (1) "Oedaleus australis var. recta [sic] Sjöst. det.", and (2) "Oedaleus senegalensis Kr. ♀ Yngve Sjöstedt det." The name "recta" is a nomen nudum and clearly a lapsus for "plana", described as "mit geradem Kiel des Pronotums." In the absence of evidence that Sjöstedt had more than one specimen before him, the Canberra female, being the only one to bear the required capture data, must be accepted as the holotype. I have now added the following label: "HOLOTYPE ANIC 8747. Oedaleus australis var. plana Sjöst., 1931. ♀", on red fluorescent card.".

1.1.5.4 Oedaleus abruptus (Thunberg, 1815)

(Figs 2,37,48,75-78,158)

Gryllus abruptus Thunberg, 1815: 233. LECTOTYPE ♂, CHINA (ZI, Uppsala) here designated [examined].

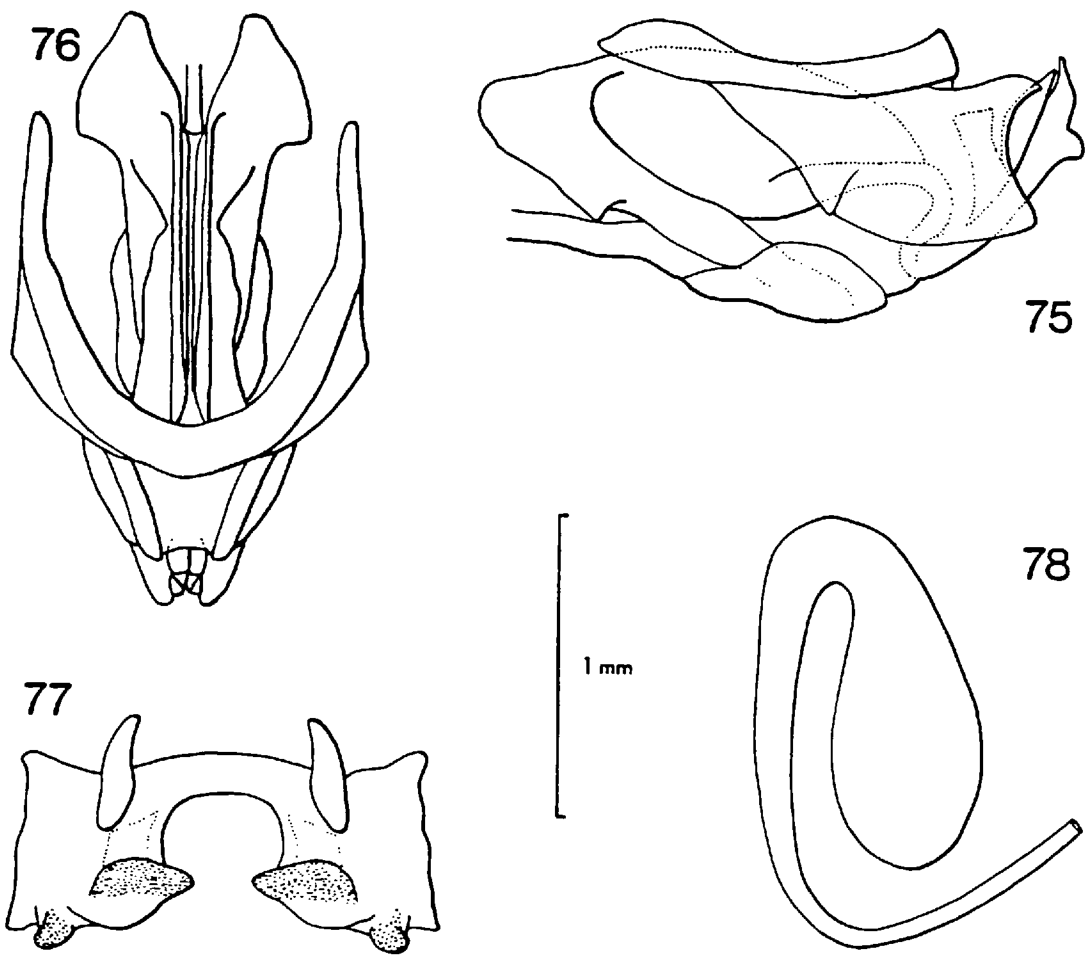
Pachytylus (Oedaleus) abruptus (Thunberg); Stål, 1873: 127.

Oedaleus (Oedaleus) abruptus (Thunberg); Saussure, 1884: 117.

Oedaleus abruptus (Thunberg); Kirby, 1910: 226.

[Oedaleus nigrofasciatus (Degeer); Barber and Jones, 1915: 163; Gabriel, 1968: 101. Misidentifications.]

Redescription. ♂. Unusually small species. Integument finely rugulose and pitted. Antennae about one and one third times as long as head and pronotum together; flagellum with 20 segments. Fastigium of vertex longer than wide, concave, narrowing to two fifths of maximum width anteriorly, with distinct lateral carinae; frons in profile slightly convex; frontal ridge constricted just below median ocellus, becoming obsolescent ventrally. Eyes about one and two fifths as long as wide, Pronotum low tectiform; median carina low arcuate, not intersected by posterior sulcus; hind margin rounded obtusangular. Tegmen surpassing folded hind knees by about one third of hind femur length with numerous long fine hairs on subcostal and radial veins. Hind tibia with 13 inner and 12 outer spines; inner apical spurs one and four fifths as long as outer, apical tarsal segment twice claw length; arolium three fifths length of claw; outer surface of ventral inner apical spur with row of conical sensilla, more marked than in other species. Cerci one and four fifths times as long as basal width. Genitalia (Figs 75-77) with cingular apodemes long and strongly curved; rami elongated with exposed portion of cingular and apical penis valves short, subapical ventral process small; epiphallus rectangular with narrow bridge; inner lobes of lophi two and a half times as wide as outer lobes; outer lobes outwardly protruding, pointed; anterior



Figs 75-78. O. abruptus, genitalia. 75, endophallus & cingulum, lateral; 76, same, dorsal; 77, epiphallus; 78, ♀ spermatheca.

projections rounded acutangular; posterior projections acutangular.

General colouration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infuscate in basal half with three or four pale transverse bands, variable in emphasis, extending from costal margin to first radial vein or as far as first cubitus, first and second bands dividing basal half of wing equally into three, band three situated distal to junction of Cu1 a and Cu1 b, band four situated about two thirds along from base, frequently obsolete; apical third of tegmen clear with variable brown blotches. Hind wing fascia (Fig. 2) widely interrupted between first radial and second anal veins, reaching or almost reaching hind margin, basal area pale yellow. Hind femora with two indistinct dark transverse bands on external upper marginal and medial areas, sometimes obsolete; internal surface mottled; ventral surface straw-coloured; hind knees dark brown; hind tibiae straw-coloured with dark basal ring and thicker subbasal pale ring.

♀. Larger and more robust. Ventral ovipositor valves (Fig. 48) strongly sclerotised with strongly curved apices. Spermatheca (Fig. 78) without subapical diverticulum.

Affinities. O. abruptus is allied to O. senegalensis on the basis of its genitalia and general appearance. However it may easily be distinguished from any other species by its small size and the distinctive hind wing fascia (Fig. 2).

Material examined. Appendix 1, p. 375.

Measurements. Tables 5, 6

Distribution (Fig. 158, and Biogeography section, p. 177). Widely distributed in mainland east Asia.

Biology. O. abruptus has at least two generations per year with eggs overwintering from November to April. These hatch to give adults June - July which lay eggs, giving a second generation of adults in August - September (Ahmed et al., 1973). The egg pod is short and fragile, laid in hard soil to a depth of 25 - 35 mm. There are 18 - 27 eggs per pod, each about 3.15 - 4.15 mm long and 0.85 - 0.95 mm across (Katiyar, 1960). In the laboratory maximum survival rates and fastest development occurred at 35°C and 8.0% humidity (Khan & Aziz, 1974). Maturation was slower and survival lower in crowded compared to solitary conditions (Khan & Aziz, 1976). The chromosomes have been studied by Asana et al. (1939), Dutt (1952, 1955), and Manna (1954). The species is a suitable experimental intermediate host of cestodes parasitic in crows and domestic fowl (Dutt & Sihha, 1961; Dutt & Mehra, 1962). The egg parasite Scelio aegyptiacus has been reared from eggs of O. abruptus in the laboratory (Ahmed et al. 1973). There are a number of reports of crop damage. Ballard (1921) recorded damage to Eleusine, and Chopard & Chatterjee (1937) reported attacks on Pinus and Shorea seedlings and sandal. Oedaleus abruptus

Table 5
Measurements (Sri Lanka, Various localites):
Oedaleus abruptus (Thunberg)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	18.97	2.69	3.07	3.32	14.27	9.34	2.19	4.26	4.64
Range	17.95-20.2	2.55-2.75	2.85-3.25	3.05-3.75	13.2 - 15.3	8.35-10.0	2.05-2.35	4.02-4.67	4.48-4.8
S.D.	1.28	0.090	0.141	0.248	0.744	0.526	0.105	0.242	0.103
No.	8	8	8	8	8	8	8	8	8
♀ Mean	24.20	3.65	3.88	4.39	18.05	11.48	2.78	4.12	4.64
Range	21.95-25.95	3.25-3.95	3.4 - 4.35	3.6 - 4.9	16.15-20.9	9.7 - 12.5	2.45-3.0	3.88-4.55	4.41-4.93
S.D.	1.286	0.215	0.284	0.355	1.136	0.769	0.157	0.188	0.157
No.	14	15	13	15	15	15	15	15	13

Table 6
Measurements cond. (China, Hainan Province, Wutoshi):
Oedaleus abruptus (Thunberg)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	21.71	2.95	3.36	3.71	16.2	10.33	2.25	4.59	4.81
Range	20.4 - 24.05	2.75-3.1	3.05-3.75	3.25-4.1	15.05-17.95	9.55-11.65	2.1 - 2.4	4.34-5.06	4.12-5.21
S.D.	1.042	0.085	0.210	0.213	0.796	0.501	0.095	0.189	0.252
No.	23	23	21	23	23	23	23	23	21
♀ Mean	26.88	3.71	4.16	4.79	20.0	12.32	2.74	4.51	4.82
Range	25.0 - 29.7	3.4 - 4.2	3.5 - 4.65	4.45-5.35	18.45-22.2	11.25-14.05	2.45-3.05	4.14-4.98	4.46-5.09
S.D.	1.207	0.180	0.267	0.266	0.986	0.713	0.168	0.280	0.167
No.	18	18	17	17	18	16	16	16	17

has also been found on maize and rice (Roffey 1964, 1965), and is said to feed also on wheat, bajra, jowar, tomato, grain pea, groundnut and other crops (Khan and Aziz, 1974).

Discussion. The measurements above indicate that specimens from Hainan are larger with relatively longer tegmina and a larger ratio of femur length to depth than those from Sri Lanka which is the southern limit for this species. It would be of interest to compare these populations with samples from Nepal on the north west limit of its range.

1.1.5.5 <u>Oedaleus virgula</u> (Snellan van Vollenhoven, 1869)

(Figs 24,42,79-82,163)

<u>Oedipoda virgula</u> Snellan van Vollenhoven, 1869: 11. Holotype ♀ [not ♂ as stated in van Vollenhoven op. cit.], MADAGASCAR (RNH, Leiden) [examined].

<u>Epacromia inclyta</u> Walker, 1870: 773. Holotype ♀, MADAGASCAR, (BMNH) [synonymised by Uvarov, 1925: 276] [examined].

<u>Oedaleus (Gastrimargus) madecassus</u> Saussure, 1884: 115. LECTOTYPE ♀, MADAGASCAR (MHN, Geneva), here designated. [Synonymised by Uvarov, 1925: 276] [examined].

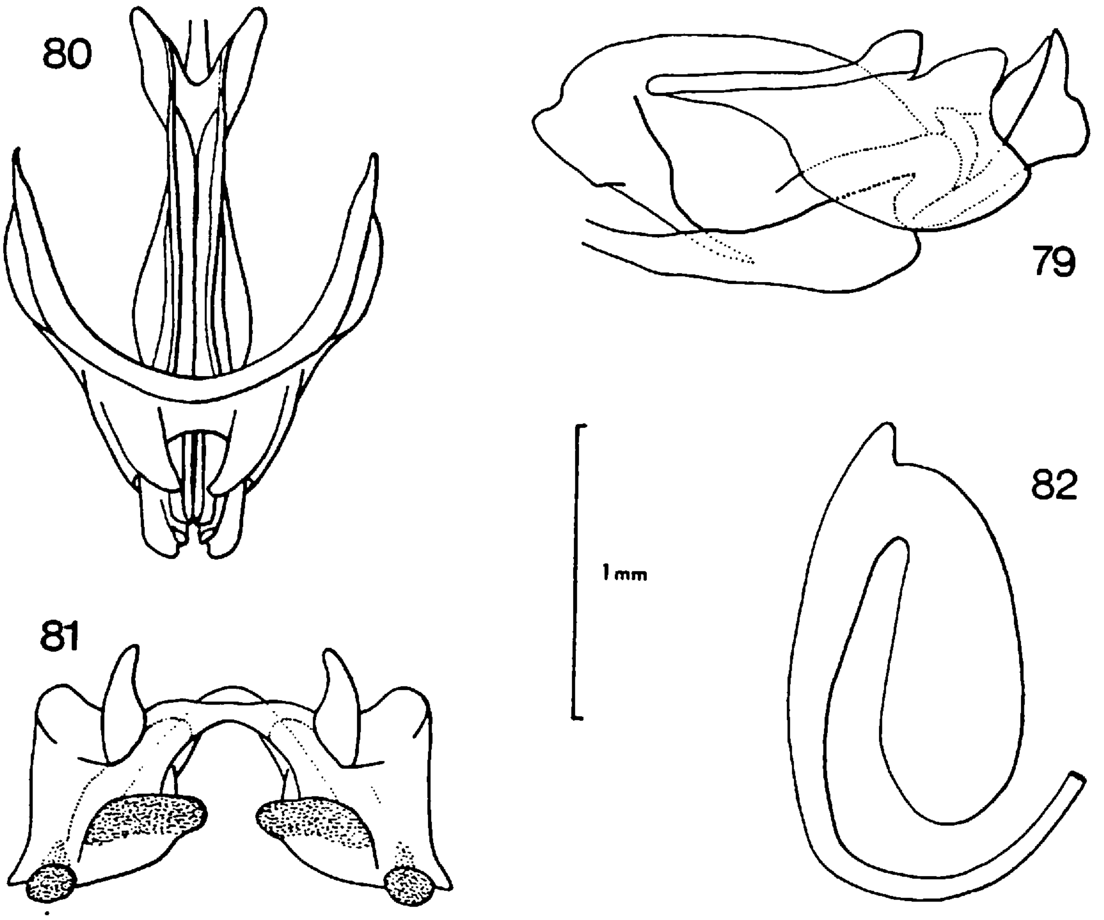
<u>Oedaleus (Oedaleus) nigro-fasciatus</u> var. <u>virgula</u> (Snellan van Vollenhoven) Saussure, 1888: 40; Kirby, 1910: 226.

<u>Oedaleus inclytus</u> (Walker) Kirby, 1910: 226.

<u>Oedaleus virgula</u> (Snellan van Vollenhoven) Kirby, 1910: 226.

<u>Oedaleus virgulus</u> (Snellan van Vollenhoven) Dirsh, 1961a: 398 [unjustified emendation].

Redescription. ♂. Integument finely rugulose and pitted. Antennae one and a quarter to one and a third times as long as head and pronotum together; flagellum with 22-24 segments. Fastigium of vertex wider than long, anterior width one third of maximum width, concave with raised margins; frons in profile straight to slightly convex, frontal ridge constricted at vertex and below median ocellus, wider between antennal bases, becoming obsolete ventrally. Eyes nearly one and a half times as deep as wide. Pronotum tectiform, finely punctate; median carina shallowly arcuate, hind margin acutangular to obtusangular. Tegmen surpassing hind knees by two fifths to one half of hind femur length. Hind tibia with 11 inner and outer spines; inner apical spurs twice as long as outer, apical tarsal segment twice length of claw, arolium more than half claw length. Cerci about two and a quarter times as long as basal width. Genitalia (Figs. 79 - 81): cingular apodemes slender, rami moderate length;



Figs 79-82. O. virgula, genitalia. 79, endophallus & cingulum, lateral; 80, same, dorsal; 81, epiphallus; 82, ♀ spermatheca.

cingular and apical penis valves short; subapical ventral process large; epiphallus almost rectangular with thin bridge; inner lobes of lophi strongly transverse, two and a half times as wide as outer lobes; anterior projections large, rounded; posterior projections small, sharply acutangular.

General colouration variable greenish or brownish, with lighter markings on frons, genae, pronotum, tegmina and hind femora. Pronotal x-marking (Fig. 24) sometimes obsolescent. Tegmen infuscate in basal half with four pale transverse bands extending from costal margin; first band one sixth along from base reaching second cubitus, second band one third along reaching first or second cubitus, third band reaching and following Cu1b as a distinct oblique white stripe; fourth band two thirds along reaches posterior medial vein; apical third of wing mottled with brown and transparent cells. Hind wing without fascia or with very pale indistinct fascia barely visible posterior to second anal vein; basal area pale yellow. Hind femur with three variable transverse dark markings on external and internal upper marginal areas, extending obliquely across external and internal medial areas, sometimes obsolescent; ventral surface of femur straw coloured, hind knee brown. Hind tibia with dark basal ring, subbasal pale area, otherwise pale blue-grey.

♀. Larger and more robust. Ventral ovipositor valves (Fig. 42) blunt, heavily sclerotised, exterior lateral surface almost straight; basivalvular sclerite coarsely rugose. Spermatheca (Fig. 82) with apical diverticulum elongate and short blunt sub-apical diverticulum.

Affinities. O. virgula belongs to the same species group as O. senegalensis and O. nigrofasciatus on the basis of the pale hind tibia and underside of the hind femur, and the close similarity of the genitalia, particularly the epiphallus (Fig. 81). It is however easily distinguished from all the other species of the group by the absence of a distinct wing band.

Material examined. Appendix 1, p. 376.

Measurements. Table 7

Distribution (Fig. 163, and Biogeography section, p. 177). Widely distributed and common within Madagascar, and newly recorded from Zanzibar and Aldabra. There is one specimen purporting to be from South Africa, but this is presumably mislabelled.

Biology. Little is known of the biology of this species. The following information is derived from Descamps & Wintrebert (1966). One egg pod was measured and found to be 57.5 mm x 5 mm, slightly bent, with 30 eggs arranged in 11 rows of 2 - 4 eggs each. The individual eggs are about 4.1 x 1 mm and have a chorionic sculpture composed of irregular dots forming indistinct rows, with neighbouring dots sometimes joined by fine lines. In the cool season incubation lasts at least 2 months. The sixth instar may last a month. Nymphs are particularly common in September, November, March, and April. There are three or possibly four generations per year with an apparent movement of adults southward at the end of the hot season. Three species of Scelio were recorded as egg parasites.

Discussion. The emendation of the specific name virgula to virgulus (Dirsh, 1961a) is here rejected because virgula, meaning a wand, is a feminine noun in apposition and not an adjective.

Table 7
Measurements (Madagascar, various localities):
<u>Oedaleus virgula</u> (Snellan van Vollenhoven)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	25.87	3.43	4.33	4.39	19.39	12.53	2.97	4.22	4.48
Range	22.15-28.7	3.2 - 3.75	3.65-5.0	4.05-4.75	16.45-21.45	11.15-13.85	2.65-3.2	3.92-4.45	3.97-4.79
S.D.	1.829	0.139	0.354	0.219	1.512	0.732	0.141	0.182	0.190
No.	21	21	21	21	21	17	17	17	21
♀ Mean	34.58	4.77	5.90	6.23	25.89	16.0	3.84	4.18	4.4
Range	29.75-38.35	4.3 - 5.15	4.9 - 5.95	5.7 - 6.9	21.8 - 28.9	14.15-18.25	2.75-4.45	3.78-5.14	3.89-4.71
S.D.	2.624	0.249	0.476	0.334	1.978	1.226	0.307	0.255	0.225
No.	33	31	34	34	34	32	31	31	33

Table 8
Measurements (Mali Republic, Adrar des Iforhas):
<u>Oedaleus johnstoni</u> Uvarov

	Total length	Caput width	Pronotum length	Pronotum width	Tegmon length	Femur length	Femur width	FL/FD	TL/PL
♂ Mean	30.18	4.88	4.87	5.97	21.90	13.80	3.88	3.74	4.56
Range	26.35-35.35	4.55-5.3	4.2 - 5.55	5.3 - 6.8	18.45-25.85	12.65-17.3	3.15-4.35	3.47-4.16	3.95-5.26
S.D.	2.267	0.223	0.357	0.476	1.864	3.126	0.384	0.211	0.373
No.	14	19	19	19	14	19	19	19	14
♀ Mean	40.09	6.67	6.38	7.90	29.03	18.58	4.79	3.89	4.55
Range	36.75-45.45	6.1 - 7.6	5.5 - 7.7	7.25-9.3	26.05-32.75	17.05-20.95	4.1 - 5.7	3.6 - 4.24	4.02-4.83
S.D.	2.69	0.425	0.633	0.630	1.934	1.269	0.474	0.188	0.23
No.	20	20	21	20	20	21	21	21	20

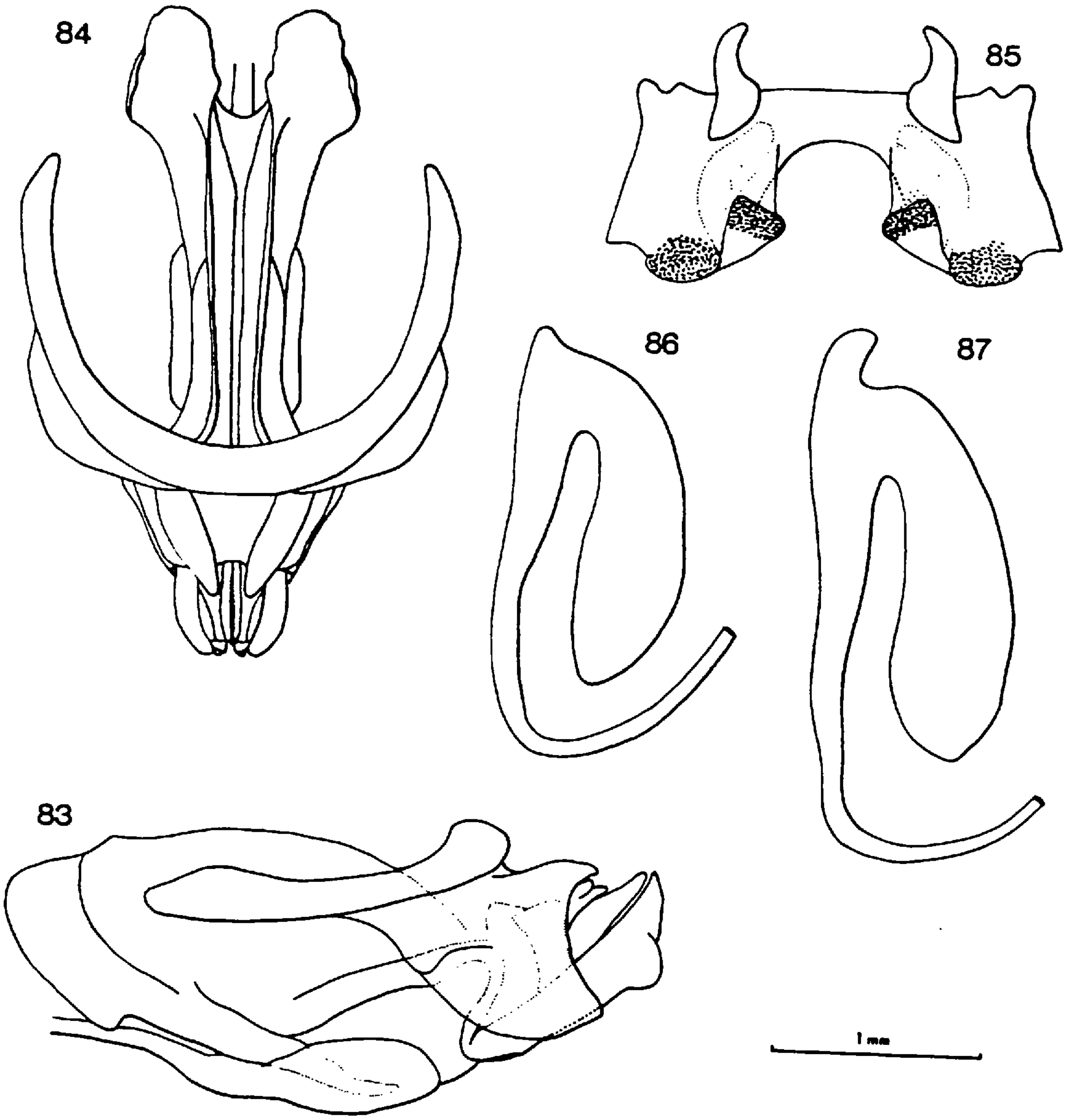
1.1.5.6 Oedaleus johnstoni Uvarov, 1941

(Figs 14,19,43,83-87,155)

Oedaleus johnstoni Uvarov, 1941: 58. Holotype ♂, SUDAN: Khartoum (BMNH) [examined].

Redescription. ♂. Integument finely rugulose. Antennae about one and two fifths length of head and pronotum together; flagellum usually 22 segmented. Fastigium wider than long, concave, with raised margins, narrowing to half maximum width anteriorly. Frons in profile flat or slightly convex; frontal ridge slightly expanded at ocellus. Eyes barely deeper than wide. Pronotum low tectiform to saddle-shaped, finely rugulose, pitted, and with well marked sulci; median carina low and cut by posterior sulcus. Hind margin of pronotum smoothly rounded. Tegmen surpassing hind knees by about one third of femur length. Hind tibia with 10 outer and 11 inner spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and a quarter times as long as claw; arolium about one third length of claw. Cerci almost twice as long as basal width. Genitalia (Figs.83-85): cingular apodemes long and strongly curved, zygoma only slightly thickened; rami long; cingular and apical penis valves short. Apical penis valves with acute apices and tumulus-shaped subapical ventral process. Epiphallus long and broad with deeply arched bridge; outer lobes of lophi wider than inner lobes; anterior and posterior projections large and acutangular.

General colouration mottled, variable, from dark brown to sandy or greenish. Head mainly light brown, sometimes with frons and vertex green. Lateral surface of pronotum and thorax mottled with variable light and dark patches. Pronotum sometimes entirely green on dorsum of prozona and metazona but laterally on metazona only. Tegmen mottled with two indistinct variable transverse bands in basal two thirds, apex



Figs 83-87. O. johnstoni, genitalia. 83, endophallus & cingulum, lateral; 84, same, dorsal; 85, epiphallus; 86, 87, ♀ spermatheca, showing variation.

with some dark speckling. Hind wing fascia (Fig. 14) incomplete, not reaching posterior margin and not passing 2A anteriorly; basal area pale yellow. Outer surface of hind femur with three indistinct oblique dark bands, inner surface with some bands visible in upper-marginal area but medial area clear straw coloured, with orange sulci in chevron pattern, lower marginal area bright orange. Hind knees with internal surface and external crescent black. Hind tibia bright orange internally, orange-yellow externally.

♀. Larger and more robust. Pronotum more rugose. Ventral ovi-positor valves (Fig. 43) barely longer than wide, slightly excavated laterally; basivalvular sclerite sclerotised and with rugose warts. Spermatheca (Figs 86,87) elongate with short, variable subapical diverticulum.

Affinities. O. johnstoni is most closely allies to O. senegalensis and O. nigeriensis, having the rounded pronotal hind margin of the former and the orange-red hind tibiae and under surface of the hind femur reminiscent of the latter. It is however quite distinct, being more heavily built and having a lighter, more indistinct pattern than either of these species.

Material examined. Appendix 1, p. 376.

Measurements. Table 8

Distribution (Fig.155, and Biogeography section, p.172). Occurs in a thin band across the northern Sahel from Mauretania to Ethiopia (Jago, 1977), and there is one known specimen from Oman, a new record which needs confirmation. An erroneous record from Senegal by Roy (1962: 130) was later identified as Oedaleus nigeriensis Uvarov (Roy, 1965: 616).

Biology. Little is known of the biology of this species. Joyce (1952) recorded it from sandstone and serpentine outcrops in East Central Sudan, and regarded it as the dominant species in sandy areas of the Gash river delta (200-300 mm annual rainfall) and the clay plains of the northern Gezira (150-200 mm rainfall). Adults were found from August to November with peak numbers in August and September. Hoppers occurred between July and October and mature females from August. Joyce postulated two annual generations, with the dry season passed in the egg stage in dry soils. There are records of damage to millet (Joyce, 1952) and to cotton (Joyce, 1956) but such damage is probably rare and of small extent.

O. johnstoni normally occurs in low densities but very high density populations have been reported. Dr. R. Skaf (personal communication) observed bands of fourth and fifth instar hoppers at a density of $100/m^2$ marching westward downwind in the Oued Edjerer (18^o 26' N 02^o 02' E) in N.E. Mali on 20.viii.74. The hoppers collected exhibited pronounced black and brown colouration like that of high density hoppers of O. senegalensis, and small numbers of adult O. senegalensis were mixed among them. On 30.ix.74 I visited the locality and found adults only at about 1 per 2-3 m^2. The decline in numbers over five weeks may be attributed to dispersal of adults by flight since the species is often caught at light some distance from areas where it can be found by day. *O. johnstoni* is the dominant grasshopper species in the flat, gravelly silt oueds flowing into the Tillemsi valley, from the rocky outcrops of the Adrar des Iforhas and its colouration is well matched to that of the extensive patches of bare soil on which it rests. The sparse vegetation consists of low hummocks of *Tribulus*, *Euphorbia*, *Indigofera*, *Farsetia*, and *Heliotropium* with *Aristida* and *Panicum turgidum*. The insects fly readily when first disturbed but land and hide within the clumps of vegetation and are then difficult to flush a second time.

Adult specimens possess a pronotal gland similar to that found in *O. senegalensis* but no hoppers were available for dissection. The ovaries of seven adult females were dissected and the mean number of ovarioles per ovary was found to be 26.8 with a range from 23 to 31.

1.1.5.7 Oedaleus nigeriensis Uvarov, 1926

(Figs 10,20,39,88-91,162)

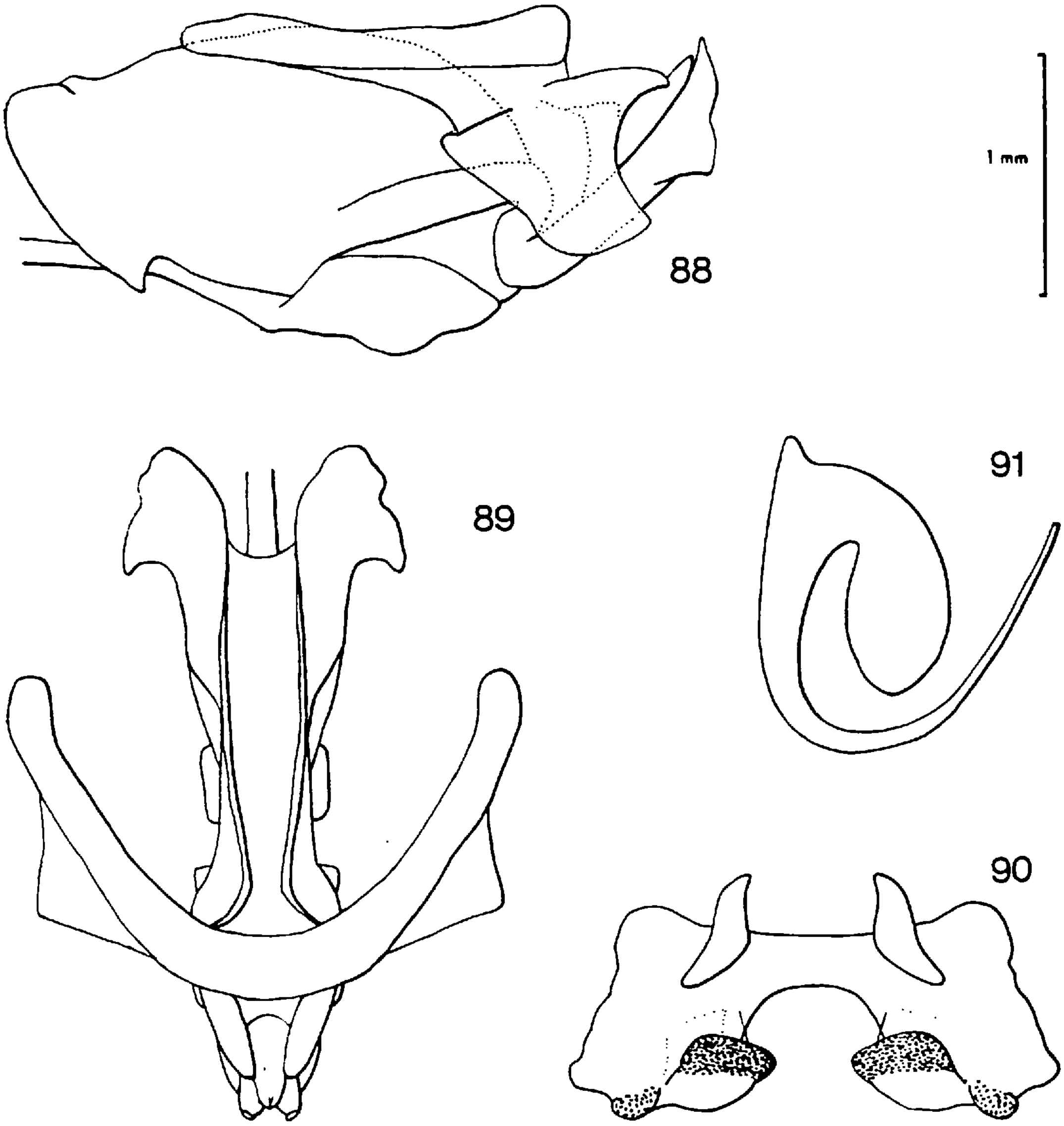
Oedaleus nigeriensis Uvarov, 1926: 437. Holotype ♂, NIGERIA (BMNH) [examined].

Oedaleus senegalensis (Krauss) var. b. Saussure, 1884: 117; I. Bolivar, 1908: 102.

Oedaleus cephalotes Uvarov, 1934: 606. Holotype ♀, ETHIOPIA (BMNH) [examined]. *Syn. n.*

Redescription. ♂. Integument finely rugulose and pitted. Antennae one and three fifths times as long as head and pronotum together, flagellum with twenty segments. Fastigium longer than wide, shallowly concave, narrowing to two fifths of maximum width anteriorly; frons in profile convex; frontal ridge barely constricted below median ocellus, becoming obsolete ventrally. Eyes one and two fifths as deep as wide. Pronotum low tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin obtusangular to rounded obtusangular. Tegmen surpassing folded hind knees by two fifths to one half of hind femur length. Hind tibia with 10-11 inner and 8-10 outer spines; inner apical spurs one and three fifths as long as outer; apical tarsal segment two and one fifth times as long as claw; arolium three fifths length of claw. Cerci barely more than twice as long as basal width. Genitalia (Figs. 88 – 90): cingular apodemes short and moderately curved; rami elongate dorsally; exposed section of cingular and apical penis valves short; subapical ventral process rectangular; epiphallus trapezoidal, bridge narrow; inner lobes of lophi twice as wide as outer lobes; anterior projections large and rounded; posterior projections rectangular.

General colouration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum and dorsal surface of folded



Figs 88-91. O. nigeriensis, genitalia. 88, endophallus & cingulum, lateral; 89, same, dorsal; 90, epiphallus; 91, ♀ spermatheca.

tegmina and hind femora. Tegmen infuscate brown in basal two thirds with irregular pale transverse bands one third and one half way along from base; apical one third clear with variable brown patches. Hind wing fascia (Fig. 10) broadly interrupted between first cubitus and second anal vein, reaching or nearly reaching to hind margin posteriorly; wing tip infumate, basal area pale yellow. Hind femur with three indistinct dark variable oblique transverse bands on outer and inner upper marginal areas and outer medial area; inner surface light reddish brown becoming pale red ventrally; hind knees dark brown; hind tibiae with dark basal ring and subbasal pale area, otherwise light red.

♀. Larger and more robust. Ventral ovipositor valves (Fig. 39) long, well sclerotised, outer margin almost straight. Apical diverticulum of spermatheca (Fig. 91) with short subapical diverticulum.

Affinities. *O. nigeriensis* is a member of the same group of species as *O. senegalensis*, characterised by the possession of large transverse inner lobes to the epiphallic lophi. It is most closely allied to *O. carvalhoi* from which it may be separated by the principal characters listed under that species (p. 82).

Material examined. Appendix 1, p. 376.

Measurements. Tables 9 - 12

Distribution (Fig. 162, and Biogeography section, p. 174). Widely distributed in moist savannah and woodland from Senegal to Ethiopia and southwards through central Africa to the southern limits of the *Brachystegia* woodland. Newly recorded from Grand Comoro I.

Biology. The life history and ecology of *O. nigeriensis* were studied in Nigeria by Golding (1948) who stated that there were probably three generations in the south but only one in the north. In West Africa as a whole adults are to be found from April through to January. In Tanzania Robertson & Chapman (1962) made an ecological study which suggested that there were two generations between January and July, but they were unable to decide whether the species survived the dry season in the egg or adult stage, or in both. They presented evidence suggesting that young adults leave the

Table 9

Measurements (Tanzania, Shinyanga, i-ii.37, (K. Burtt)):

Oedaleus nigeriensis Uvarov

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	25.22	3.36	3.79	4.62	18.37	11.58	2.96	3.91	4.86
Range	23.5 - 27.45	3.05- 3.7	3.4 - 4.2	4.2 - 4.95	16.85- 20.9	10.85- 12.75	2.75- 3.2	3.71- 4.13	4.39- 5.32
S.D.	1.266	0.170	0.181	0.193	1.034	0.500	0.138	0.114	0.245
No.	26	28	27	28	26	27	27	27	25
♀ Mean	32.03	4.60	4.97	6.16	23.45	14.69	3.76	3.91	4.72
Range	28.9 - 37.85	4.2 - 5.85	4.25- 6.5	5.55- 7.6	21.35- 27.7	12.95- 28.5	3.4 - 4.5	3.67- 4.11	4.23- 5.21
S.D.	1.957	0.338	0.468	0.417	1.514	1.074	0.227	0.137	0.244
No.	26	26	25	26	26	26	26	26	25

Table 10

Measurements contd. (Zambia, Musosa, xi-xii.40., (H. J. Bredo) [beginning of rainy season]):

Oedaleus nigeriensis Uvarov

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	23.99	3.33	3.725	4.66	17.75	11.44	2.87	3.98	4.73
Range	22.15- 25.8	3.1 - 3.65	3.35- 4.1	4.35- 4.9	16.7 - 18.7	10.45- 12.6	2.75- 3.0	3.65- 4.43	4.27- 5.33
S.D.	0.999	0.152	0.216	0.169	0.661	0.661	0.071	0.200	0.222
No.	16	17	16	17	16	17	17	17	15
♀ Mean	29.99	4.47	4.78	6.25	22.22	13.96	3.64	3.83	4.66
Range	26.5 - 33.5	3.95- 5.0	4.25- 5.25	5.55- 6.7	19.6 - 25.45	12.0 - 15.4	3.15- 3.95	3.6 - 4.07	4.22- 5.19
S.D.	1.558	0.223	0.275	0.246	1.331	0.819	0.165	0.128	0.235
No.	20	20	20	20	20	20	20	20	20

Table 11

Measurements contd. (Zambia, Musosa, iv-v.41., (H. J. Bredo) [end of rainy season]):

Oedaleus nigeriensis Uvarov

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	29.05	4.33	4.57	5.36	21.36	14.82	3.39	4.37	4.69
Range	27.0 - 30.4	4.15- 4.65	4.25- 5.1	4.95- 5.75	20.1 - 22.35	14.4 - 15.45	3.05- 3.65	4.15- 4.68	4.23- 5.14
S.D.	1.051	0.186	0.261	0.226	0.790	0.530	0.204	0.172	0.231
No.	10	10	10	10	10	9	10	9	10
♀ Mean	36.49	5.78	5.71	7.15	26.57	18.42	4.31	4.28	4.67
Range	34.75- 37.8	5.55- 6.15	5.25- 6.2	6.95- 7.35	25.45- 27.75	16.8 - 20.2	4.2 - 4.5	4.0 - 4.81	4.38- 4.98
S.D.	1.286	0.239	0.417	0.169	0.896	1.323	0.134	0.313	0.222
No.	5	5	5	5	5	5	5	5	5

Table 12

Measurements contd. (Ethiopia, Nefasit, 28.viii.68. (J. Tunstall)):

Oedaleus nigeriensis Uvarov

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	23.62	3.72	3.9	4.8	17.04	12.54	3.14	3.99	4.38
Range	22.35- 26.1	3.45- 4.2	3.6 - 4.25	4.5 - 5.1	16.15- 19.1	11.5 - 13.45	2.9 - 3.35	3.67- 4.19	3.94- 4.70
S.D.	1.267	0.210	0.227	0.207	0.937	0.592	0.148	0.156	0.224
No.	11	11	11	10	11	11	11	11	11
♀ Mean	32.24	5.36	5.24	6.43	22.66	16.69	4.07	4.1	4.33
Range	28.95- 35.85	4.85- 5.7	4.55- 5.75	5.45- 7.05	20.8- 24.9	14.45- 19.1	3.65- 4.4	3.83- 4.39	4.06- 4.66
S.D.	1.905	0.279	0.369	0.46	1.088	1.141	0.224	0.177	0.176
No.	12	12	12	12	12	12	12	12	12

grasslands and enter the woodland to feed or oviposit. In Cameroon Descamps (1953) postulated two generations with an embryonic diapause. The egg pod and eggs have been described by Chapman and Robertson (1958) who found 12-42 eggs per pod. The species has been recorded damaging maize (Descamps, 1954; Mallamaire, 1956), Pennisetum and Eleusine millet (Risbec, 1950; Golding, 1946; Libby, 1968; Harris, 1949), rice seedlings (Risbec and Mallamaire, 1949), groundnuts and sweet potato (Risbec, 1950) and tobacco and yams (Libby, 1968).

Discussion. The measurements of specimens from Musosa, Zambia (Tables 10, 11) show the remarkable change in size exhibited by the species over six months. The ranges of measurements from the two samples barely overlap, and are clearly significantly different. Less obviously the ratio of femur length to depth is also significantly different as indicated by a 't' test ($P < 0.001$♂, < 0.1♀). It is not clear whether the two samples at either end of the rainy season represent two different generations of the same population or rather a migration into the locality of a population from elsewhere between the two sampling periods. For present purposes however these figures provide an indication of the range of size within the species. Series from Ethiopia and Tanzania (Tables 9, 12) fall within the extremes recorded from Zambia. Material from Ethiopia was originally named as a separate species cephalotes by Uvarov (1934) at a time when relatively little material of nigeriensis was known and only from Nigeria. It has become clear that the same species is to be found without a break right across Africa. The original description of cephalotes made no comparison with material of previously described Oedaleus species.

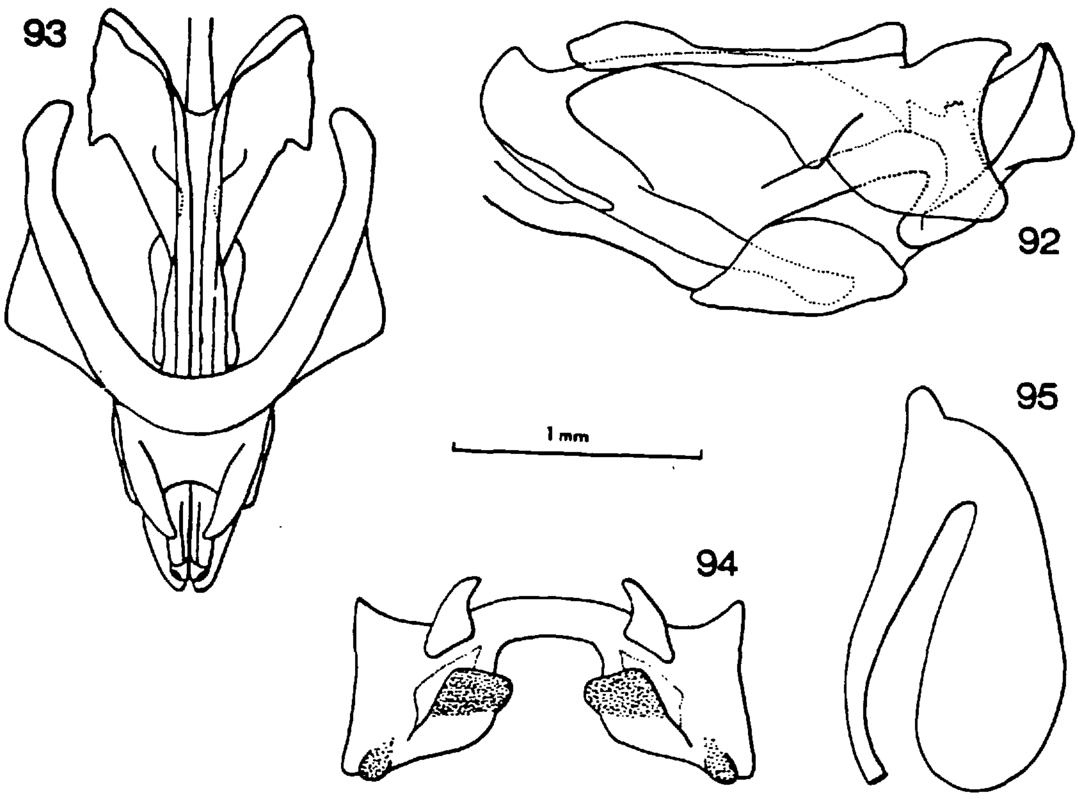
1.1.5.8 Oedaleus carvalhoi I. Bolivar, 1889

(Figs 15,23,44,92-95,152)

Oedaleus carvalhoi I. Bolivar, 1889: 103. Syntypes (?) ♂♀, ANGOLA: Lourenço Marques, (Monteiro) (lost). NEOTYPE ♂, ANGOLA (BMNH), here designated [examined].

Redescription. ♂. Integument finely rugulose and pitted. Antennae barely longer than head and pronotum together, flagellum with 21 segments. Fastigium of vertex longer than wide, concave, narrowing to less than half of its maximum width anteriorly, with distinct lateral carinae; frons in profile straight, frontal ridge barely constricted below median ocellus, becoming obsolete ventrally. Eyes one and a third times as deep as wide. Pronotum tectiform, median carina arcuate, not intersected by posterior sulcus; hind margin forming an obtuse angle with concave sides (Fig. 23). Tegmen surpassing hind knees by one quarter to one eighth of hind femur length. Hind tibia with 12 inner and outer spines; inner apical spurs one and a half times outer; apical tarsal segment one and three quarter times claw length; arolium half claw length. Cerci twice as long as basal width. Genitalia (Figs. 92 - 94): cingular apodemes long and incurved; rami elongate with short cingular and apical penis valves; subapical ventral process large, rounded; epiphallus rectangular with narrow bridge, inner lobes of lophi strongly transverse, more than twice width of outer lobes; anterior projections large, acute; posterior projections small, rounded.

General colouration variable, brown, with lighter brown or green markings on frons, vertex, genae, pronotum and dorsal surface of folded tegmina. Pale x-marking of pronotum often surrounded by longitudinal dark brown area. Tegmen matt brown in basal half with two irregular pale transverse bands one third and one half distance from base, sometimes obsolete; apical half becoming clear with irregular brown



Figs 92-95. O. carvalhoi, genitalia. 92, endophallus & cingulum, lateral; 93, same, dorsal; 94, epiphallus; 95, ♀ spermatheca.

markings. Hind wing fascia (Fig. 15) interrupted between first cubitus and second anal vein, reaching or almost reaching hind margin of wing; apex of wing infumate, basal area pale yellow. Hind femur with three indistinct variable oblique transverse dark bands on external medial and upper marginal area; inner surface brown, indistinctly mottled, ventral surface dull brown; hind knees dark brown, hind tibiae with dark basal ring and pale subbasal area, otherwise dull brown.

♀. Larger and more robust. Hind wings sometimes barely exceeding folded hind knees. Ventral ovipositor valves short, well sclerotised, hardly incurved externo-laterally (Fig. 44). Spermatheca (Fig. 95) with short subapical diverticulum.

Affinities. O. carvalhoi is most closely allied to O. nigeriensis from which it differs by the following principal characters. Tibiae and ventral surface of hind femur pale straw-coloured, not red. Pronotum with finer cross-shaped marking and more pointed hind margin (Figs 23, 20). Tegmina and wings shorter in relation to body size and pronotum length (compare TL / PL ratios given for both species).

Material examined. Appendix 1, p. 376.

Measurements. Table 13

Distribution (Fig. 152, and Biogeography section, p. 158). Widely distributed in the eastern half of southern Africa.

Biology. Little is known of the biology of this species. Nolte (1939) in his comparative study of seven species of acrididae in the Transvaal states that adult females have 18 ovarioles per ovary. Adults were mainly found from October to April but sometimes in July and August also. The species has a karyotype of 2N = 22 chromosomes. O. carvalhoi has been reported damaging cotton in Mozambique (Del Valle y Marche, 1968).

Table 13
Measurements (Transvaal, Louis Trichardt):
Oedaleus carvalhoi Bolivar

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	23.32	3.47	4.31	4.54	16.85	12.21	3.01	4.06	3.92
Range	21.5 - 25.2	3.05- 4.6	3.9 - 5.05	3.95- 5.1	15.45- 18.25	10.3 - 14.1	2.7 - 3.45	3.68- 4.37	3.57- 4.29
S.D.	1.131	0.333	0.301	0.293	0.864	0.948	0.199	0.211	0.181
No.	20	20	20	20	20	20	20	20	20
♀ Mean	26.88	4.69	5.42	6.15	18.77	14.26	3.65	3.91	3.47
Range	24.8 - 28.65	4.5 - 5.0	5.1 - 5.85	5.7 - 5.65	17.0 - 19.65	13.55- 15.05	3.45- 3.9	3.57- 4.22	3.15- 3.74
S.D.	1.032	0.139	0.204	0.207	0.781	0.482	0.149	0.173	0.172
No.	15	15	15	15	15	15	15	15	15

Table 14
Measurements (S.W. Africa, various localities):
Oedaleus plenus plenus (Walker)

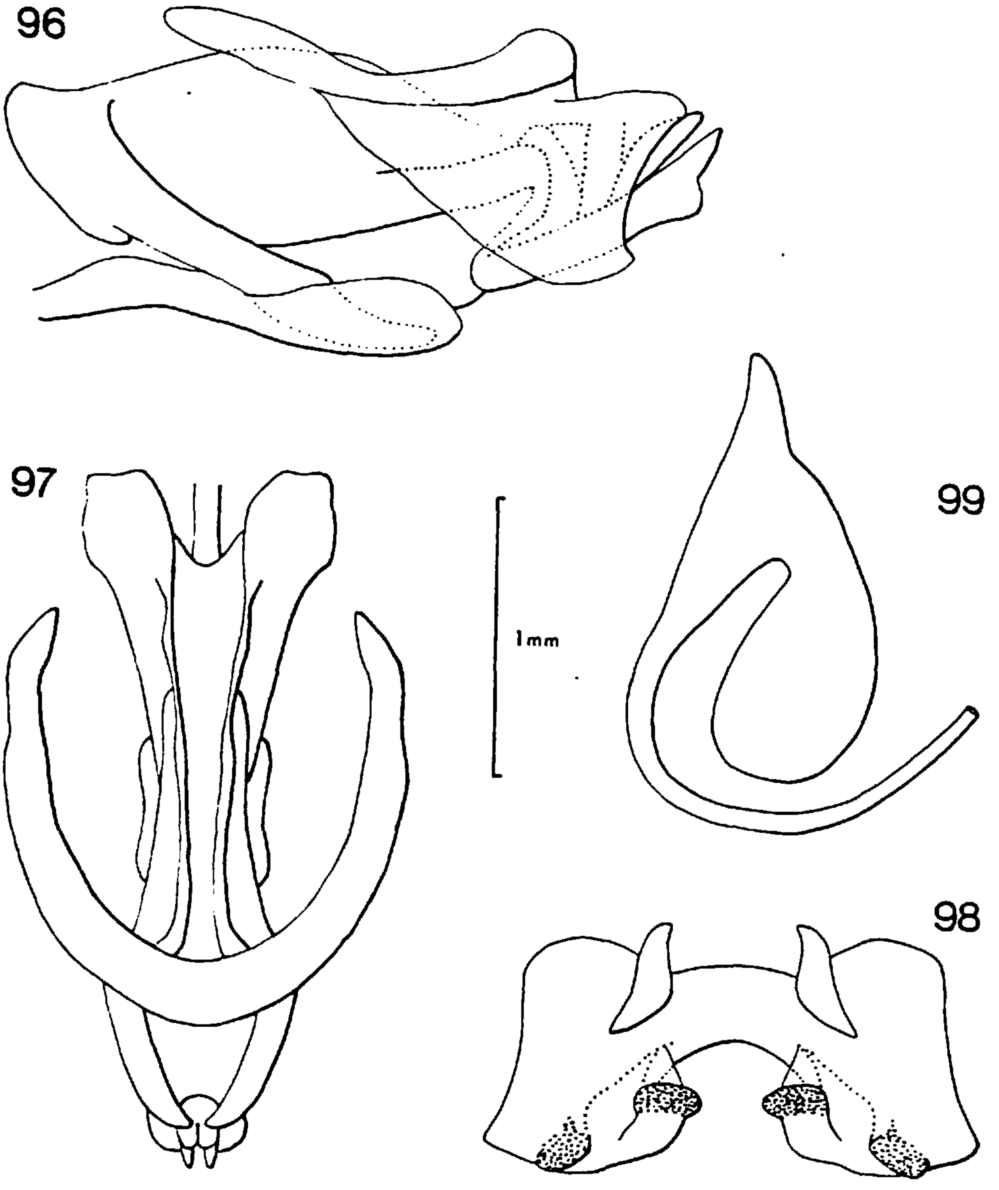
	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	26.18	3.6	4.73	5.01	19.59	12.32	3.33	3.70	4.15
Range	24.3 - 27.4	3.35- 3.8	4.3 - 5.05	4.75- 5.4	18.3 - 20.7	11.2 - 12.85	3.1 - 3.55	3.51- 3.89	3.81- 4.59
S.D.	0.867	0.113	0.228	0.217	0.727	0.503	0.129	0.119	0.214
No.	14	14	14	14	14	14	14	14	14
♀ Mean	31.44	4.72	5.76	6.35	23.48	14.6	3.9	3.75	4.08
Range	29.0 - 33.0	4.3 - 5.0	5.35- 6.05	5.75- 7.0	21.8 - 25.0	13.35- 15.7	3.5 - 4.3	3.38- 4.04	3.83- 4.44
S.D.	1.202	0.188	0.239	0.364	0.887	0.676	0.234	0.194	0.177
No.	15	15	15	15	15	15	15	15	15

1.1.5.9 Oedaleus plenus (Walker) (Figs 6,22,45,96-99,153)

This species is divided into two subspecies under which the specific synonyms are separately listed below.

Redescription. ♂. Integument finely rugulose. Antennae about one and a third times as long as head and pronotum together; flagellum with 22 segments. Fastigium longer than wide narrowing to about three quarters of maximum width anteriorly; lateral carinae distinct; forns in profile slightly convex, frontal ridge constricted at vertex and below median ocellus, wider between antennal bases. Eyes one and two fifths as deep as wide. Pronotum tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin from slightly acutangular to slightly obtusangular. Tegmen normal, surpassing hind knees by one third to one half of hind femur length. Hind tibia with 10 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and one third times claw length; arolium three fifths of claw length. Cerci little more than twice as long as basal width. Genitalia (Figs. 96 - 98): cingular apodemes long, strongly curved; rami long; exposed portion of cingular valves and apical penis valves short, subapical ventral process rounded; anterior projections large, rounded; posterior projections rectangular.

General colouration variable, brown, grey brown, or greenish; green forms rare, brown forms with lighter brown markings on frons, genae, and dorsal surface of pronotum, tegmen, and hind femur; green forms have green markings here and on vertex. Tegmen infuscate in basal half, with irregular pale transverse band one third along from base usually extending from costal margin to subcostal vein but sometimes less developed; second band half way along usually reaches from costal margin to second cubitus but may be obscure or poorly developed;



Figs 96-99. O. plenus, genitalia. 96, endophallus & cingulum, lateral; 97, same, dorsal; 98, epiphallus; 99, ♀ spermatheca.

apical third of tegmen clear or speckled. Hind wing fascia (Fig. 6) incomplete, interrupted between first cubitus and first anal vein (in O. plenus browni more broadly interrupted or almost obsolete) reaching hind margin of wing posteriorly; basal area pale yellow or colourless, wing tip sometimes infumate. Hind femur with irregular transverse oblique bands on exterior surface and interior upper marginal area; interior medial area straw-coloured; ventral surface orange red; hind tibia with dark basal ring, subbasal pale area, otherwise orange red.

♀. Larger, more robust. Ventral ovipositor valves (Fig. 45) elongate, weakly sclerotised, longer than wide, exterior lateral margins only slightly excavated; basivalvular sclerite smooth. Spermatheca (Fig. 99) with conical, slightly recurved subapical diverticulum.

The two subspecies of Oedaleus plenus may be separated by the following key:

1. Hind wing fascia absent or restricted to posterior half of wing, seldom passing third anal vein anteriorly but occasionally reaching posterior branch of second anal vein (2Aa) (E. Transvaal, E. Cape Province, Lesotho) Oedaleus plenus browni subsp. n.

-. Hind wing fascia only interrupted between first cubitus and first anal vein, reaching costal margin of wing anteriorly (southern Africa, N.E. Tanzania) ... ... Oedaleus plenus plenus (Walker)

Oedaleus plenus plenus (Walker, 1870)

Epacromia plena Walker, 1870: 769. Lectotype ♂, SOUTH AFRICA (BMNH), designated by Uvarov, 1925: 276 [examined].

Oedaleus (Oedaleus) nigro-fasciatus var. caffer Saussure, 1888: 41.
LECTOTYPE ♀, SOUTH AFRICA (MHN, Geneva), here designated [synonymised by Uvarov, 1925: 276] [examined].

Oedalus [sic] plena (Walker); Distant, 1892: 260.

Chortoicetes plena (Walker); Kirby, 1902a: 70.

Oedaleus plenus (Walker); Kirby, 1910: 225.

Oedaleus caffer Saussure; Kirby, 1910: 225.

Oedaleus dilutus Miller, 1929: 74. Holotype ♂, TANZANIA (BMNH) [examined]. Syn. n.

Material examined. Appendix 1, p. 376.

Measurements. Table 14

Oedaleus plenus browni subsp. n.

Material examined. Appendix 1, p. 377.

Measurements. Table 15

Affinities. O. plenus is a member of the rather homogeneous group of species which includes O. senegalensis and O. nigeriensis, but is in some respects intermediate between this group and the O. instillatus - obtusangulus - rosescens group having a tendency to overall grey-brown coloration, with green forms rare, and epiphallic lophi with small, equal-sized lobes (Fig. 98).

Distribution (Fig. 153, and Biogeography section p. 158). Widely distributed in southern Africa, with a population in Tanzania, isolated on the northern edge of the Brachystegia woodland. The records from Namibia, Angola, and Zambia appear to be new. Johnsen (1978) has recently recorded the species from Botswana. The record by Dirsh (1956:

Table 15
Measurements (type series):
Oedaleus plenus browni subsp. n.

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	23.16	3.74	4.57	4.92	16.85	12.26	3.51	3.49	3.73
Range	22.25-24.05	3.3 - 4.1	4.25-5.1	4.55-5.25	15.85-18.05	11.15-13.55	3.3 - 3.9	3.33-3.64	3.52-4.03
S.D.	0.658	0.247	0.287	0.265	0.769	0.742	0.188	0.111	0.168
No.	6	9	9	9	7	9	9	9	7
♀ Mean	30.28	5.22	5.81	6.55	21.92	15.13	4.27	3.55	3.78
Range	29.1 - 31.55	4.8 - 5.55	5.15-6.3	5.65-7.25	20.35-23.95	14.0 - 15.85	3.95-4.6	3.37-3.69	3.55-3.95
S.D.	1.012	0.275	0.461	0.520	1.489	0.703	0.246	0.116	0.164
No.	5	6	6	6	6	5	5	5	6

Table 16
Measurements (Algeria, Djelfa, 9.x.38., (M. N. Korsakoff)):
Oedaleus decorus decorus (Germar)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	38.2	5.69	6.23	6.51	28.27	18.86	4.42	4.27	4.56
Range	32.85-43.15	5.06-6.21	5.2 - 7.4	5.8 - 7.15	23.6 - 31.3	16.3 - 21.65	3.81-5.1	4.0 - 4.63	4.14-4.97
S.D.	2.55	0.27	0.525	0.39	1.890	1.39	0.32	0.17	0.17
No.	27	27	27	27	23	26	26	26	23
♀ Mean	44.25	7.09	7.26	8.01	31.93	21.47	5.16	4.16	4.47
Range	40.85-48.75	6.44-8.0	6.4 - 8.45	7.65- [illegible]	30.05-35.9	19.0 - 24.85	4.7 - 5.82	3.82-4.45	4.27-4.83
S.D.	2.66	0.38	0.61	0.55	1.86	1.64	0.34	0.18	0.14
No.	24	28	28	28	14	28	28	28	14

325, 265) from Lesotho should be referred to O. plenus browni which is apparently restricted to high ground above about 1500 m in the eastern half of South Africa, and Lesotho.

Biology. Unknown. Cuthbertson (1934) reported this species among the prey of the asilid fly Alcimus rubiginosus.

Discussion. Walker's type material almost certainly came from south west Cape Province. Specimens from this climatically distinct zone usually have the posterior arms of the pronotal x-marking thin, less than one and a half times as wide as the anterior arms, whereas elsewhere the posterior arms are usually about three times as wide as the anterior arms. Despite the evident discontinuity in the distribution of this character (Fig. 153) it is not an absolutely reliable distinction between populations, so the name plenus plenus is here used to refer to all the material available whatever its pronotal characteristics, except for material referred to plenus browni for other reasons.

Miller's O. dilutus, described from Tanzania, is identical in all respects with material from south of the Brachystegia woodland zone and is here considered to be a junior synonym of O. plenus plenus. If the SW Cape population should later be conclusively shown to have consistent characters meriting subspecies status then the name O. plenus plenus could be restricted to this population and dilutus would again be available for material of the species from other areas. Measurements of eight males and seven females from SW Cape Province including Walker's type series were found to give rather high mean values for the length/depth ratio of the hind femur (FL/FD: 4.00 ♂, 4.09 ♀). There is however a likelihood of bias with such low numbers and dubious locality data and a study of fresh material from this area is needed.

Statistical comparison by 't' test of all available material of

O. p. browni (Table 15) with a series of *O. p. plenus* (Table 14) reveals interesting differences. Femur length and pronotum length do not differ significantly, but in females head width is very significantly greater in *O. p. browni* than in *O. p. plenus* ($P < 0.001$), while tegmen length is significantly less, particularly in the male ($P < 0.001$ ♂, < 0.05 ♀). Head width variation is enigmatic, but decrease in wing length is very commonly associated with adaptation to montane conditions in grasshoppers at and below species level. Not surprisingly TL / PL is significantly greater in the nominate subspecies ($P < 0.001$ ♂, < 0.002 ♀) than in *O. p. browni* but less accountably the FL / FD ratio is also higher in the former than the latter ($P < 0.001$ ♂, < 0.002 ♀). Presumably decreasing flight capability is correlated with decreased take-off capability in the form of shorter femora.

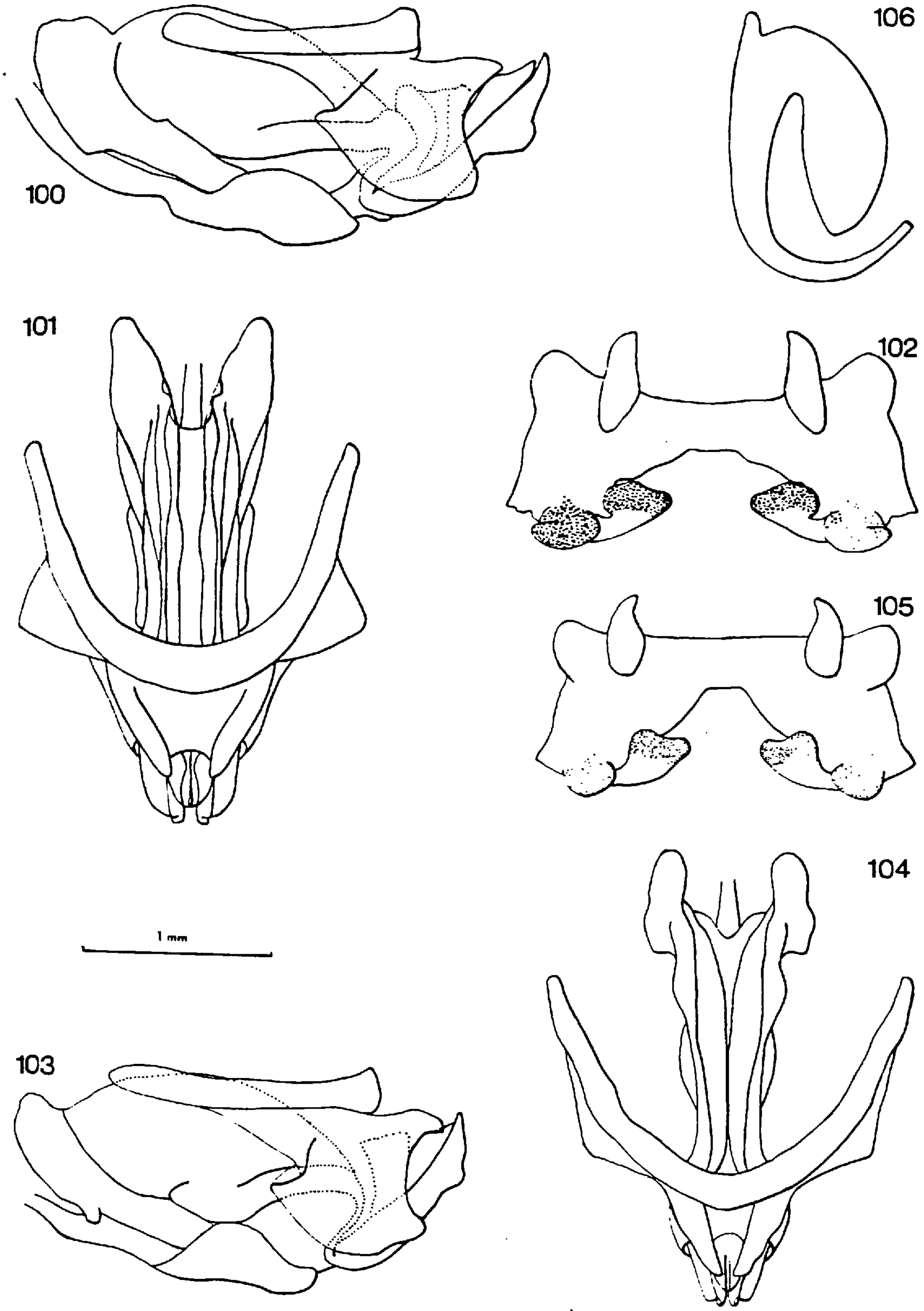
The new subspecies is named in honour of its discoverer, Dr H. D. Brown.

1.1.5.10 Oedaleus decorus (Germar, 1826)
(Figs 11,28,29,51,100-106,159,164)

This species is here divided into two subspecies under which the specific synonyms are separately listed below.

Redescription. ♂. Integument finely rugulose and pitted. Antennae about one and a third times as long as head and pronotum together, flagellum with 22 segments. Fastigium longer than wide, concave, narrowing to two fifths of maximum width anteriorly; lateral carinae distinct, faint median carina sometimes visible; frons in profile straight or slightly convex; frontal ridge, slightly expanded and coarsely punctate between antennal bases. Eyes about one and two fifths as long as wide. Pronotum low tectiform; median carina arcuate, not intersected by posterior sulcus. Tegmen surpassing hind knees by about one third of femur length. Hind tibia with 11-12 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment about twice claw length; arolium half claw length. Cerci about twice as long as basal width. Genitalia (Figs 100 - 105): cingular apodemes normal, rami well developed, cingular and apical penis valves short; subapical ventral process small; epiphallus variable, trapezoidal, with thick bridge; inner and outer lobes of lophi of equal size; anterior projections large, rounded; posterior projections rectangular.

General colouration variable, brown, with light brown or green markings on frons, genae, pronotum, basal quarter of tegmina, and hind femora. Tegmen infuscate brown in basal half with variable transverse pale bands situated one sixth, one third, and one half along from base; apical half clear with brown specks. Hind wing fascia (Fig. 11) complete, not reaching hind margin of wing, wing tip tinged with brown; basal area of wing pale yellow with distinct pale bluish tinge on wing vein bases. Hind femora with three oblique transverse bands on inner



Figs 100-106. *O. decorus*, genitalia. 100-102, *O. decorus decorus*. 100, endophallus & cingulum, lateral; 101, same, dorsal; 102, epiphallus. 103-105, *O. decorus asiaticus*. 103, endophallus & cingulum, lateral; 104, same, dorsal; 105, epiphallus; 106, *O. decorus decorus*, ♀ spermatheca.

and outer surfaces, ventral surface red, knees black; hind tibiae with black basal ring, basal one third pale straw-coloured, apical two thirds reddish.

♀. Larger and more robust. Frons in profile convex. Ventral ovipositor valves (Fig. 51) blunt, strongly sclerotised. Spermatheca (Fig. 106) with apical diverticulum bulbous with acutely rounded apex, and short subapical diverticulum.

The two subspecies of Oedaleus decorus may be separated by the following key:

1. Generally larger (except in northern France), body length 24.0-36.3 mm male, 31.1-49.0 mm female; pronotal hind margin more angular (Fig. 28); hind wing fascia thicker, and terminating posteriorly within 1 mm of wing margin (Fig. 11); interior surface of epiphallic bridge weakly arched (Fig. 102) (N. Africa, S. Europe, Middle East, S.W. U.S.S.R. as far as E. Kazakh S.S.R., W. Sinkiang province of China) Oedaleus decorus decorus (Germar)

-. Generally smaller, body length 25.0-27.5 mm male, 32.0-37.6 mm female; pronotal hind margin more rounded (Fig. 29); hind wing fascia thinner, terminating posteriorly more than 1 mm from wing margin; interior surface of epiphallic bridge strongly arched (Fig. 105) (Mongolia, Transbaikalia, Hopeh and Shantung provinces of China) ... Oedaleus decorus asiaticus B.-Bienko

Oedaleus decorus decorus (Germar, 1826)

Acrydium decorum Germar, 1826: plate 17. Holotype ♂ (?), U.S.S.R.: 'Podolia australi (Besser)' '(Mus. Besseri)' (lost). NEOTYPE ♂, U.S.S.R.: Daghestan (BMNH), here designated [examined.]

[Acridium flavum (Linnaeus) Costa, 1836: 11. Misidentification.]

[Oedaleus nigrofasciatus (Degeer) Bormans, 1879: 407; Brunner, 1882: 169; Bonnet & Finot, 1884: 220; Bormans, 1884: 179, 1885: 109; Olivier, 1892: 45; Frey-Gessner, 1894: 106; Finot, 1895: 479; Krauss & Vosseler, 1896: 531; Fenard, 1896: 107; I. Bolivar, 1898: 76; Burr, 1898: 179; Vosseler, 1902: 359, 1902a: 116, 1902b: 84; Finot, 1902: 434; Giglio-Tos, 1907: 8; Burr, 1912: 31; I. Bolivar, 1914: 188; Werner, 1914: 397; Steck, 1915: xiv; Plotnikov, 1921: 9; Giglio-Tos, 1923: 5; Rabaud, 1923: 18; Zanon, 1924: 246; Salfi, 1925: 93; Hollande, 1926: 374; Werner, 1934: 6; Jovančić, 1953: 99; Barbut, 1954: 339; Costatino, 1954: 4. Misidentifications.]

[Oedipoda nigrofasciata (Degeer) Serville, 1831: 288; Burmeister, 1838: 645. Misidentifications.]

[Acrydium nigrofasciatum (Degeer) Latreille, 1805: 157. Misidentification.]

[Gryllus nigrofasciatus (Degeer) Charpentier, 1825: 140. Misidentification.]

[Gryllus flavus (Linnaeus) Rambur, 1838: 82. Misidentification; Uvarov, 1948: 384.]

Oedaleus decorus (Germar) Uvarov, 1923: 69.

Material examined. Appendix 1, p. 377

Measurements. Tables 16-19, 21

Table 17

Measurements contd. (France, Gironde Department, S. of Soulac-sur-Mer, 11.viii.77., (N. D. Jago)):
Oedaleus decorus decorus (Germar)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	25.0	3.81	4.25	4.425	18.58	12.65	3.12	4.06	4.88
Range	23.95-26.65	3.60-4.15	3.90-4.75	4.15-4.95	17.85-20.25	11.60-14.05	2.90-3.30	3.75-4.32	4.62-5.11
S.D.	0.748	0.181	0.239	0.270	0.657	0.726	0.148	0.164	0.169
No.	10	10	10	10	10	10	10	10	10
♀ Mean	34.17	5.33	5.82	6.5	25.28	16.75	4.20	3.99	4.74
Range	32.75-35.55	5.15-5.45	5.30-6.20	6.20-6.75	24.30-26.50	16.00-17.35	3.90-4.45	3.83-4.31	4.61-4.91
S.D.	1.070	0.115	0.272	0.199	0.823	0.412	0.164	0.129	0.096
No.	12	13	13	13	12	13	13	13	12

Table 18

Measurements contd. (France, Bouches-du-Rhône, 22 kms S.E. of Arles, 1-17.vii.60, (Goodings & Philpot)):
Oedaleus decorus decorus (Germar)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	28.43	4.42	4.56	5.12	20.76	14.65	3.47	4.24	4.55
Range	27.05-31.35	4.2 - 4.65	4.1 - 5.0	4.8 - 5.5	18.4 - 23.25	13.35-15.55	3.24-3.79	3.98-4.57	4.09-4.89
S.D.	1.42	0.14	0.23	0.20	1.35	0.57	0.16	0.15	0.21
No.	13	13	13	13	13	13	13	13	13
♀ Mean	40.85	6.49	6.75	7.44	30.31	20.69	4.75	4.37	4.5
Range	38.3 - 42.85	6.05-6.8	6.1 - 7.15	6.45-8.2	28.5-31.85	19.0 - 21.8	4.22-5.19	3.97-5.05	4.19-4.78
S.D.	1.54	0.25	0.48	0.57	1.13	0.92	0.34	0.36	0.18
No.	8	8	8	8	8	8	8	8	8

Table 19

Measurements contd. (Western U.S.S.R., various localities):

Oedaleus decorus decorus (Germar)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	27.92	4.31	4.44	5.19	20.6	14.26	3.39	4.23	4.66
Range	26.15-30.35	3.95-4.65	3.95-5.05	4.7 - 5.7	18.95-22.5	12.95-15.7	3.0 - 3.95	3.53-4.5	4.24-5.15
S.D.	1.35	0.28	0.37	0.38	1.16	0.92	0.32	0.32	0.35
No.	8	8	8	8	8	7	7	7	8
♀ Mean	38.87	6.22	6.27	7.58	28.8	19.16	4.57	4.2	4.61
Range	33.0 - 42.1	5.15-6.85	4.95-7.1	6.15-8.2	24.8 - 30.9	15.75-20.65	3.65-4.95	4.0 - 4.32	4.35-5.07
S.D.	2.64	0.47	0.61	0.63	1.9	1.62	0.45	0.13	0.29
No.	9	9	9	9	9	7	7	7	7

Table 20

Measurements (all available material):

Oedaleus decorus asiaticus Bei-Bienko

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	25.73	3.65	3.84	4.24	19.11	12.09	2.85	4.24	4.98
Range	24.9 - 27.45	3.55-3.75	3.6 - 4.15	4.1 - 4.6	18.25-20.95	11.75-12.45	2.82-2.9	4.11-4.41	4.69-5.25
S.D.	0.926	0.071	0.22	0.19	0.95	0.25	0.034	0.12	0.19
No.	6	6	6	6	6	5	5	5	6
♀ Mean	35.79	4.41	5.57	6.36	26.33	16.29	3.75	4.34	4.74
Range	32.1 - 37.65	4.95-5.75	4.95-5.8	5.45-6.95	23.9 - 28.35	14.95-18.2	3.43-4.06	4.25-4.48	4.54-5.07
S.D.	1.80	0.26	0.37	0.47	1.24	0.92	0.19	0.082	0.175
No.	9	9	9	9	9	9	9	9	9

Table 21. Significance levels of 't' tests on comparisons of mean measurements of populations of Oedaleus decorus

Paired comparisons of mean values	Sex	Caput width	Pronotum length	Tegmen length	Femur length	FL/FD	TL/PL
Algeria/Bouches du Rhône	♂	< 0.001	<0.001	<0.001	<0.001	n.s.	n.s.
	♀	< 0.001	<0.02	<0.02	n.s.	n.s.	n.s.
BDR/Gironde	♂	< 0.001	<0.01	<0.001	<0.001	<0.02	<0.001
	♀	< 0.001	<0.001	<0.001	<0.001	<0.01	<0.01
BDR/Russia	♂	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	♀	n.s.	n.s.	n.s.	<0.05	n.s.	n.s.
Gironde/Russia	♂	< 0.001	n.s.	<0.001	<0.002	n.s.	n.s.
	♀	<0.001	n.s.	<0.001	<0.002	<0.01	<0.05
Gironde/asiaticus	♂	<0.05	<0.01	n.s.	<0.05	<0.05	n.s.
	♀	n.s.	n.s.	<0.05	n.s.	<0.001	n.s.
Russia/asiaticus	♂	< 0.001	<0.01	<0.05	<0.001	n.s.	<0.05
	♀	< 0.001	<0.01	<0.01	<0.001	<0.05	n.s.

Table 22

Measurements (Japan, Nishigo, Uzen):

Oedaleus infernalis Saussure

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	31.45	4.43	5.73	5.79	23.37	16.52	4.18	3.95	4.08
Range	28.75-34.75	4.2 - 4.65	5.3 - 6.2	5.4 - 6.15	21.25-26.3	15.25-17.8	3.9 - 4.45	3.77-4.23	3.8 - 4.38
S.D.	1.377	0.144	0.259	0.254	1.229	0.697	0.155	0.109	0.142
No.	21	21	21	21	21	21	21	21	21
♀ Mean	42.29	6.28	7.88	8.2	31.28	22.03	5.37	4.10	3.97
Range	38.6 - 45.8	6.0 - 6.85	7.4 - 8.7	7.5 - 9.1	28.05-34.1	20.75-25.45	5.0 - 5.95	3.94-4.28	3.69-4.23
S.D.	1.912	0.246	0.578	0.433	1.616	1.146	0.242	0.113	0.157
No.	19	19	19	19	19	19	19	19	19

Oedaleus decorus asiaticus Bei-Bienko, 1941 comb. et stat. n.

Oedaleus asiaticus Bei-Bienko, 1941: 152. Holotype ♂, U.S.S.R.: Buryat A.S.S.R., Kiakhta distr., Ust-Kiakhta, 20.viii.29, (A.N. Strakhovsky), (ZI, Leningrad).

Material examined. Appendix 1, p. 377.

Measurements. Tables 20, 21

Affinities. O. decorus is most closely allied to O. senegalensis, O. nigeriensis, and O. infernalis in having strongly transverse inner lobes to the epiphallic lophi. The red ventral surface of the hind femur is shared with O. infernalis from which however O. decorus is easily distinguished by its general colouration, and the form of the pronotal x-marking and hind wing fascia.

Distribution (Figs 159, 164, and Biogeography section, pp. 170, 179). Europe, North Africa, Middle East, with subspecies decorus extending into SW Russia, and subspecies asiaticus continuing eastwards across Transbaikalia, Mongolia, and China.

Biology. O. decorus has probably received more attention than any other species in the genus except O. senegalensis. Adults of O. decorus decorus are found in N Africa from June until January and in the middle east from April to September. In southern Europe they occur from May to October with a gradually shortening and later season towards the northern limit of the species. O. decorus asiaticus has been recorded in eastern U.S.S.R., Mongolia, and China from July to September. It is probable that one generation is the norm outside Africa. However the longer season in north Africa may allow a second generation, since laying has been reported in July (A-L.R.C. Unpublished Report 6114-135) in Libya. Berezhkov (1956) gives five as the number of nymphal instars. The egg pod has been described by Zimin (1938), and Morales Agacino (1951), who found 10 to 35 eggs per pod. Waloff (1954) records 18 and 20 ovarioles per ovary in two females dissected.

Ivanov (1934) made a study of the biology and ecology of O. decorus in Central Asia and Stebaev (1957a) found that it was seasonally mobile between different types of habitat. It was recorded in the French Alps up to 1300 m by Dreux (1961) who stated that the species distribution in France is bounded by the 16° July isotherm. In U.S.S.R. Bei-Bienko and Mishchenko (1951) regarded it as a characteristic species of stony mountain sides with xerophytic vegetation, and in the Pyrenees Marty (1969) found that this species constituted 20% of all Orthoptera in the littoral zone. In Turkestan (Zacher, 1949) the species lays in damp areas with Cynodon dactylon and Hordeum murinum. O. decorus has been reported damaging wheat, vines, and lentils in Libya (A-L.R.C. Unpublished Report 6114-135), maize and tobacco in Morocco (Lépiney and Mimeur, 1932) and cotton, lucerne, and wheat in Iran (Farahbaksh, 1961). O. decorus asiaticus was described as a pasture pest in Transbaikal region (Bei-Bienko and Mishchenko, 1951a). Predation of adults of O. decorus by asilid flies was reported by Adamovic (1968) and four species of Blaesoxipha (Greathead, 1963; Léonide and Léonide, 1969; 1973) and one Nemestrinid (Léonide, 1963) have been reared from adults. Integumental colouration in relation to humidity temperature, and background colour have been studied by Jovančic (1953) and Ergene (1954, 1955 , 1955a, 1955b, 1956). The thoracic repugnatorial gland has been described by Vosseler (1902b), and Hollande (1926) who considered the gland to be eversible. If this is so it would contrast with the purely internal gland of other Oedaleus species.

Discussion. The measurements and 't' tests given above indicate the very considerable range of variation in morphometrics shown by this species. The largest specimens, judged by femur or tegmen length, are found in Algeria, but from here northwards through western Europe there is a decline in size with specimens from Gironde on the west coast of France significantly smaller than those from the Rhône delta in all respects and with a significantly higher ratio of tegmen length to pronotum length and a significantly thicker femur in relation to its length. Surprisingly, the Rhône delta specimens are closest to those from the western U.S.S.R. in all measurements though differing significantly from them in the female femur length. The western U.S.S.R. material differs significantly in all measurements from material of O. decorus asiaticus from further east though in the two ratios significance is less marked. These differences might suggest morphometric support for the separate species status of asiaticus, but overall there is an equally significant difference between the western U.S.S.R. material and that from the Gironde region of western France. Comparing material of asiaticus with Gironde specimens, differences are generally of low significance (<5 >2%) or none at all excepting pronotum length which in male asiaticus is markedly smaller and the femur length to depth ratio (FL/FD) which is significally smaller in the Gironde population than in asiaticus.

Bei-Bienko and Mishchenko (1951a: 578, 579) distinguish asiaticus from decorus on the basis of minor differences of colouration and shape which have not been found reliable in the material used in this study. At present asiaticus may be considered as a subspecies or race of decorus but may prove on further study not to justify even racial status. Its small size and rounded posterior angle of the pronotum are features also found in specimens from Gironde and elsewhere on the north western limit of the species distribution in France, and are probably a response to harsh conditions in both cases.

1.1.5.11 Oedaleus infernalis Saussure, 1884
(Figs 5,36,52,107-110,164)

Oedaleus (Oedaleus) infernalis Saussure, 1884: 116. LECTOTYPE ♂, JAPAN (NM, Vienna), here designated [examined].

Oedaleus (Oedaleus) infernalis var? Saussure 1884: 117 [based on 1♂, U.S.S.R.: Amur (NM, Vienna), see below].

Oedaleus infernalis var. amurensis Ikonnikov, 1911: 255. LECTOTYPE ♂, U.S.S.R.: Amur (NM, Vienna), here designated. [Emendation attributed erroneously to Saussure, op. cit.] [examined]. Syn. n.

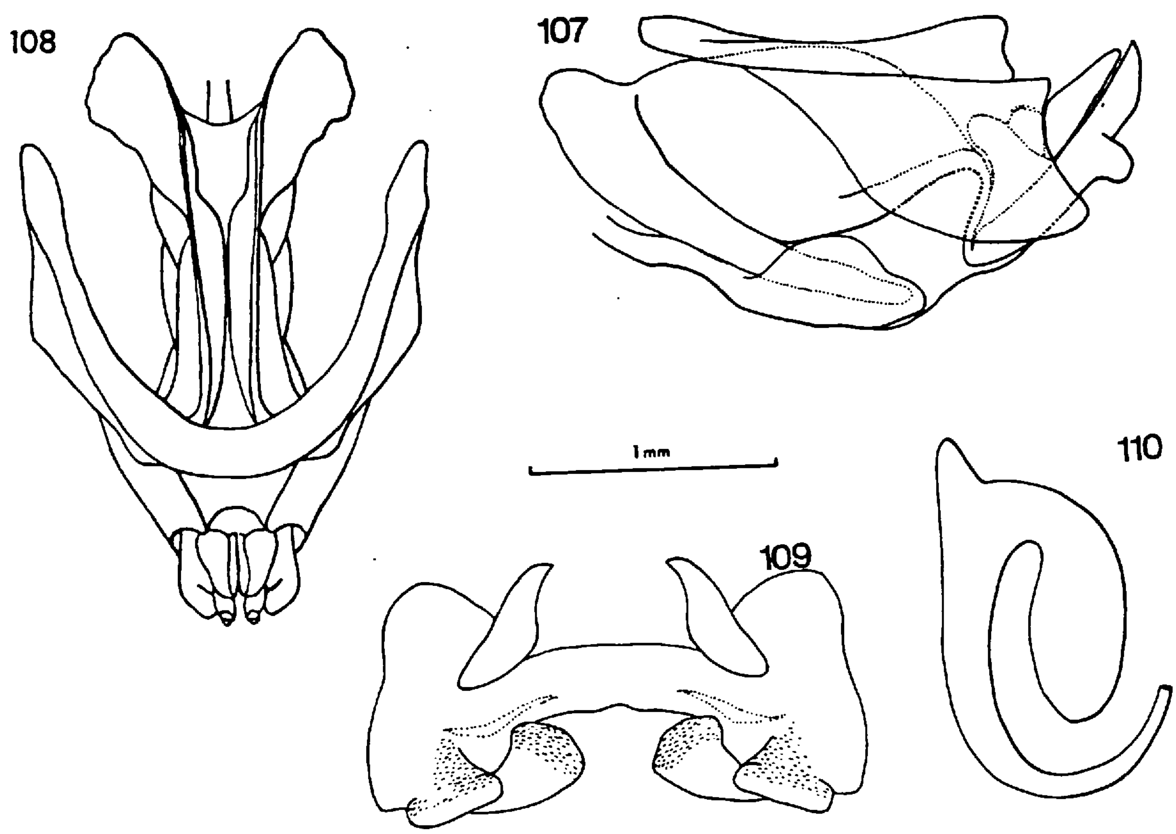
Oedaleus infernalis amurensis Ikonnikov; Bei-Bienko, 1941: 154.

Oedaleus manjius Chang, 1939: 21. Holotype ♂, CHINA: Chekiang, Wenchow, 15.ix.1933, (K.S. Chang) (lost). Syn. n.

Oedaleus infernalis montanus Bei-Bienko, 1951a: 577. Holotype ♂, CHINA, N. slope of Burkhan-Budda, defile Khatu, c.10,800 ft., end VI- beginning VII. 1901, (P.C. Kozlov) (ZI, Leningrad). Syn n.

Oedaleus infernalis (Saussure) Jacobson & Bianchi, 1905: 256.

Redescription. ♂. Integument finely rugulose and pitted. Antennae barely longer than head and pronotum together; flagellum 24 segmented. Fastigium of vertex as long as wide, concave with raised margins, narrowing to half maximum width anteriorly. Frons in profile convex, frontal ridge constricted at vertex and below median ocellus, ventrally obsolescent. Eyes about one and a third times as deep as wide. Pronotum tectiform, median carina arcuate, lateral lobes coarsely punctate in metazona, hind margin acutangular to rectangular. Tegmen surpassing folded hind knees by one quarter to one half of hind femur length. Hind tibia with 12 inner and 12 outer spines; inner apical spurs less than twice outer; apical tarsal segment more than two and a half times claw length; arolium little more than half claw length. Cerci about twice as long as wide. Genitalia (Figs. 107-109): rami, apodemes, cingular and apical penis valves of moderate length; subapical process large and protruding; epiphallus rectangular, twice as long as wide;



Figs 107-110. O. infernalis, genitalia. 107, endophallus & cingulum, lateral; 108, same, dorsal; 109, epiphallus; 110, ♀ spermatheca.

outer lobes of lophi wider than inner lobes; anterior projections large, rounded; posterior projections small.

General colouration dark mottled brown, occasionally green. Brown form with pale x-marking on pronotum (♀, Fig. 36), and pale band on genae; green form with variable degree of green on frons, genae, pronotum (obscuring x-marking), thorax and hind femora. Tegmen infuscate in basal half with four variable pale transverse bands extending from costal margin. First band one sixth along from base reaching subcostal vein, sometimes obsolescent; second band one third along reaching first or second cubitus; third band half along reaching Cu1c or Cu2; fourth band two thirds along variable, often reaching hind margin but without a distinct border towards apex of wing which is clear with variable dark patches. Hind wing fascia (Fig. 5) complete; wing tip infumate, basal area pale yellow. Hind femur with 3 variable oblique transverse dark bands on external and internal surface. On internal surface two basal bands combine to form U-shaped marking in medial area. Ventral surface of hind femur red, sometimes faded; hind knees black; tibiae basally black, subbasally pale straw, (sometimes tinged with red), remainder red.

♀. Larger and more robust. Hind tibiae and ventral surface of hind femur brown, not red. Ventral ovipositor valves (Fig. 52) elongated and ridged; basivalvular sclerite rugose. Spermatheca (Fig. 110) with short conical subapical diverticulum.

Affinities. _O. infernalis_ is most closely related to _O. decorus_ by its overall shape, the continuous band of the hind wing and the red ventral surface of the hind femur. It is however easily distinguished by its more sombre pattern, the poorly defined pronotal x-marking (Fig. 36), and hind wing fascia (Fig. 5), and the rather short cingular rami of the male genitalia (Fig. 108). The bases of the main veins of the hind wing are never tinged with pale blue in this species. In the female the ventral ovipositor valves are longer and more ridged than those of _O. decorus_ (Figs 52, 51).

Material examined. Appendix 1, p. 377.

Measurements. Tables 22 - 25

Distribution (Fig. 164, and Biogeography section, p. 179). Widely distributed in SE Asia.

Biology. Little is known of the biology of this species. Adults are found from July to October. There are records of damage to citrus (Chen & Wong, 1936), rice (Cheo, 1937; Shiraki, 1952) and sugar cane (Butani, 1961; Box, 1953), the latter from almost every country in

Table 23

Measurements contd. ("amurensis", E. Manchuria and Ussuri region of U.S.S.R., including lectotype): Oedaleus infernalis Saussure

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	25.9	3.71	4.66	4.75	19.01	12.98	3.30	3.96	4.08
Range	23.7 - 30.6	3.55- 4.05	4.25- 5.05	4.1 - 5.55	17.1 - 23.2	11.95- 14.3	3.05- 3.65	3.5 - 4.33	3.39 4.36
S.D.	1.957	0.163	0.350	0.367	1.608	0.870	0.178	0.185	0.158
No.	12	13	13	13	13	13	12	12	13
♀ Mean	38.71	5.66	7.05	7.47	28.65	18.58	4.71	3.95	4.06
Range	34.55- 46.75	5.2 - 6.35	6.3 - 8.2	6.75- 8.25	25.3 - 35.7	17.25- 19.1	4.35- 5.3	3.61- 4.15	3.83- 4.36
S.D.	3.806	0.394	0.654	0.459	3.295	1.180	0.319	0.163	0.201
No.	10	10	10	10	10	9	9	9	10

Table 24

Measurements contd. ("montanus" ♂ paratype and 2♀ from Lifan, Szechuan)): Oedaleus infernalis Saussure

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂	22.6	3.65	4.25	3.95	15.9	12.25	3.35	3.66	3.74
♀	38.3	6.15	7.95	8.85	28.05	20.55	5.55	3.70	3.53
♀	53.9	7.65	10.2	9.35	40.25	23.15	5.95	3.89	3.95

Table 25

Measurements contd. ("menjius", Szechuan, Wei Chow, 65 mls N.W. of Chengtu, 5 000 ft, -.viii.33 (Graham)): *Oedaleus infernalis* Saussure

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	26.01	4.04	5.02	5.26	18.65	13.98	3.77	3.70	3.71
Range	23.35-29.15	3.7 - 4.4	4.5 - 5.75	5.0 - 5.65	16.5 - 21.85	13.35-14.75	3.65-3.95	3.61-3.83	3.43-3.89
S.D.	2.039	0.198	0.352	0.220	1.766	0.449	0.096	0.077	0.149
No.	12	12	12	12	12	8	8	8	12
♀ Mean	36.01	5.96	7.33	7.79	25.83	18.75	5.0	3.76	3.53
Range	32.1 - 40.25	5.4 - 6.75	6.4 - 8.4	7.0 - 8.6	23.3 - 29.25	17.05-20.4	4.55-5.75	3.51-4.16	3.35-3.82
S.D.	2.097	0.320	0.509	0.424	1.491	1.011	0.294	0.140	0.135
No.	25	25	25	25	25	25	25	25	25

Table 26

Measurements (all known specimens): *Oedaleus formosanus* (Shiraki)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	25.82	3.94	4.89	4.68	18.2	12.91	2.98	4.35	3.71
Range	22.45-29.55	3.65-4.5	4.45-5.5	4.2 - 5.0	15.65-20.9	12.05-14.35	2.4 - 3.25	4.13-5.02	3.52-3.95
S.D.	2.337	0.292	0.365	0.290	1.754	0.833	0.287	0.312	0.156
No.	6	7	7	7	6	7	7	7	6
♀ Mean	34.34	5.94	7.16	7.2	23.97	17.74	4.25	4.17	3.34
Range	29.85-41.0	5.55-6.65	6.5 - 8.55	6.9 - 7.95	19.7 - 29.25	15.9 - 20.85	3.95 - 4.8	3.83-4.34	3.03-3.48
S.D.	4.725	0.487	0.944	0.502	3.950	2.15	0.376	0.231	0.207
No.	4	4	4	4	4	4	4	4	4

which the insect is found. The records of rice damage in Taiwan (Box, 1953; Bei-Bienko and Mishchenko, 1951; Cheo, 1937) have not been confirmed by examination of specimens during this study, though the species may be expected to occur there. Genetical studies of O. infernalis have been made by Lu (1951-2), Kawamura (1957), Takizawa and Narasawa (1971), and Inoue (1972). The Meloid beetle Epicauta gorhami was recorded as an egg predator in Japan (Nagatomi and Iwata, 1958).

Discussion. At the commencement of this study there were two recognised subspecies of Oedaleus infernalis, and one closely related species, O. manjius Chang. All three taxa are here synonymised because the characters given by Chang (1939) and by Bei-Bienko and Mishchenko (1951a) cannot be considered sufficient to differentiate populations at species or subspecies level when comparative examination has been made of material from the whole range of the species.

Oedaleus infernalis was originally described from Japan. No locality was given but the species is known to extend from Kyushu island in the south to at least the central region of Honshu island in the north. Measurements for a series from Japan are given above (p. 97). The subspecies O. infernalis amurensis Ikonnikov was an emendation by Ikonnikov of the unnamed variety O. infernalis var? from Amur described by Saussure (1884: 117). The varietal name amurensis, incorrectly attributed by him to Saussure, should therefore be considered as his own, as was correctly assumed by Bei-Bienko and Mishchenko (1951a: 577) when elevating the variety to subspecific status. However, because Ikonnikov attributed his name to Saussure he therefore did not designate his material as types or place the words "*var. n.*" after the name as he did elsewhere in the same paper when describing new taxa. In any case his material, originally housed in the Zoologischen Museum der Kais, Moscow University, is presumably lost to science. The unique male in Saussure's collection at Geneva is here regarded as the type and accordingly designated as the lectotype of *Oedaleus infernalis amurensis* Ikonnikov, 1911. Measurements of a series of specimens of both sexes from the type locality are given above together with measurements of the lectotype (p. 106). Compared to Japanese specimens they are noticeably smaller though the ranges overlap. However the shape, as judged by TL/PL and the length/depth ratio of the hind femur, is substantially identical.

Oedaleus manjius Chang, 1939 was described from material collected in Chekiang and Szechwan provinces of China. The measurements of a series collected at 5,000 feet in Szechwan and loaned to me by Dr. A.B. Gurney of the United States National Museum, Washington are given above (p. 107). The series was studied by Chang and one specimen (not measured) had been labelled "*Oedaleus wenchowensis* Chang, det. Chang 1936". I am indebted to Dr. Gurney for the following information:

"Chang's material, which had been borrowed here, was never returned from China, so that we do not have types or other material except what he named while in the United States, where he studied at Cornell University. In China he was at St. John's University, Shanghai, but whether anything of his remains there is unknown to us here. It is probable that he did not survive the war. My last word from him was in April 1939, at which time conditions there were very much upset.

The name Oedaleus wenchowensis Chang which he placed on a label here in 1936 evidently applies to what he described in 1939 as O. manjius, the former just being a manuscript name of no permanent validity. I knew K.S. Francis Chang here in the summer of 1936 when he visited for perhaps a week, a fine appearing, most friendly and cooperative young man seemingly of great promise. His use of English and knowledge of many things in this country were superior to my own in many ways, and his later apparent loss after returning to China was thought of by those here who knew him as a great tragedy."

Unfortunately Chang's diagnostic characters for O. manjius are unreliable since specimens from one locality exhibit great variation in minor details of the morphology of the head and pronotum and the colour of the hind tibiae and the ventral surface of the hind femora, all characters which he considered as conclusive in distinguishing his species from O. infernalis.

Oedaleus infernalis montanus Bei-Bienko, 1951 was described from material collected in "Szechwan, Nan Shan Mts., and range of Burkhan-Budda". The male only was described and distinguished by its author from other subspecies by the colour of the hind femora, by its small size, and by minute differences in the length of the "median segments of antennae". Of these characters only size is of any objective validity. The holotype was unavailable for study but the measurements of a paratype from Lifan are given above. Bei-Bienko and Mishchenko (1951a: 577) gave the range of tegmen length of the type series as 16.5-20.0 mm though the specimen measured here is actually smaller than this. Measurements of two females from near Lifan are given for comparison. One of these is very large indeed, suggesting that the

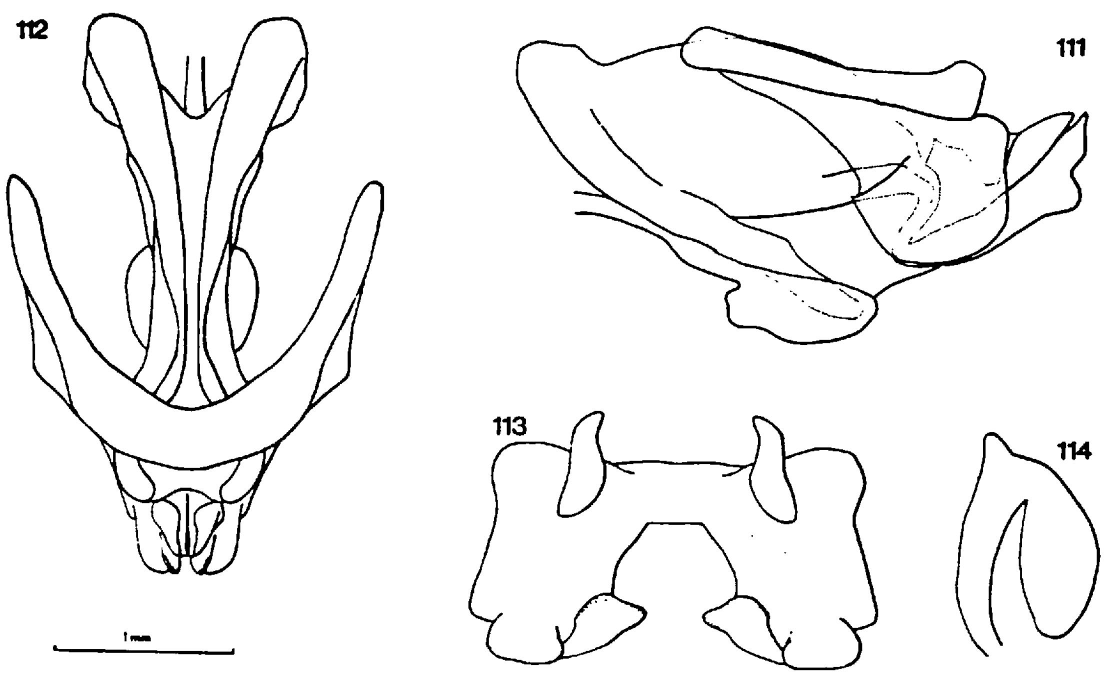
Himalayan population is not composed exclusively of dwarf individuals, though doubtless specimens caught at high altitude have a tendency to small size and relatively short tegmina and hind femora, a well known phenomenon in montane Acridoidea (Uvarov, 1977: 436). Tegmen length of Bei-Bienko's series has an almost identical range to that of the specimens studied by Chang mentioned above and overall there is consistency within the material from south west China. From the measurements given it is evident that the TL/PL ratio is different for both sexes of the Szechuan population compared to the L. Khanka population which is essentially lowland-living (♂♂: $t = 6.03$, $P < 0.01$; ♀♀: $t = 7.67$, $P \ll 0.001$). A careful analysis of the effects of altitude on morphometrics in this species would be most interesting but at present there is no evidence of any genuinely geographically based variation worthy of subspecies status. In any case morphometric variation even within one population is so great that subspecies divisions based on only a few specimens from widely scattered localities are biologically meaningless.

1.1.5.12 Oedaleus formosanus (Shiraki, 1910) comb. n.
(Figs 7,38,53,111-114,164)

Oedipoda formosana Shiraki, 1910: 89. NEOTYPE ♂, TAIWAN: Taikaizan (BMNH), here designated [examined].

♂. Integument finely rugulose and sparsely hairy. Antennae about one and a third times as long as head and pronotum together, flagellum with 19 segments. Fastigium of vertex longer than wide, narrowing to half maximum width anteriorly, concave, with raised margins; frons in profile flat, frontal ridge narrowed just below vertex and again just below median ocellus. Eyes nearly one and a half times as deep as wide; genae sparsely hairy. Pronotum tectiform, finely rugose and pitted; median carina arcuate, intersected by posterior sulcus; lateral lobes of pronotum sparsely covered with long hairs; hind margin nearly rectangular; lateral surface of meso-and metathorax sparsely hairy. Tegmen surpassing folded hind knees by less than one quarter of hind femur length. Hind tibia with 10 outer and 11 inner spines; inner apical spurs about one and a half times as long as outer; apical tarsal segment three times as long as claw; arolium more than one third length of claw. Cerci more than two and a half times as long as wide. Genitalia (Figs. 111-113): cingular apodemes medium length, strongly curved, zygoma thickened; rami short, cingular and apical penis valves short, the latter with acute apices; subbasical ventral process tumuliform; epiphallus long and broad with deeply arched bridge; lophi large, outer lobes wider than inner; anterior projections large, rounded, posterior projections rectangular.

General colouration brown, with darker brown markings. Head brown with oblique dark striations on genae and frons, vertex speckled. Pronotal x-marking forming a light area on shoulders of pronotum bounding dark medial area on dorsum; lateral surface of pronotum and meso- and metanotum with variable light and dark specks. Tegmen



Figs 111-114. O. formosanus, genitalia. 111, endophallus & cingulum, lateral; 112, same, dorsal; 113, epiphallus; 114, ♀ spermatheca.

infuscate brown throughout except for irregular pale triangle on costal margin one third along from base and transparent specks in apical half visible when wing is open. Hind wing fascia (Fig. 7) complete and fusing posteriorly with infuscate wing tip; basal area pale greenish yellow. Outer surface of hind femora with three oblique dark bands, inner surface with three transverse bands partially elided; interior ventral carina and ventral surface of hind femur scarlet; hind knees black; hind tibiae with thin black basal ring, otherwise coral to scarlet.

♀. Larger and more robust. Frons in profile convex. Ventral ovipositor valves (Fig. 53) narrow, almost triangular, strongly sclerotised, with curved apices. Spermatheca (Fig. 114) with apical diverticulum abruptly rounded apically, with conical subapical diverticulum.

Affinities. _O. formosanus_ appears to be most closely allied to _O. infernalis_, but is quite distinct by virtue of its dark colouration and the extensive shading of the hind wing (Fig. 7), both features which are common to many high altitude oedipodine grasshoppers.

Measurements. Table 26

Material examined. Appendix 1, p. 377.

Distribution (Fig. 164, and Biogeography section, p.179). Known only from montane areas of Taiwan.

Biology. Unknown.

Discussion. This species was not fully described by Shiraki (1910), probably as a result of an oversight, and it is known only from Plate II fig. 3 and the legend '*Oedipoda formosana* n. sp.'. In 1929, four specimens of this species were donated to the British Museum (Natural History) via the Commonwealth Institute of Entomology, and these were entered in the C.I.E. donations book on April 6th as four cotypes of *Oedaleus formosanus*. There are a number of problems posed by this situation. Firstly, only the two females actually bear manuscript labels identifying them as cotypes, though it is probable that in his correspondence with C.I.E. Shiraki described them all as cotypes. This cannot now be verified since all pre-war C.I.E. correspondence was pulped during World War II. The second problem is that specimens collected several years after the publication of a species cannot possibly be cotypes (or in modern usage, syntypes). It is conceivable that they were designated in a later publication, but if so this cannot now be traced. What is clear is that by 1929 Shiraki had realised that his species was an *Oedaleus* and he labelled the specimens he sent to C.I.E. accordingly. However, since no publication of this combination is known, it is here given as a new combination. Presumably Shiraki had specimens before him when writing his 1910 paper which he intended to designate as types but this material is now apparently lost. Dr Syoziro Asahina has kindly checked Shiraki's collection at Hokkaido University, Sapporo, and he informs me that there is no named specimen of *Oedipoda formosana*. For this reason, and to establish the identity of the species, one male from Shiraki's later series is here designated as neotype.

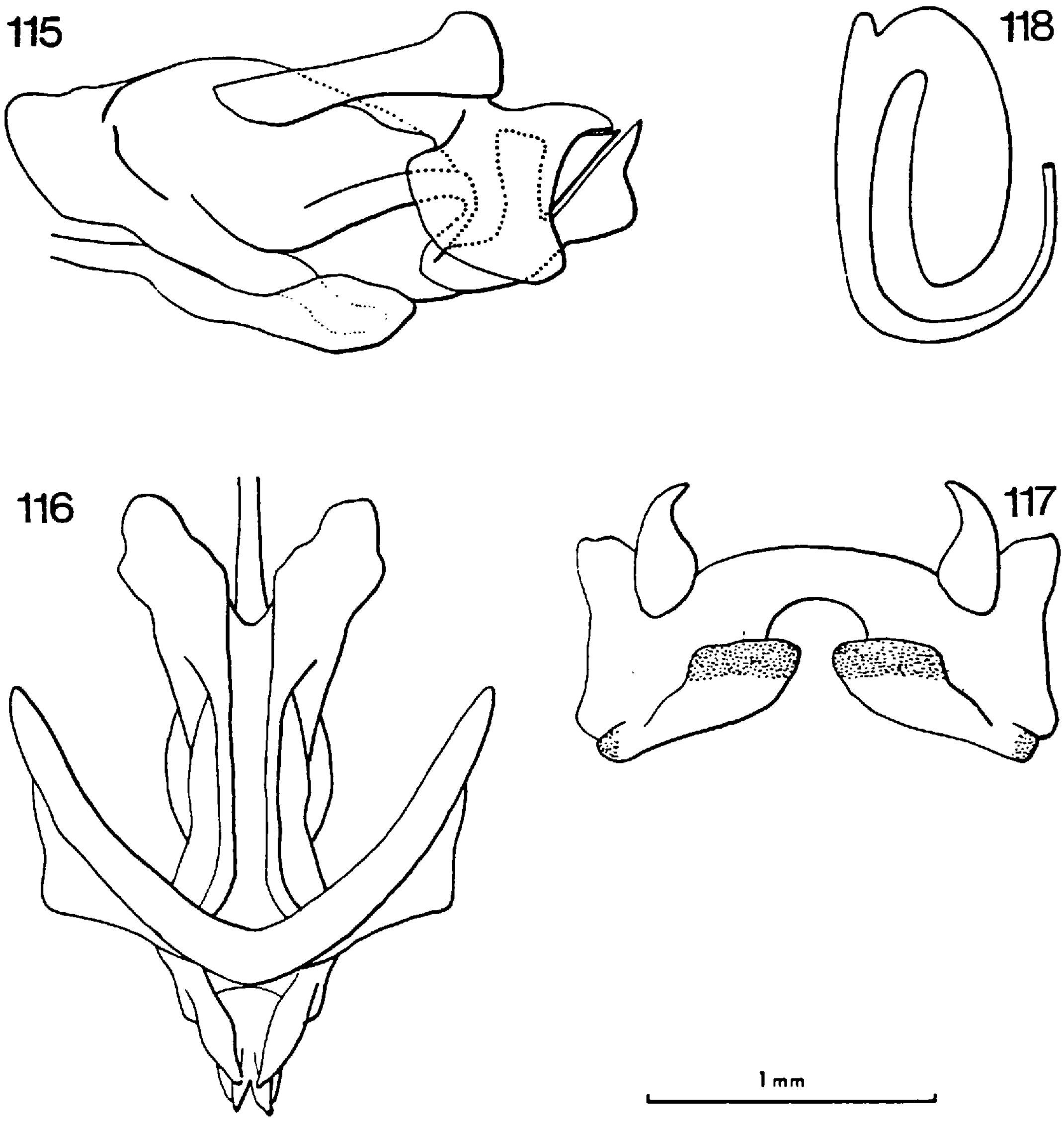
1.1.5.13 Oedaleus interruptus (Kirby 1902)
(Fig. 13,26,46,115-118,152)

Chortoicetes interruptus Kirby, 1902a: 232. LECTOTYPE ♂, SOUTH AFRICA: Transvaal (BMNH), here designated [examined].

Oedaleus interruptus (Kirby) Uvarov, 1925: 275.

Redescription. ♂. Integument finely rugulose and pitted. Antennae one and a quarter times as long as head and pronotum together; flagellum 20 segmented. Fastigium of vertex subtriangular, longer than wide with well defined margins, narrowing anteriorly to one third of maximum width. Frons in profile slightly convex. Frontal ridge slightly expanded dorsal to median ocellus, ventrally obsolescent. Eyes about one and a third times as deep as wide. Pronotum low tectiform, median carina arcuate, blade-like, not intersected by posterior sulcus. Posterior margin of pronotum acutangular to rectangular. Tegmen surpassing folded hind knees by one fifth to one third of hind femur length. Hind tibia with 11-12 inner and 11-13 outer spines. Inner apical spurs about one and a half times as long as outer. Apical tarsal segment about twice length of claw, arolium half length of claw. Cerci elongate more than two and a half times as long as wide. Genitalia (Figs. 115-117): cingular apodemes short, of medium thickness; rami long, slender; cingular and apical penis valves short, subapical ventral process large; epiphallus rectangular, bridge narrow, inner lobes of lophi three times as wide as outer lobes.

General colouration variable, brown, with lighter brown or green markings on vertex, frons, genae, pronotum, dorsal and lateral surface of folded tegmina and dorsal surface of hind femora. Pale x-marking of pronotum thin and distinct (♀ Fig. 26). Tegmen infuscate brown or brown and green in basal half with four pale transverse bands one quarter, one third, one half, and three fifths along from base; apical two fifths clear with variable smoky patches. Hind wing fascia (Fig. 7)



Figs 115–118. O. interruptus, genitalia. 115, endophallus & cingulum, lateral; 116, same, dorsal; 117, epiphallus; 118, ♀ spermatheca.

narrowly interrupted between second cubitus and first anal vein, or more widely, reaching margin of wing posteriorly; wing tip sometimes slightly infuscate, basal area of wing pale yellow. Hind femur with two transverse brown bands on external upper marginal area and one longitudinal brown streak on external medial area; ventral surface of hind femur suffused (often indistinctly) with rose pink. Hind tibia basally pale straw, otherwise brown suffused with pink. Hind knees brown or greenish.

♀. Larger and more robust. Ventral ovipositor valves (Fig. 46) moderately sclerotised, slender. Spermatheca (Fig. 118) with finger-like subapical diverticulum.

Affinities. O. interruptus is probably most closely related to O. carvalhoi with which it shares the characteristics of very fine x-markings on the pronotum, red hind tibiae and undersides of hind femora, and incomplete wing band. It is easily distinguished by its smaller and slenderer appearance and the acutely angled pronotal hind margin, an unusual feature in Oedaleus.

Material examined. Appendix 1, p. 377.

Measurements. Table 27

Distribution (Fig. 152, and Biogeography section, p. 158). Known only from eastern montane areas of South Africa.

Biology. Unknown. There is one report of damage to wheat at Bloemfontein (13.iv.51, D.H. Botha) recorded in the C.O.P.R. collection index: 'The edges of the fields were severely damaged and in some cases had to be reploughed and resown. The fliers mostly roosted in grass outside the wheat fields and flew into them daily to feed on the green wheat'.

Table 27
Measurements (all available material):
Oedaleus interruptus (Kirby)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	23.18	3.63	4.49	4.33	17.28	12.57	3.2	3.93	3.87
Range	21.1 - 25.05	3.35- 3.95	4.0 - 5.15	3.85- 4.8	15.45- 19.05	10.95- 13.55	2.85- 3.6	3.76- 4.19	3.49- 4.32
S.D.	1.06	0.195	0.356	0.253	1.047	0.786	0.230	0.120	0.234
No.	9	11	10	10	11	10	10	10	10
♀ Mean	27.68	4.64	5.08	5.41	20.08	13.82	3.53	3.92	3.97
Range	25.1 - 31.6	4.25- 5.0	4.1 - 5.9	4.95- 6.1	17.9— 22.85	12.65- 15.85	3.15 - 4.0	3.77- 4.11	3.64- 4.51
S.D.	2.052	0.240	0.430	0.339	1.566	0.998	0.267	0.111	0.262
No.	12	13	12	13	13	12	12	12	12

Table 28
Measurements (Kenya, El Wak, 2°47'N, 40°55'E, 5.xii.44., (Kevan)):
Oedaleus instillatus Burr

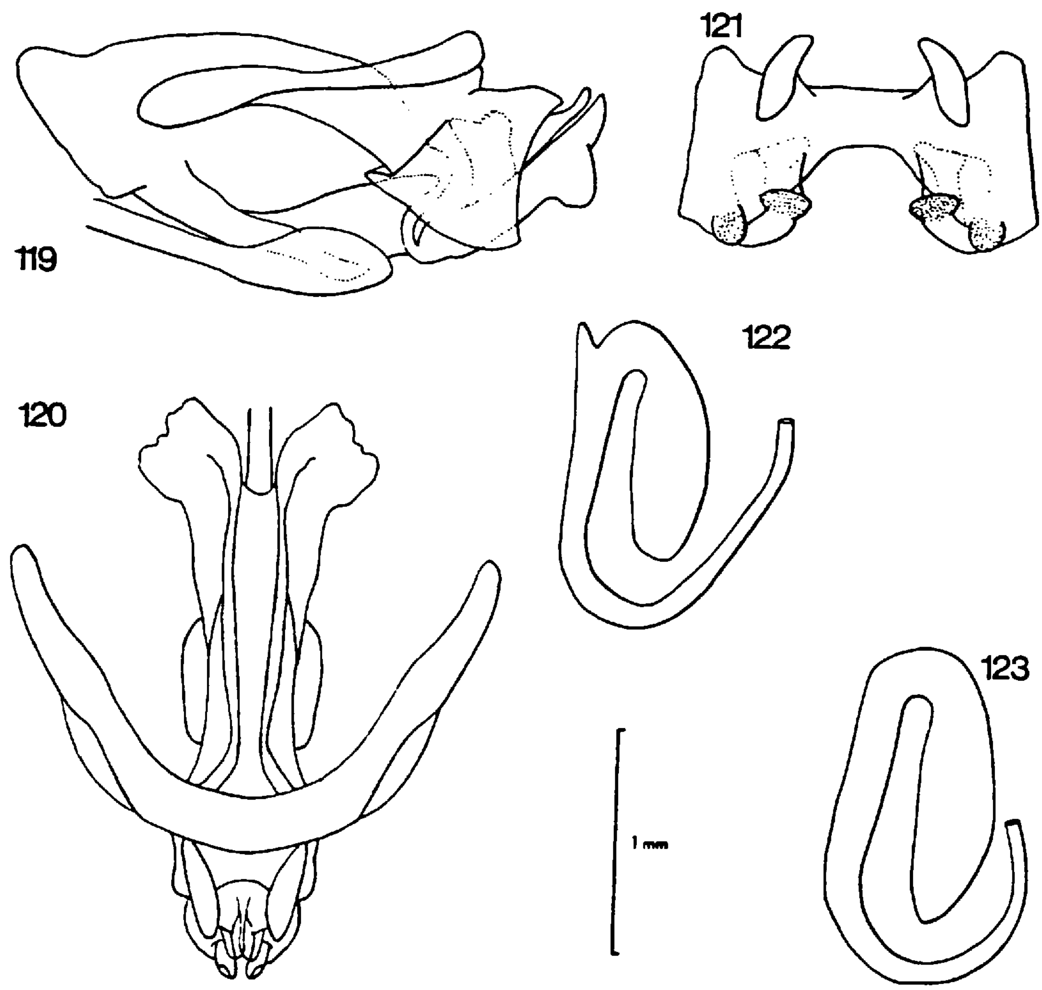
	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	26.97	3.56	4.59	4.76	18.97	11.9	3.01	4.16	4.14
Range	23.85- 27.6	3.3 - 3.85	4.2 - 5.3	4.25- 5.15	17.55- 20.7	11.2 - 12.75	2.8 - 3.2	3.7 - 6.9	3.56- 4.59
S.D.	7.045	0.142	0.287	0.238	0.82	0.411	0.125	0.795	0.259
No.	28	29	26	29	29	14	14	14	25
♀ Mean	32.61	4.90	5.77	6.33	24.11	15.15	3.83	3.95	4.20
Range	28.2 - 37.3	4.35- 5.75	4.65- 6.9	5.5 - 7.35	22.0 - 27.35	12.95- 18.0	3.3 - 4.5	3.83- 4.13	3.61- 4.71
S.D.	1.946	0.339	0.589	0.466	1.429	1.404	0.328	0.106	0.316
No.	25	24	25	25	25	14	14	14	25

1.1.5.14 Oedaleus instillatus Burr, 1900 (Figs 12,33,56,119-123,156)

Oedaleus instillatus Burr, 1900: 39. LECTOTYPE ♂, SOMALI REPUBLIC (UM, Oxford), here designated [examined].

Redescription. ♂. Integument finely rugulose and pitted. Antennae one and a quarter times as long as head and pronotum together; flagellum with 22 segments. Fastigium longer than wide, concave, narrowing to two fifths of maximum width anteriorly; frons in profile slightly convex; frontal ridge slightly expanded at and narrowed below median ocellus. Eyes one and a third times as deep as wide. Pronotum tectiform; median carina arcuate not intersected by posterior sulcus; hind margin rectangular to acutangular. Tegmen surpassing folded hind knees by one third to one half of femur length. Hind tibia with 12 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and a half times claw length; arolium two fifths of claw length. Cercus one and four fifths as long as wide. Genitalia (Figs 119-123): cingular apodemes of moderate thickness and curvature; rami fully developed with cingular and apical penis valves short; subapical ventral process large; epiphallus rectangular, inner and outer lobes of lophi small, subequal; anterior projections rounded, acute; posterior projections obtusangular.

General colouration variable, brown, with lighter brown (or, rarely, pale green) markings on frons, vertex, genae, pronotum, and dorsal surface of folded hind tegmina and hind femora. Tegmen infuscate in basal two thirds with three pale transverse bands situated one third, one half, and two thirds along from base, commencing from costal margin. Hind wing fascia (Fig. 12) complete, reaching hind margin of wing, basal area pale yellow, wing tip infuscate. Hind femur with three oblique transverse bands on external medial and upper marginal areas; internal surface with basal pair of bands elided to form dark area;



Figs 119-123. O. instillatus, genitalia. 119, endophallus & cingulum, lateral; 120, same, dorsal; 121, epiphallus; 122, ♀ spermatheca.

ventral surface pale red; hind knees dark brown, hind tibia with dark basal ring, thick subbasal pale area, otherwise pale red.

♀. Larger and more robust. Hind femur and tibia with very pale red pigment often appearing light brown. Ventral ovipositor valves (Fig. 56) elongate, moderately sclerotised, with exterior margin deeply incurved. Spermatheca (Fig. 122) with or without a short finger-like subapical diverticulum.

Affinities. O. instillatus is allied to O. rosescens and O. obtusangulus on the basis of its epiphallus morphology (Fig. 121), the lophi being small and of nearly equal size. It also shares with them its sombre colouration, green forms being relatively rare. This reflects the open dry habitats favoured by these species.

Material examined. Appendix 1, p. 377.

Measurements. Table 28

Distribution (Fig. 156, and Biogeography section, p. 167). Widely distributed and common throughout the drier areas of eastern Africa.

Biology. Almost nothing is known of the biology of this common species. from label data it is apparent that adults may be seen at all times of the year. One hopper has been collected in January and one copulation observed in May. It is notable that specimens are rarest in March and July, both months of low rainfall, the latter also having lowest temperatures. Peak numbers have been collected in May and November, in each case one month after the two months of peak rainfall (Griffiths, 1972: 139). It is clear that there are at least two generations corresponding to these peaks and perhaps more in years of above-average rainfall. There is one record of night-flying 'swarms' of O. instillatus observed at El Wak in NE Kenya, on 5.xii.44 between 20.00 and 22.00 h (Kevan & Knipper, 1955: 312) but no details of density or behaviour were given. The measurements given in Table 28 are for a series from this swarm.

1.1.5.15 Oedaleus obtusangulus Uvarov, 1936

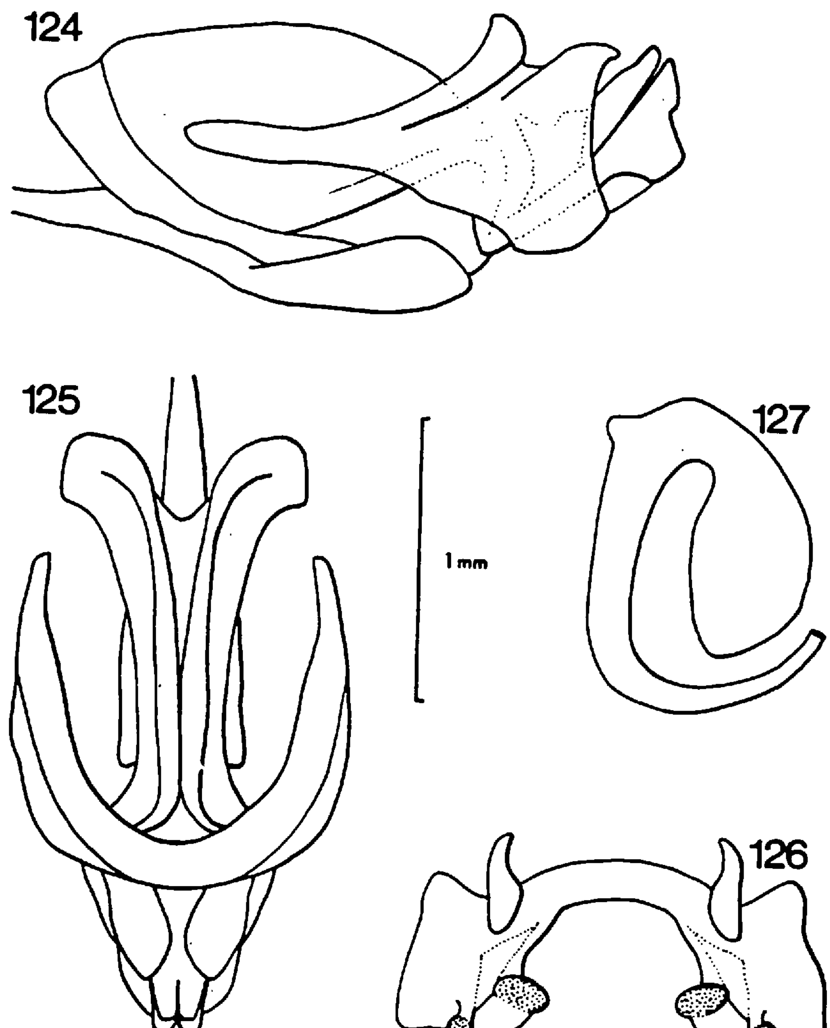
(Figs 3,35,55,124-127,156)

Oedaleus obtusangulus Uvarov, 1936: 542. Holotype ♀, ARABIA (BMNH) [examined].

Oedaleus villiersi Chopard, 1950: 139. Holotype ♀, NIGER REPUBLIC (MNHN, Paris) [examined]. Syn. n.

Redescription. ♂. Integument finely rugulose and pitted. Antennae one and a third times as long as head and pronotum together, flagellum with 22 segments. Fastigium of vertex longer than wide narrowing to half maximum width anteriorly, concave with raised margins; frons in profile slightly convex; frontal ridge constricted at vertex, slightly widened between antennal bases, constricted below median ocellus. Eyes one and a third times as deep as wide. Pronotum tectiform, rugose, with deep sulci; median carina arcuate, hind margin rectangular to obtusangular. Tegmen surpassing folded hind knees by one half to one third of length of hind femur. Hind tibia with 11 inner and 10-11 outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment twice length of claw; arolium less than half length of claw. Cerci twice as long as basal width. Genitalia (Figs. 124-126): cingular apodemes long, strongly curved; rami well developed; cingular and apical penis valves short; subapical ventral process large; epiphallus elongate trapezoidal with thin arched bridge; inner lobes of lophi small, twice as wide as outer lobes; anterior projections large, rounded acutangular; posterior projections smaller rounded acutangular.

General colouration greyish brown with lighter markings on frons, genae, pronotum, tegmina, and hind femora. Tegmen infuscate in basal half, with two irregular pale transverse bands extending from costal margin, first band one third along from base reaching at least to subcostal vein, sometimes to second cubitus posteriorly; second band



Figs 124-127. O. obtusangulus, genitalia. 124, endophallus & cingulum, lateral; 125, same, dorsal; 126, epiphallus; 127, ♀ spermatheca.

half way along wing reaching first cubitus posteriorly. Apical third of tegmen clear with variable degree of infuscate speckling. Hind wing fascia (Fig. 3) variable in emphasis, widely but variably interrupted around first cubitus reaching hind margin of wing posteriorly; basal area pale yellow or colourless. Hind femur with three variable transverse markings on external and internal upper marginal area extending indistinctly obliquely forward across external medial area; inner and ventral surfaces of hind femur straw coloured; hind tibia with dark basal ring, subbasal pale area, otherwise straw coloured.

♀. Larger and more robust. Ventral ovipositor valves (Fig. 55) elongate, weakly sclerotised, laterally excavated; basivalvular sclerite smooth. Spermatheca (Fig. 127) with short rounded apical diverticulum and very short subapical diverticulum.

Affinities. O. obtusangulus is most closely allied to O. instillatus and O. rosescens on the basis of general shape and colour and in particular the morphology of the epiphallus, which in all three species has small inner and outer lobes of equal size.

Material examined. Appendix 1, p. 378.

Measurements. Tables 29, 30

Distribution (Fig. 156, and Biogeography section, p.156). This species has a relict montane distribution in the western Sahara and south west Arabia.

Biology. Unknown.

Table 29

Measurements (Arabia, various localities):

Oedaleus obtusangulus Uvarov

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	21.52	3.32	3.85	4.36	15.62	10.08	2.72	3.71	4.08
Range	18.6 - 24.0	2.9 - 3.45	3.55-4.25	3.7 - 4.9	13.75-17.5	9.15-11.55	2.25-3.05	3.54-3.98	3.61-4.63
S.D.	1.339	0.171	0.280	0.278	1.007	0.672	0.202	0.123	0.269
No.	20	21	21	21	20	21	21	21	20
♀ Mean	28.43	4.62	5.21	6.12	20.44	13.61	3.59	3.79	3.93
Range	25.25-32.9	4.1 - 5.3	4.65-6.1	5.25-6.6	18.1 - 23.9	11.9 - 15.45	3.1 - 4.0	3.55-4.11	3.65-4.29
S.D.	2.079	0.381	0.393	0.371	1.474	0.976	0.236	0.147	0.164
No.	16	16	16	15	16	16	16	16	16

Table 30

Measurements contd. (Niger Republic: Aïr, all available material of "villiersi"):

Oedaleus obtusangulus Uvarov

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂	23.05	3.45	4.15	4.6	17.0	10.9	2.85	3.82	4.10
Paratype ♂	21.95	3.2	3.8	4.2	16.4	9.7	2.8	3.46	4.32
Paratype ♂	23.8	3.45	4.1	4.8	17.75	10.4	2.7	3.85	4.33
Paratype ♀	28.7	4.85	5.35	6.35	20.9	13.35	3.8	3.51	3.91
Holotype ♀	28.1	4.6	5.25	6.1	20.4	13.65	3.65	3.74	3.89

Discussion. The measurements given above indicate that the few known specimens of *O. villiersi* fall well within the range of size of *O. obtusangulus*. In all other respects the two separated populations appear to be morphologically identical. Chopard was probably unaware of the Arabian species previously described by Uvarov when he described *O. villiersi*.

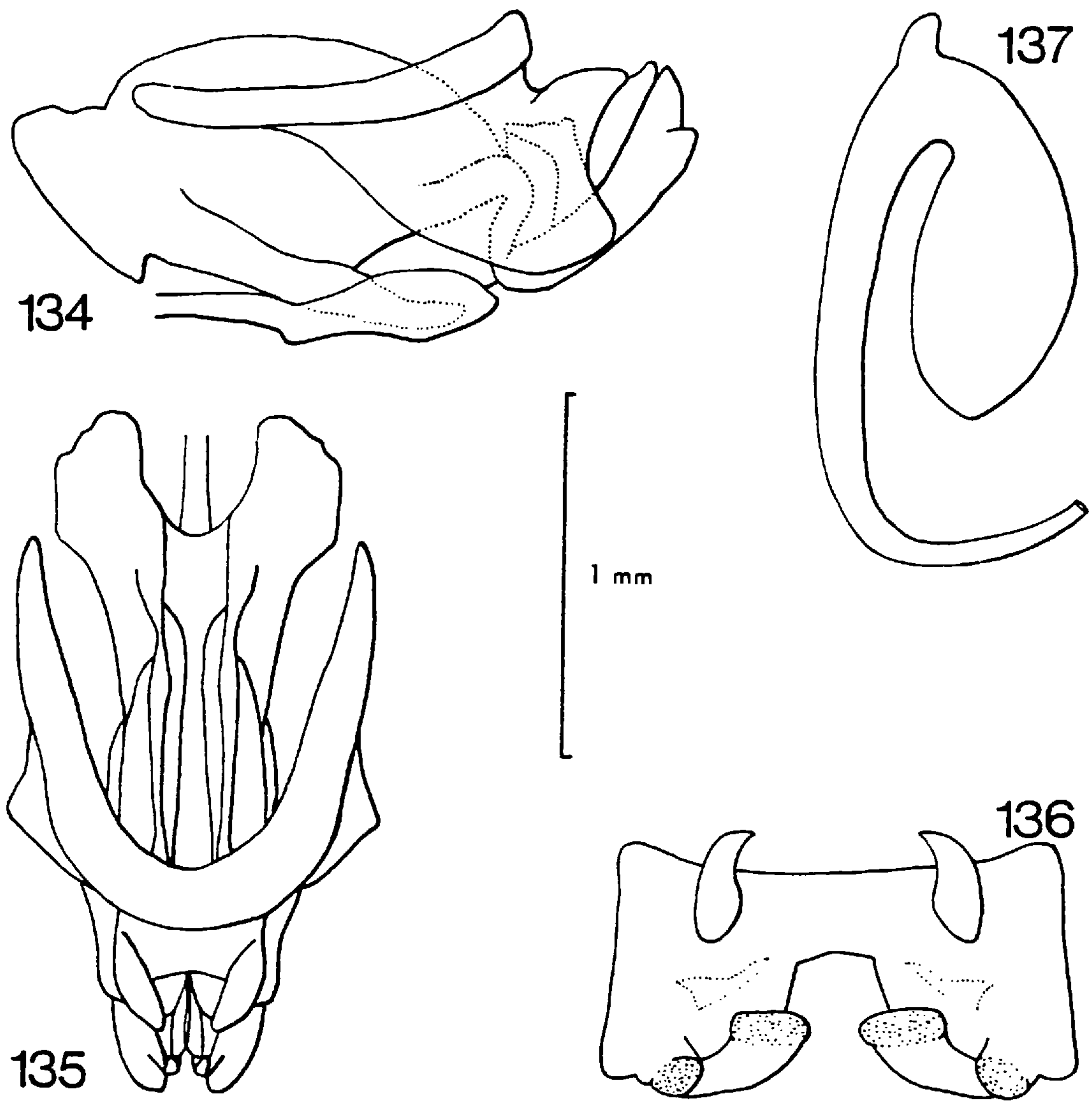
1.1.5.16 Oedaleus rosescens Uvarov, 1942

(Figs 4,31,54,134-137,158)

Oedaleus rosescens Uvarov, 1942: 582. Holotype ♂, INDIA (BMNH) [examined].

Redescription. ♂. Integument finely rugulose and pitted. Antennae one and a half times as long as head and pronotum together; flagellum with 22 segments. Fastigium of vertex much longer than wide, concave, narrowing to about half of maximum width anteriorly, with well-defined margins; frons in profile convex; frontal ridge slightly expanded at median ocellus. Eyes 1.3 times as deep as wide. Pronotum low tectiform; median carina arcuate, barely intersected by posterior sulcus; hind margin obtusangular. Tegmen surpassing hind knees by about one third of hind femur length. Hind tibia with 10 outer and 11 inner spines; inner apical spurs one and a half times as long as outer; apical tarsal segment twice claw length; arolium half claw length. Cerci twice as long as basal width. Genitalia (Figs. 134-136): cingular apodemes long and strongly curved; rami well-developed with short cingular valves and apical penis valves; subapical ventral process small; epiphallus rectangular with narrow thick straight bridge angled within; inner lobes of lophi one and a half times wider than outer lobes; ancorae small; anterior and posterior projections rounded rectangular.

General colouration reddish brown with lighter brown markings on frons, genae, pronotum, tegmina and hind femora. Tegmen infuscate brown in basal half, with irregular pale transverse band extending from costal margin to first cubitus posteriorly, situated one third along from base, second transverse band reaching first cubitus about half way along wing; apical third of tegmen clear with variable brown speckling. Hind wing fascia (♀ Fig. 4) complete, slightly sigmoid, reaching hind margin of wing; basal area of wing pale pink. Hind



Figs 134-137. *O. rosescens*, genitalia. 134, endophallus & cingulum, lateral; 135, same, dorsal; 136, epiphallus; 137, ♀ spermatheca.

femur with three indistinct transverse dark markings on external upper marginal area. Internal lateral surface of hind femur black in basal half with black transverse band one third back from apex; ventral surface of hind femur pink, hind knee internally black; hind tibia with dark basal ring, subbasal pale area, otherwise pale pink.

♀. Larger and more robust. Ventral ovipositor valves (Fig. 54) short with strongly curved apices. Spermatheca (Fig. 137) with apical diverticulum rounded, with short subapical diverticulum.

Affinities. O. rosescens is most closely allied to O. instillatus and O. obtusangulus on the basis of general shape and colouration and more specifically the epiphallus shape (Fig. 136). It is however quite distinct by virtue of the continuous fascia (Fig. 4) and pink basal area of the hind wing.

Material examined. Appendix 1, p. 378.

Measurements. Table 31.

Distribution (Fig. 158, and Biogeography section, p. 169). NW India and NE Pakistan.

Biology. Unknown.

Table 31
Measurements (all available specimens):
Oedaleus rosescens Uvarov

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	22.2	3.24	3.63	4.11	16.31	10.39	2.94	3.55	4.47
Range	20.65-23.95	3.0 - 3.55	3.4 - 3.95	3.8 - 4.45	15.2 - 17.9	9.7 - 11.15	2.65-3.2	3.48-3.72	4.34-4.56
S.D.	1.202	0.178	0.213	0.252	0.912	0.516	0.177	0.09	0.083
No.	8	8	7	8	8	8	8	8	7
♀ Mean	27.96	4.41	4.77	5.84	20.46	13.37	3.79	3.53	4.31
Range	25.9 - 29.15	4.05-4.7	4.4 - 4.95	5.3 - 6.15	18.6 - 21.8	12.4 - 13.95	3.4 - 3.95	3.36-3.69	4.06-4.69
S.D.	1.154	0.218	0.202	0.278	1.083	0.647	0.212	0.125	0.204
No.	7	8	8	8	7	8	8	8	7

Table 32
Measurements (Kenya, Hola, 1°30'S, 40°00'E, (I. A. D. Robertson)):
Oedaleus miniatus Uvarov

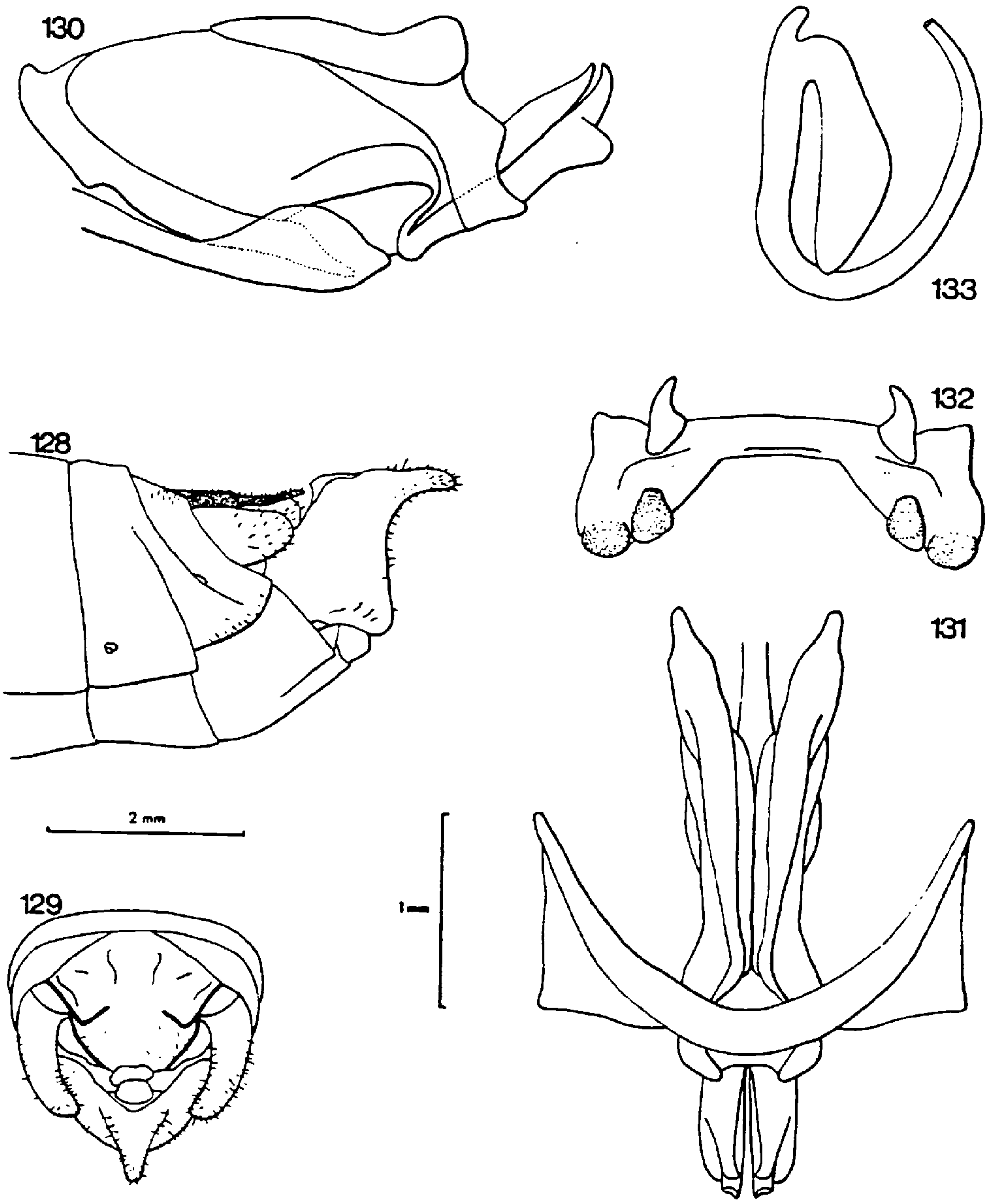
	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	25.67	3.88	5.26	5.34	18.36	12.47	3.63	3.44	3.51
Range	23.35-27.9	3.55-4.35	4.5 - 6.2	4.35-6.3	16.65-20.1	10.9 - 14.0	3.15-4.05	3.31-3.76	3.12-3.81
S.D.	1.465	0.265	0.534	0.512	1.078	0.884	0.272	0.126	0.219
No.	10	11	11	11	10	11	11	11	10
♀ Mean	28.1	6.08	7.1	8.21	18.29	15.01	4.58	3.28	2.58
Range	26.4 - 29.2	5.75-6.5	6.7 - 7.55	7.55-8.85	17.2 - 18.95	14.45-16.0	4.4 - 4.8	3.08-3.52	2.5 - 2.71
S.D.	1.267	0.309	0.382	0.514	0.763	0.621	0.168	0.156	0.097
No.	5	5	5	5	5	5	5	5	5

1.1.5.17 Oedaleus miniatus Uvarov, 1930

(Figs 16,32,59,128-133,156)

Oedaleus miniatus Uvarov, 1930: 177. Holotype ♀, SOMALI REPUBLIC (BMNH) [examined].

♂. Integument rugose and wrinkled. Antennae slightly longer than head and pronotum together, distinctly flattened, ensiform; flagellum with 22 segments. Fastigium of vertex longer than wide, concave, with well-defined lateral carinae, narrowing to one third of maximum width anteriorly; frons in profile flat or slightly concave with projecting angle between frons and vertex; frontal ridge strongly narrowed just ventral to fastigium, expanded at and slightly constricted ventral to median ocellus. Eyes about one and a half times as long as wide. Pronotum tectiform, strongly rugose; median carina arcuate, intersected by posterior sulcus; anterior arms of pronotal x-marking placed on narrow raised ridges; hind margin acutangular to rectangular. Tegmen surpassing folded hind knees by one third of length of hind femur. Hind tibia with 11-13 spines inside and out; inner apical spurs about twice as long as outer; apical tarsal segment twice length of claw; arolium less than one third length of claw. Cerci twice as long as basal width; subgenital plate with an acute dorsal posterior process (Figs 128, 129). Genitalia (Figs 130-132): cingular apodemes short, thin crescent-shaped, obtusely curved; rami short, reduced, with apices of cingular valves and apical penis valves long and exposed, the latter with acute flattened chisel-like tip and pronounced subapical ventral processes; epiphallus short and wide, with broad, thin, flat bridge, lophi with inner and outer lobes small and nearly of equal size; ancorae small; anterior projections small, rectangular; posterior projections obsolete.



Figs 128-133. O. miniatus, genitalia. 128, apex of ♂ abdomen, lateral; 129, same, dorsal; 130, endophallus & cingulum, lateral; 131, same, dorsal; 132, epiphallus; 133, ♀ spermatheca.

General colouration variable, brown, with lighter brown or green markings on frons, vertex, genae, and pronotum. Eyes with four light vertical stripes sometimes visible in anterior half (Fig. 31). Tegmen infuscate brown in basal half with irregular pale transverse band on costal margin, reaching second anal vein posteriorly, situated one third along from base, continuous when folded with light band on hind femur; secondary light band between half and two thirds along from base sometimes visible. Hind wing fascia (Fig. 4) complete, angled at dividing vein, spreading towards base and tip of wing along costal margin, basal area of wing bright scarlet, apical portion of wing slightly clouded. Outer surface of hind femora with three oblique transverse dark bands separated by lighter areas; interior surface with three transverse brown bands partially elided; interior ventral carina and ventral surface of hind femur orange red; hind knees blackish, tibiae with incomplete narrow dark basal ring, subbasal wide pale ring, otherwise orange red.

♀. Larger and more robust . Frons in profile concave to convex; head large. Pronotum rugose, warty. Tegmen shorter, just surpassing hind knees, narrowing towards apex; costal margin subbasally expanded. Hind wing scarlet, faded to salmon pink in some specimens, with dark fascia almost obsolete on small specimens. Hind femora with interior ventral carina suffused with orange red; hind tibiae orange. Ventral ovipositor valves (Fig. 54) with weakly sclerotised apices. Spermatheca (Fig. 137) with apical diverticulum tapering proximally and distally, and with short finger-like subapical diverticulum.

Affinities. O. miniatus is most closely allied to O. nadiae, under which species the principal similarities and differences are discussed. The unique features of this species include the very wide epiphallus (Fig. 136) and the curiously elongated subgenital plate (Figs 128, 129). The female possesses the least sclerotised ovipositor valves of any member of the genus, which suggests some ecological difference in oviposition between this species and its near relatives. Conceivably egg pods are deposited in the roots of vegetation clumps rather than in the more resistant soil. This however is merely a hypothesis. The small equal-sized lobes of the epiphallic lophi suggest a tenuous link between miniatus and nadiae on the one hand, and the obtusangulus - rosescens - instillatus group on the other. However it is clear that O. miniatus has undergone a long period of evolutionary divergence from the main stem of Oedaleus.

Uvarov (1930: 177) felt that O. miniatus might merit a separate genus, but incorrectly allied it to O. carvalhoi to which it is not closely related. With the discovery of O. nadiae, an intermediate species between O. miniatus and the rest of the genus, there seems less reason to erect a new genus for the latter.

Material examined. Appendix 1, p. 378.

Measurements. Table 32

Distribution (Fig. 156, and Biogeography section, p. 165). Known only from the Somali Republic and Kenya.

Biology. Unknown.

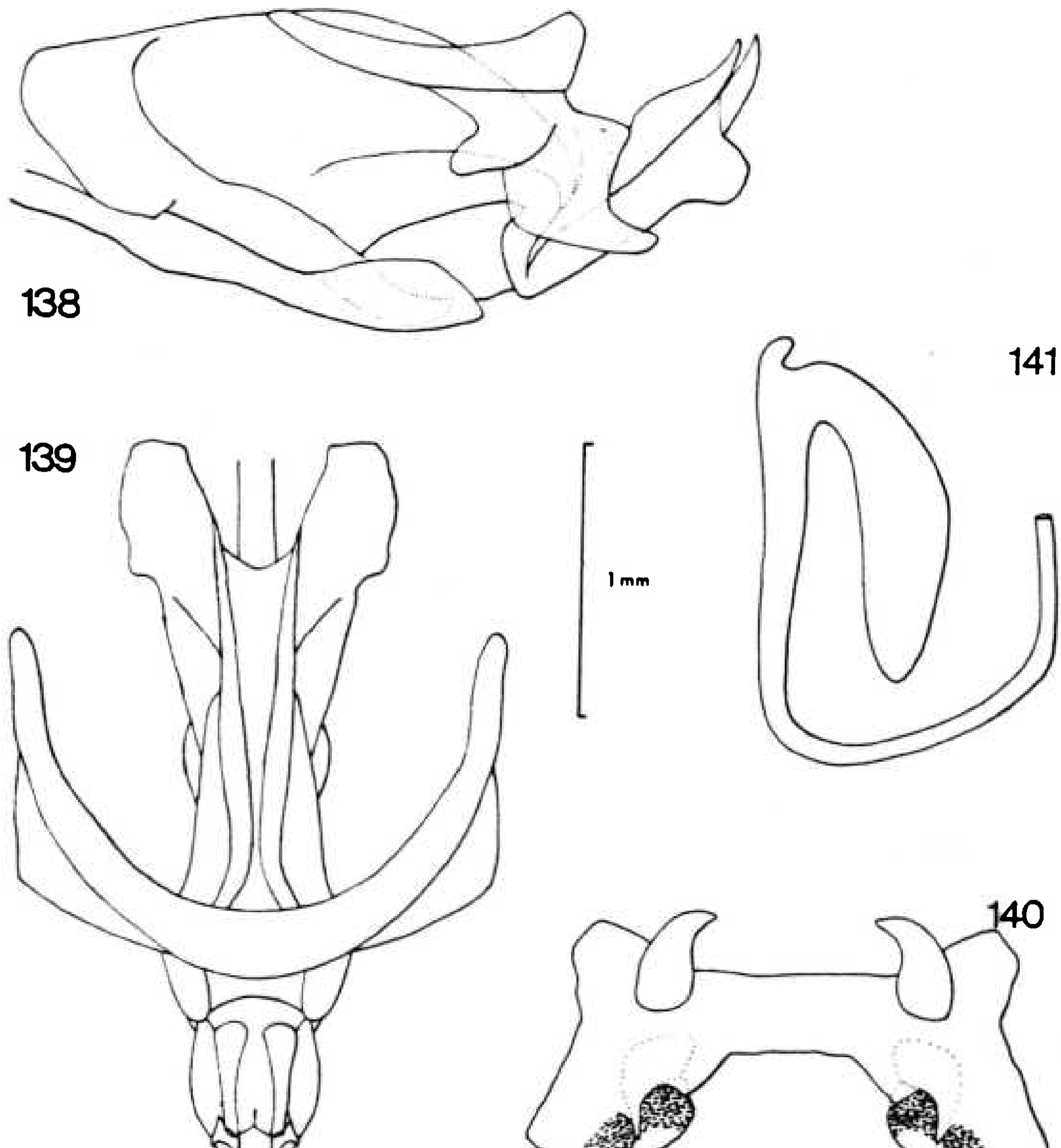
Discussion. The original description of O. miniatus by Uvarov (1930: 177) was based on a single female specimen collected at 6750 ft in the Surud Range of N Somalia. More recently specimens have been collected in southern Somalia and in Kenya which are much larger, with the hind wing fascia better developed. A close comparison with the holotype is no longer possible since it has been reduced by insect damage to a shell consisting of the pronotum, tegmina, hind wings, and left mid leg. However, all the known specimens appear to belong to one species, though further collecting in northern Somalia may demonstrate that the population from which the holotype came is a montane relict which has diverged sufficiently from the main population of the species further south to be considered as a separate subspecies. The male of this species, previously unknown, is here described for the first time.

1.1.5.18 Oedaleus nadiae sp. n.

(Figs 30,58,138-141,156,157)

♂. Integument rugose and wrinkled. Antennae slightly longer than head and pronotum together. Flagellum 20 segmented. Fastigium of vertex longer than wide, subtriangular, concave, with well defined margin; frons in profile slightly convex, almost straight; frontal ridge strongly narrowed just below fastigium and with a slight constriction just ventral to median ocellus. Eyes about one and a half times as deep as wide. Pronotum tectiform, strongly rugose, median carina arcuate, intersected by posterior sulcus; anterior arms of pronotal x-marking placed on raised ridges; hind margin acutangular; mesosternal interspace anteriorly narrower than metasternal but wider posteriorly. Tegmen surpassing folded hind knees by one tenth to one third of hind femur length; tibia with 10 outer and 11-12 inner spines; inner apical spurs nearly twice as long as outer; apical tarsal segment twice claw length; arolium about half claw length. Cerci length twice basal width. Genitalia (Figs. 138-140): cingular apodemes medium length evenly tapering; rami short, apices of cingular and apical penis valves long and exposed, the latter with acute chisel-like apices and pronounced lobular subapical ventral process. Epiphallus trapezoidal with lateral plates indented; bridge flat and thick, lophi with inner and outer lobes subequal in size. Anterior projections large, rectangular, posterior projections rectangular.

General colouration mottled brown with light brown or green markings on frons, vertex, genae, and pronotum. Eyes with four light vertical stripes sometimes visible in anterior half. Broad pale pronotal x-marking (Fig. 58) sometimes continuous posteriorly with pale band fringing hind margin of pronotum. Tegmen infuscate brown in basal two thirds with two pale transverse bands reaching to first anal



Figs 138–141. *O. nadiae*, genitalia. 138, endophallus & cingulum, lateral; 139, same, dorsal; 140, epiphallus; 141, ♀ spermatheca.

vein posteriorly; apical third of tegmen clear, with dark speckles. Hind wing lacking fascia, with pale crimson basal area and darkened main veins. Outer surface of hind femora with three oblique dark bands separated by lighter areas; internal surface with dark brown medial area; interior ventral carina orange; hind knees blackish, tibiae orange.

♀. Larger and more robust than male. Antennae 22 segmented. Pronotum heavily rugose, warty. Ovipositor valves pale with weakly sclerotised excurved apices (Fig. 58). Spermatheca (Fig. 141) with apical diverticulum elongated, tapering, with short finger-like subapical diverticulum.

Affinities. O. nadiae is most closely allied to O. miniatus. Principal characters in common are the general shape (rather stocky in the female), red hind wing, short cingular rami with exposed cingular and apical penis valves with very large subapical ventral processes (Fig. 138), and inner and outer lobes of epiphallic lophi small and nearly equal in size. The principal differences are that O. nadiae has an unbanded hind wing, a less elongated epiphallus, and the male subgenital plate not produced into a sharp point.

Material examined. Appendix 1, p. 378.

Measurements. Table 33

Distribution (Figs 156, 157, and Biogeography section, p. 166). This species is known only from the northern region of Somalia.

Biology. Unknown.

Discussion. This species is named in honour of Dr Nadia Waloff.

Table 33
Measurements (all known specimens):
Oedaleus nadiae sp. n.

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	23.68	3.96	4.78	5.17	16.88	11.83	3.53	3.35	3.54
Range	21.6 - 25.4	3.65- 4.15	4.35- 5.35	4.75- 5.55	15.4 - 18.45	10.65- 12.6	3.25- 3.85	3.27- 3.48	3.22- 3.99
S.D.	1.252	0.170	0.314	0.294	1.04	0.725	0.207	0.085	0.276
No.	8	8	8	8	8	8	8	8	8
♀ Mean	31.96	6.05	7.18	7.91	22.05	15.41	4.53	3.41	3.10
Range	27.45- 36.5	5.4 - 6.65	5.96- 8.6	6.55- 9.4	18.55- 25.5	12.75- 17.85	3.7 - 5.3	3.19- 3.97	2.8 - 3.35
S.D.	2.835	0.472	0.840	0.923	2.067	1.556	0.547	0.173	0.161
No.	16	17	17	17	16	17	17	17	16

Table 34
Measurements (N. Somalia, various localities):
Oedaleus inornatus Schulthess-Schindler

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	33.16	5.11	6.08	6.54	23.88	17.14	4.36	3.93	3.92
Range	27.4 - 37.3	4.4 - 5.65	5.25- 6.75	5.55- 7.1	19.55- 27.0	15.1 - 19.3	3.55- 4.85	3.73- 4.13	3.62- 4.22
S.D.	3.658	0.453	0.528	0.554	2.754	1.63	0.40	0.157	0.207
No.	12	12	12	12	12	12	12	12	12
♀ Mean	43.16	6.98	7.83	8.86	30.82	21.12	5.3	3.99	3.91
Range	33.65- 48.9	6.25- 7.85	6.4 - 9.25	7.35- 10.3	23.65- 35.2	16.7 - 25.25	4.3 - 6.05	3.8 - 4.35	3.5 - 4.47
S.D.	4.57	0.556	0.766	0.735	3.357	2.155	0.508	0.156	0.271
No.	18	19	19	19	18	19	19	19	18

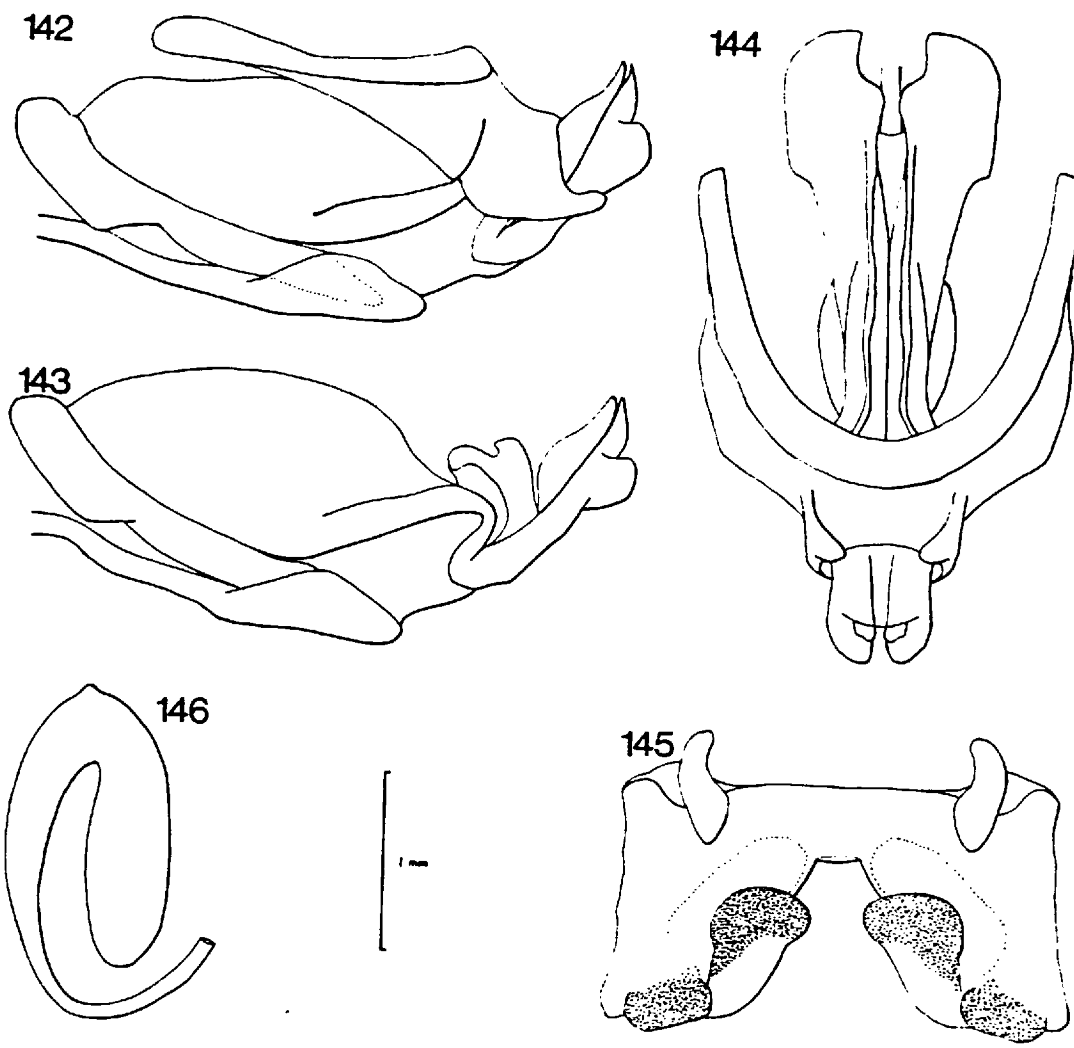
1.1.5.19 Oedaleus inornatus Schulthess-Schindler, 1898

(Figs 25,57,142-146,156)

Oedaleus inornatus Schulthess-Schindler, 1898: 27. Holotype ♀, SOMALI REPUBLIC: Dolo, -.viii.1893, (E. Ruspoli)(MCSN, Genoa).

Redescription. ♂. Integument rugulose and pitted. Antennae one and one third times as long as head and pronotum together, flagellum 22-23 segmented. Fastigium longer than wide, shallowly concave, narrowing to half maximum width anteriorly, margins only slightly raised; frons in profile slightly convex; frontal ridge slightly expanded above median ocellus. Eyes one and two fifths as deep as wide. Pronotum tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin obtusangular. Tegmen surpassing folded hind knees by one quarter to one third of hind femur length. Hind tibia with 13 inner and 11-12 outer spines; inner apical spurs about one and one third times as long as outer; apical tarsal segment nearly twice claw length; arolium half claw length. Cerci twice as long as basal width. Genitalia (Figs. 142-145): cingular apodemes long and of moderate thickness and curvature; rami short, cingular and apical penis valves protruding strongly; subapical ventral process large; epiphallus rectangular, bridge thick, narrow, lophi very large and heavily sclerotised, inner lobes larger than outer; anterior and posterior projections lobate, acutely rounded.

General colouration brown, with light brown or green markings on vertex, frons, genae, pronotum, and dorsal surface of folded tegmina and hind femora; green forms relatively rare. Tegmen infuscate brown in basal half with three variable transverse bars or blotches situated one sixth, one third, and one half of distance along from base; apical half clear with variable brown patches. Hind wing without fascia but with infuscate wing tip, and occasionally, faint traces of fascia near



Figs 142-146. O. inornatus, genitalia. 142, endophallus & cingulum, lateral; 143, same, cingulum removed; 144, endophallus & cingulum, dorsal; 145, epiphallus; 146, ♀ spermatheca.

hind margin; basal area pale yellow. Hind femur with three variable oblique dark bands on outer medial and upper marginal areas, basal pair of bands elided on inner surface to form large black area; ventral surface scarlet; hind knees black, hind tibia with narrow dark basal ring and broad pale subbasal area, otherwise scarlet.

♀. Larger and more robust. Hind femora and tibiae less distinctly red than male. Ventral ovipositor valves (Fig. 57) elongate triangular, well sclerotised, with smoothly incurved exterior margins. Spermatheca (Fig. 146) with apical diverticulum vestigial.

Affinities. O. inornatus is characterised by the total absence of a wing band and by the very robust genitalia, in particular the epiphallus with its very large lophi. It is impossible to relate this species to the others with any degree of certainty. It may possibly be an offshoot of the senegalensis group.

Material examined. Appendix 1, p. 378.

Measurements. Table 34

Distribution (Fig. 156, and Biogeography section, p. 166). Widely distributed but not common throughout the drier areas of northeastern Africa.

Biology. Unknown. A gynandromorph specimen of this species has been described (Ritchie, 1978a).

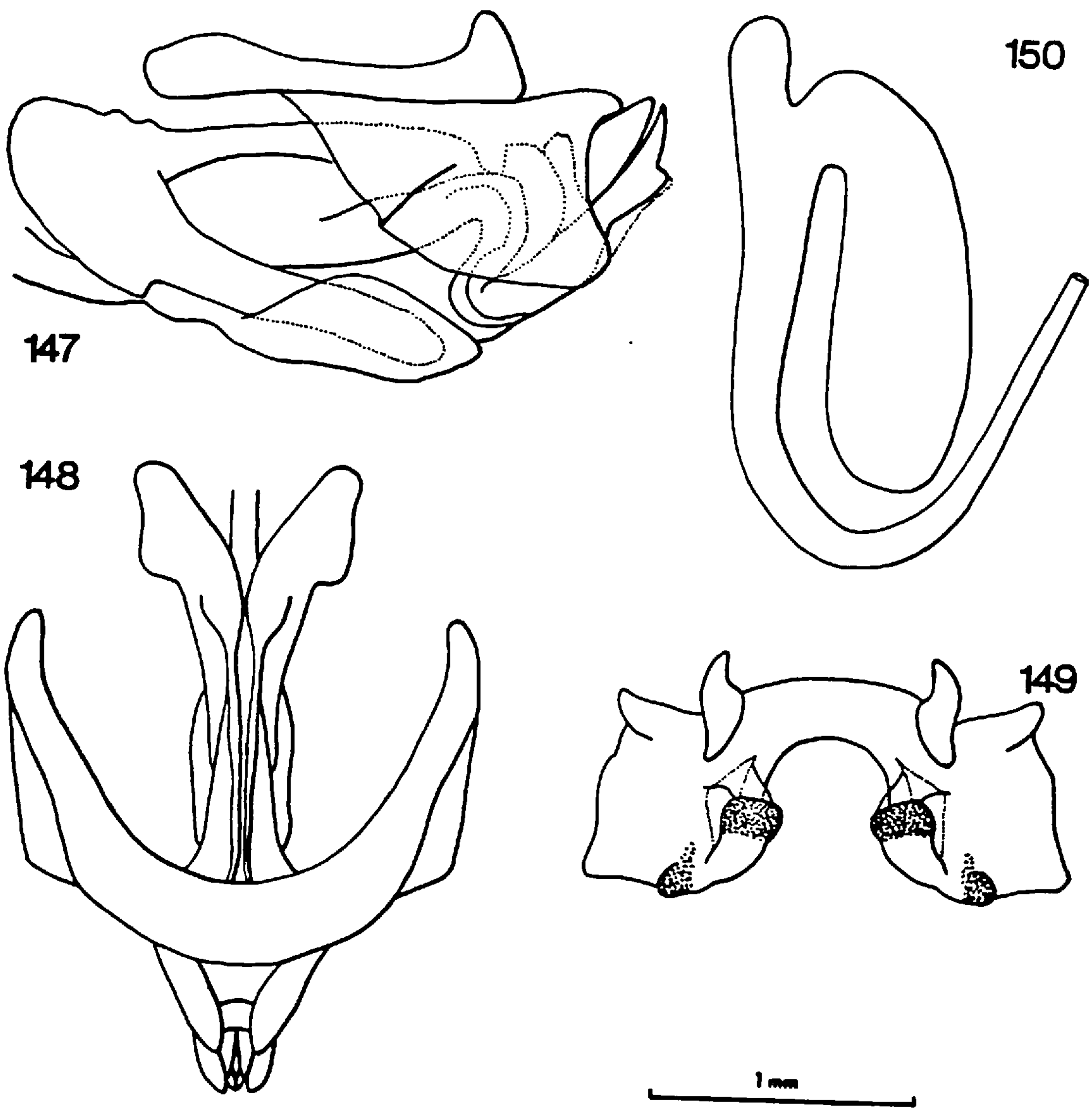
1.1.5.20 Oedaleus flavus (Linnaeus, 1758)

(Figs 17,34,49,50,147-150,155)

This species is here divided into two subspecies under which the specific synonyms are separately listed below.

Redescription. ♂. Integument finely rugose and warty. Antennae slightly longer than head and pronotum together, flagellum with 22 segments. Fastigium longer than wide, widest medially, tapering both anteriorly and posteriorly, concave, with well defined margins; frons in profile convex; frontal ridge almost parallel sided, slightly divergent between antennal bases. Eyes about one and two fifths times as long as wide. Pronotum tectiform with sparse warts, at least in prozona; median carina arcuate, intersected by posterior sulcus; hind margin of pronotum acutangular. Tegmen surpassing folded hind knees by about one fifth to one third of hind femur length. Hind tibia with 12 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment one and four fifths length of claw; arolium less than half claw length. Cerci two and a half times as long as basal width. Genitalia (Figs 147-149): cingular apodemes medium length, medially thickened; rami slender, elongate, cingular valves and apical penis valves short; subapical ventral process small; epiphallus trapezoidal, lateral plates slightly excurved; bridge arched, thick; lophi with inner lobes larger than outer; anterior projections small, acutely rounded; posterior projections rectangular, rounded.

General colouration dark brown, with lighter brown (or rarely green) markings on frons, vertex, genae, and pronotum. Tegmen infuscate brown in basal two thirds with three pale transverse bars at intervals of one quarter, one half, and two thirds along from base; apical third clear with brown speckles. Hind wing fascia (Fig. 17) complete, continued half way towards apex of wing between first radial vein and radial



Figs 147-150. O. flavus, genitalia. 147, endophallus & cingulum, lateral; 148, same, dorsal; 149, epiphallus; 150, ♀ spermatheca.

sector; wing tip variably infuscate; basal area of wing bright opaque lemon yellow. Outer surface of hind femora with three oblique dark bands; hind knees blackish, hind tibiae orange red.

♀. Larger and more robust. Dorsal surface of pronotum with large warts and posterior arms of x-marking very thick (Fig. 34). Hind wing tip not clouded. Ovipositor valves strongly sclerotised and excurved. Spermatheca (Fig. 150) with apical diverticulum bulbous, preapical diverticulum stout.

The two subspecies of Oedaleus flavus may be separated by the following keys:

MALES

1. Interior surface of hind femur with one transverse and one U-shaped dark band, not intersecting the internal ventro-lateral carina; basal half of interior surface, internal ventro-lateral carina, and ventral surface suffused with red (E. Africa) ... ... Oedaleus flavus somaliensis (Sjöstedt)

-. Interior surface of hind femur with dark bands enlarged and crossing internal ventro-lateral carina onto ventral surface; central portion of interior surface suffused with mauve or black, never red (S. Africa) ... Oedaleus flavus flavus (Linnaeus)

FEMALES

1. Ventral surface of hind femur, particularly internal ventro-lateral carina, suffused with red, sometimes discoloured, never black; basivalvular sclerite of ventral ovipositor valves smooth (Fig. 50) ... Oedaleus flavus somaliensis (Sjöstedt)

-. Ventral surface of hind femur, particularly in inner half,

suffused with black, never red; basivalvular sclerite of ventral ovipositor valves with raised warts in posterior half (Fig. 49)
... ... *Oedaleus flavus flavus* (Linnaeus)

Oedaleus flavus flavus (Linnaeus, 1758)

Gryllus Locusta flavus Linnaeus, 1758: 433. Lectotype ♀, AFRICA (ZIUU, Uppsala) Dirsh, 1961: 317 [*not* in LS, London, as stated by Dirsh, *op. cit.*] [examined].

Gryllus flavus (Linnaeus) Fabricius, 1775: 292 [locality: Piedmont, indicates partial confusion with *Oedaleus decorus* (Germar)].

Acrydium flavum (Linnaeus) Olivier, 1791: 227 [incorrectly gives *Acrydium nigrofasciatum* Degeer, 1773 as synonym].

Gryllus flavus (Linnaeus) Petagna, 1792: 319 [incorrectly gives *Acrydium nigrofasciatum* Degeer as synonym].

Oedipoda flava (Linnaeus) Serville, 1831: 288.

Oedipoda flava (Linnaeus) Burmeister, 1838: 643 [incorrectly gives *Acrydium nigrofasciatum* Degeer as synonym].

Pachytylus (*Oedaleus*) *flavus* (Linnaeus) Stål, 1873: 125.

Humbella flava (Linnaeus) Saussure, 1884: 107.

Oedaleus nigrofasciatus var. *citrinus* Saussure, 1888: 41. LECTOTYPE ♂, SOUTH AFRICA: 'Cap.' (MHN, Geneva) [synonymised by Dirsh, 1961: 317], here designated [examined].

Oedalus (sic) *citrinus* (Saussure) Distant, 1892: 260.

Oedaleus citrinus (Saussure) Kirby, 1910: 225.

Oedaleus flavus (Linnaeus) Kirby, 1902: 73 [incorrectly gives *Oedaleus nigrofasciatus* as synonym].

Humbe flava (Linnaeus) Kirby, 1910: 215.

Oedaleus flavus (Linnaeus) Dirsh, 1961: 317 [reinstates original usage].

Material examined. Appendix 1, p. 378.

Measurements. Table 35

<u>Oedaleus</u> <u>flavus</u> <u>somaliensis</u> (Sjöstedt, 1931) comb. et stat. n.

<u>Gastrimargus</u> <u>somaliensis</u> Sjöstedt, 1931a: 26. Holotype ♀, SOMALI REPUBLIC (NR, Stockholm) [examined].

Material examined. Appendix 1, p. 379.

Measurements. Table 36

Affinities. <u>O</u>. <u>flavus</u> is probably allied to <u>O</u>. <u>instillatus</u> on the basis of its epiphallus having small lophi (Fig. 149) and the same characteristic suggests a link with <u>O</u>. <u>plenus</u> with which it may be confused on superficial examination. The bright yellow basal area of the hind wing is however a sufficient diagnostic character.

Distribution (Fig. 155, and Biogeography section, p. 161). Widely distributed in eastern and southern Africa with a broad discontinuity corresponding with the <u>Brachystegia</u> woodland zone.

Biology. Little is known of the biology of this species. It was reported by Ballard (1914) as a pest of tobacco in Malawi. Phipps (1959) recorded mean numbers of 35.0 and 36.8 ovarioles per female in two samples of two and four specimens respectively in Tanzania. Nolte (1939) reports a karyotype of 2N = 22 in this species.

Table 35
Measurements (South Africa, various localities):
Oedaleus flavus flavus (Linnaeus)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	28.19	4.27	5.45	5.39	20.99	13.92	3.71	3.75	3.85
Range	26.4 - 29.85	3.95- 4.65	5.1 - 5.85	4.7 - 5.9	19.6 - 22.4	12.9 - 15.2	3.3 - 4.15	3.61- 4.0	3.7 - 3.98
S.D.	1.212	0.206	0.228	0.301	1.041	0.762	0.264	0.126	0.093
No.	11	11	11	11	11	11	11	11	11
♀ Mean	37.0	5.79	7.04	7.47	27.58	17.78	4.93	3.61	3.93
Range	34.8 - 39.85	5.05- 6.25	6.35- 7.75	6.9 - 7.95	26.0 - 29.5	16.15- 19.4	4.3 - 5.2	3.39- 3.76	3.72- 4.31
S.D.	1.537	0.346	0.402	0.390	1.015	0.844	0.277	0.114	0.165
No.	11	11	11	11	11	11	11	11	11

Table 36
Measurements (Kenya, various localities):
Oedaleus flavus somaliensis (Sjöstedt)

	Total length	Caput width	Pronotum length	Pronotum width	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂ Mean	27.4	4.11	5.12	5.05	20.56	13.45	3.59	3.74	4.03
Range	24.75- 29.3	3.7 - 4.45	4.55- 5.55	4.6 - 5.45	18.5 - 22.15	11.65- 15.1	3.3 - 3.95	3.38- 3.97	3.64- 4.52
S.D.	1.216	0.217	0.303	0.221	1.004	0.865	0.183	0.136	0.231
No.	22	22	22	22	22	22	22	22	22
♀ Mean	38.74	6.18	7.1	7.19	29.08	18.49	5.11	3.62	4.10
Range	33.3 - 45.55	5.5 - 6.45	6.1 - 7.8	6.2 - 8.0	24.7 - 34.35	15.7 - 21.6	4.5 - 5.65	3.38- 3.82	3.84- 4.46
S.D.	2.752	0.385	0.472	0.517	2.147	1.294	0.324	0.130	0.208
No.	14	14	13	14	14	14	14	14	13

Discussion. Gastrimargus somaliensis Sjöstedt (1931a) is here considered as a subspecies or geographical race of Oedaleus flavus. The external morphology and male genitalia of the two forms are identical apart from the minor differences detailed in the key above (p. 147). Despite these consistent differences the overall shape and size of the animals has remained remarkably constant in the two disjunct populations. Tegmen length is slightly significantly ($P < 0.05$) larger in East African females than in South African, but in males there is no significant difference. Pronotum length is significantly smaller ($P < 0.002$) in East African males than South African, but in females there is no significant difference. The TL/PL ratio is significantly higher in East African specimens ($P < 0.01$ ♂, < 0.05 ♀) and the sexual dimorphism as measured by mean T♀/T♂ (Farrow, 1972) is greater in the former (1.414) than the latter (1.314).

The present interrupted distribution of the two races probably resulted from the recent interposition of the Brachystegia woodland across a previously continuous range of savannah (Van Zinderen Bakker, 1976). As described above (p. 89) Oedaleus plenus plenus also has two populations separated by the woodland, but without having undergone any apparent morphological divergence. For this reason and in view of the small amount of divergence which can be observed in the two populations of O. flavus, the process of speciation is considered to be incomplete.

1.2 BIOGEOGRAPHY OF THE GENUS OEDALEUS

1.2.1 Relationships within the genus Oedaleus

The genus Oedaleus comprises a homogeneous group of oedipodine grasshoppers colonising a wide range of grassland habitats throughout the tropical and warmer temperate regions of the Old World. Before any analysis of the influences that have shaped the present distribution of the genus can be attempted it is necessary to describe the groupings of species which can be made on morphological grounds. These are tabulated below:

Group I

O. senegalensis
O. nigrofasciatus
O. australis
O. abruptus
O. virgula
O. johnstoni
O. nigeriensis
O. carvalhoi
O. plenus
O. decorus
O. infernalis
O. formosanus
O. interruptus

Group II

O. instillatus
O. obtusangulus
O. rosescens

Group III

O. miniatus
O. nadiae sp. n.

Ungrouped species

O. inornatus
O. flavus

Group I are linked by the possession of the following combination of characters: 1. similar genitalia having epiphallic lophi with unequal sized lobes, 2. the basal area of the hind wing pale yellow, 3. smooth integument with pronounced green-brown polymorphism. O. interruptus is unusual in having a strongly acutangular hind margin to the pronotum, but is otherwise a member of this group. Group II have the epiphallus almost square with small, equal sized lobes to the lophi. Group III have pink wings and rugose integument and are probably closely related although each species has peculiarities which suggest that they have been genetically isolated one from the other over a long period. O. rosescens, another species with pink wings, is placed in group II since it resembles the other two species of that group in all other characters.

1.2.2 Geographical origin of the genus

Analysis of the existing distribution of the genus strongly suggests an origin within the Ethiopian Region. The evidence for this can be summarised as follows:

1. The species endemic to Africa show the greatest range of inter-specific morphological diversity, whereas those outside Africa can be placed in one or other of the African groups of species.
2. More than half of the known species (13) are found in Africa south of the Sahara. One other is known from North Africa and yet another species is endemic to Madagascar.
3. The genera most closely related to Oedaleus are either endemic to the Ethiopian Region (e.g. Humbe, Oreacris, Locustana), or are Malagasian (e.g. Pycnocrania), or are at least well represented in Africa (e.g. Locusta, Gastrimargus).

La Greca (1970) has drawn attention to the danger of assuming an Ethiopian origin for groups which may have entered Africa from Southern Europe or Western Asia, and whose present distribution may represent a relic of a much more extensive fossil or prehistoric range which would have included those areas. He cites the examples of the Lion and the Rhinoceros whose present limited distribution has been reduced largely by human activity. As to the savannah grasshoppers however, it seems improbable that anything short of major habitat degradation would have brought about multiple extinctions. In Australia some flightless members of the endemic subfamily Morabinae are reported to survive only in graveyards and other refuges where sheep grazing is prevented (Key, 1974). However Oedaleus together with several other Oedipodines is able to survive under a wide range of ecological conditions, largely because of its effective egg diapause and the high mobility of the adults. For these reasons an African origin, or at least a primary radiation within Africa, seems most probable. To gain some idea of the forces which could have brought about the present day radiation of species it is necessary to examine some of the major features, past and present, of the African biomes.

1.2.3. The Pleistocene in Africa

Moreau (1966), in his study of the bird faunas of Africa, has reviewed the climatic changes of the Pleistocene in Africa, and has presented strong circumstantial evidence for his belief that the forces that have shaped the avian fauna have, for the most part, operated within the last 70,000 years. At present there is no coherent chronological scheme that would harmonise all the known geological changes which have occurred in different parts of Africa within that period of time. However it is possible to date some Pleistocene features in Africa and to relate them to events both in different parts of Africa itself and in Europe.

The two major influences on vegetation in the past have been changes in temperature and humidity and the most significant fluctuations in both have been associated with glaciation. As well as a direct lowering of temperature, glaciation has a complex effect on atmospheric circulation which in turn causes changes in the rainfall pattern which are the subject of opposed theories. In the last one million years there have been four glaciations, each with a similar temperature minimum and each separated by an interglacial period with higher peak temperatures than at present. The course of the last glaciation is better known than that of the previous ones and serves as a model in considering some of the dramatic changes which have repeatedly affected both the climate and vegetation of Africa. There is however the important reservation that human influence has been much more significant since the last glaciation than at any earlier period.

The last glaciation began around 70,000 years B.P. (before present), and its last severe stage lasted from 25,000 - 15,000 B.P. with a peak at 19,000 correlated with arctic conditions in central Europe. From around 16,000 B.P. the temperature rose very sharply except for brief cold relapses around 10,500 B.P. and again between 5,500 and 4,700 B.P. (Van Zinderen Bakker, 1969). Present temperatures were reached around 8,000 B.P. then exceeded by as much as 2°C around 6,000 B.P. Finally, between 1400 and 1850 AD temperatures were slightly lower than now (Moreau, 1966). These cyclical temperature changes, which are presumed to be of cosmic origin, have excercised a profound effect on plant and animal distribution patterns both directly and through their influence on precipitation, evaporation, and ocean currents. The results of this influence are discussed below on a regional basis in relation to the distribution of the species of the genus Oedaleus.

1.2.4 The southern African Oedaleus fauna

According to Moreau (1966), the most stable parts of Africa during the Pleistocene have been the Namib and Kalahari deserts of southern Africa and the Somali peninsula of eastern Africa. Van Zinderen Bakker (1975) has reviewed evidence relating to the age, origins, and movements of the Namib and Kalahari and concludes that they originated in the Oligocene about 40 - 45 million years B.P. At glacial maxima these deserts have enlarged and moved northwards in response to the growth of the polar ice-cap and the attendant shift towards the equator of the climatic belts and cold upwelling at the convergence of the Benguela and Angola currents on the west coast of southern Africa. Other effects of glaciation would have included decreased precipitation from colder oceanic water and an increase in the incidence of violent winds (Van Zinderen Bakker, 1976), both of which would have an aridifying influence. Successive enlargements of the Kalahari have pushed the Brachystegia woodland and the lowland forest zones back towards the equator, at the same time dissecting them into a number of separate refuges. Van Zinderen Bakker (1976) has produced tentative vegetation maps of Africa south of the Sahara during a glacial and an interglacial maximum showing how open savannah and dry grassland would have increased in extent, offering contact between eastern and southern Africa for the semi-arid biota including Oedaleus (Fig.151). Conditions at the height of the last glaciation would have provided an opportunity, perhaps the most recent of several, for species of the east African savannah and semi-arid zones to mix with those occupying similar habitats south of the equator, and vice versa, in the temporary absence of the woodland barrier which is at present more than 500 miles wide. At the same time much of South Africa and Botswana would have deteriorated from Acacia grassland to desert or near desert. The montane grassland of southern Transvaal, Orange Free State, Lesotho, and south east Cape Province would have descended as much as 1000 metres but would apparently have suffered no reduction in area and may have constituted a relatively

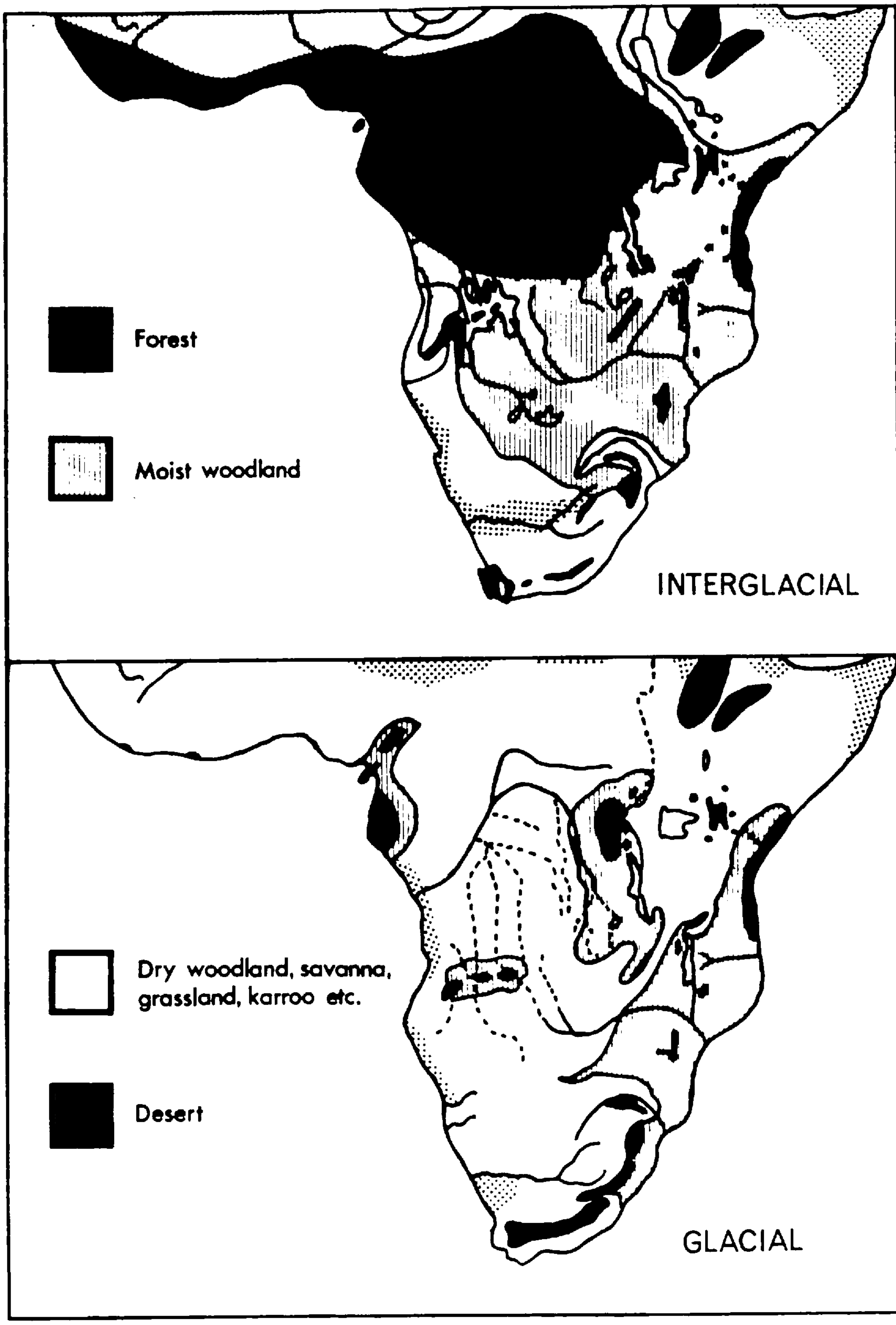


Fig. 151. Tentative vegetation maps of Africa south of the Sahara during a glacial and an interglacial maximum (simplified from Van Zinderen Bakker, 1976).

stable habitat during the Pleistocene. Certainly Oedaleus interruptus, the most distinct of the southern African species, is restricted to this habitat (Fig.152) though apparently not found above about 2500 m. Oedaleus nigrofasciatus, another southern species, also favours the montane grassland (Fig.152), whereas O. carvalhoi does not occur there (Fig.152) although both species are found together further north and west across the Acacia and 'Mopane' wooded savannah. Both species bear a marked similarity to species found to the north of the Brachystegia belt. O. nigrofasciatus is morphologically almost indistinguishable from O. senegalensis, while O. carvalhoi shows a strong resemblance to O. nigeriensis. It is probable that these and other southern species and subspecies have been able to evolve in isolation from northern populations because of the periodic fragmentation of the humid woodland barrier described above. The importance of this barrier in the development of the African biota and the evidence in favour of it are discussed below (p. 188).

The two subspecies of Oedaleus plenus, a southern African species (Fig.153), have a geographically and ecologically wide distribution within the different vegetation types mapped by Keay (1959). The most widely distributed subspecies O. plenus plenus, is found in N.E. Tanzania in open Acacia savannah with a grass cover dominated by Themeda triandra (Rattray, 1960). To the south, the Brachystegia woodland belt and rift valley separate this population from the main population of the subspecies which forms a continuous belt across the drier 'Mopane' wooded savannah from S.W. Angola to Mozambique and the steppe country of Botswana with a grass cover dominated by Eragrostis. Evidently the openness of the vegetation and the rainfall regime are of greater importance in delimiting the range of this subspecies than is the species composition of the grasslands which is quite different in the northern and southern savannahs. Further south there are two

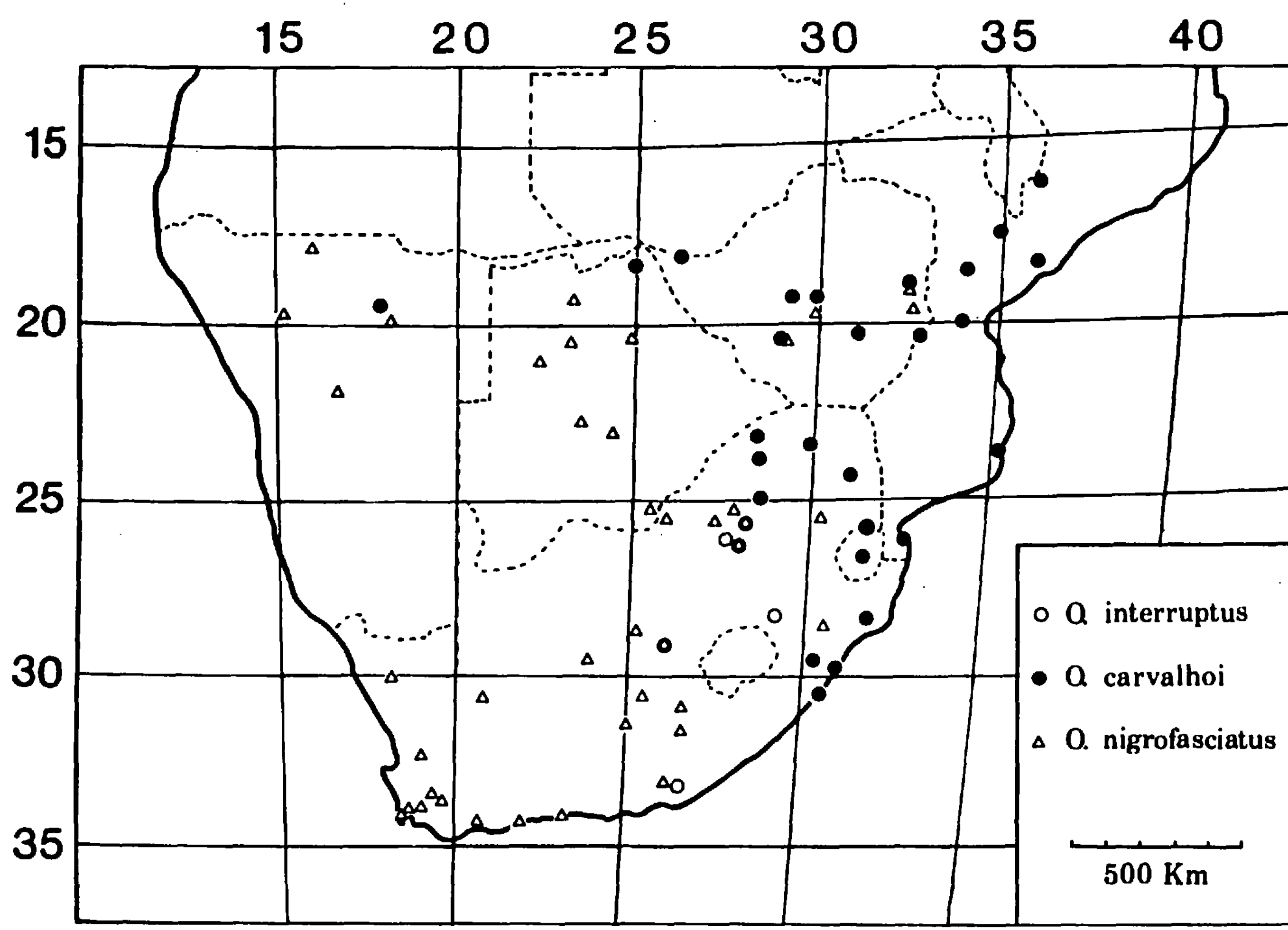


Fig. 152. Distribution of Oedaleus species in Southern Africa. Open circles, O. interruptus; closed circles, O. carvalhoi; open triangles, O. nigrofasciatus.

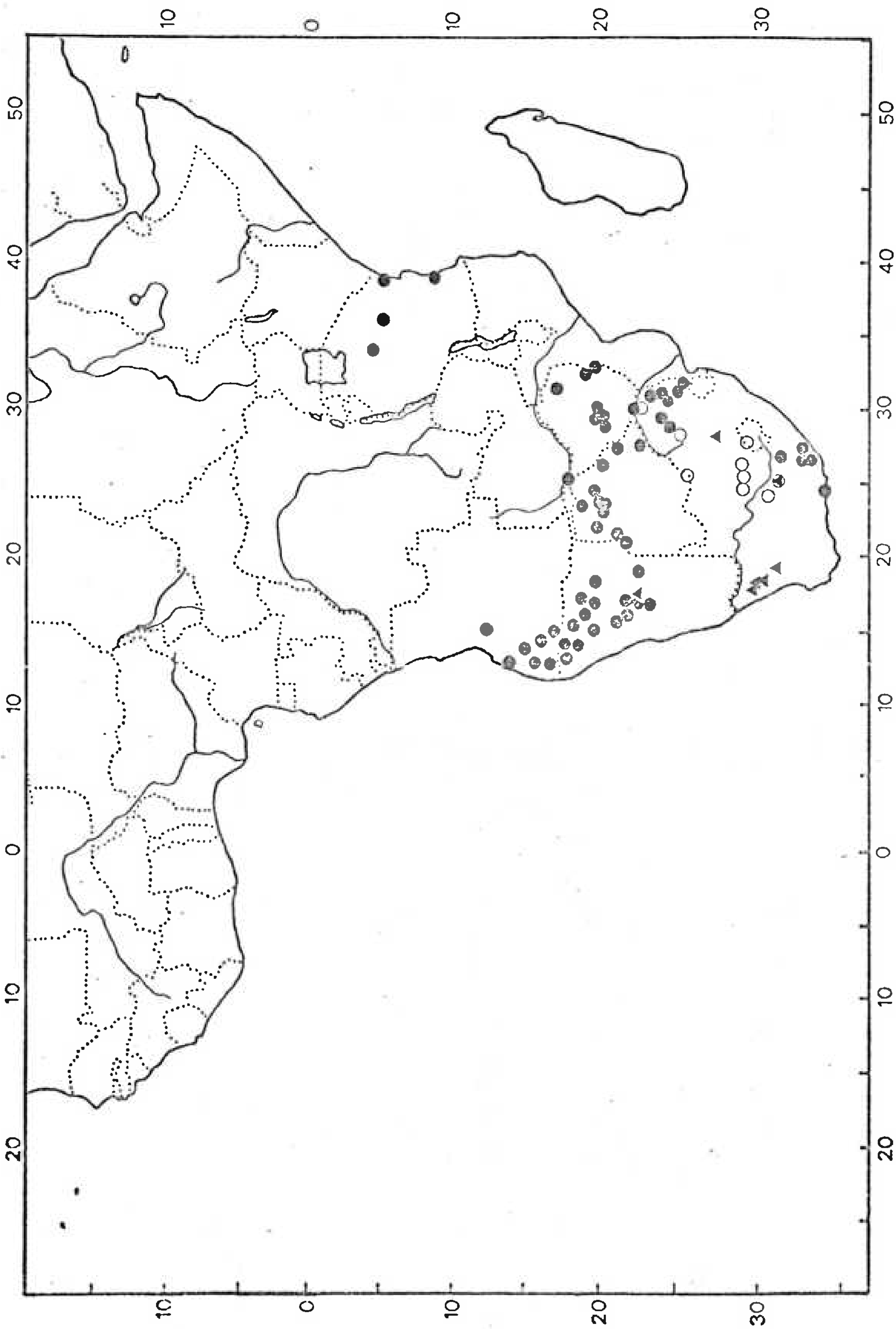


Fig. 153. Distribution of subspecies of *Oedaleus plenus* in southern Africa. Closed triangles, *O. p. plenus*, thin-lined form; closed circles, *O. p. plenus*, thick-lined form; open circles, *O. p. browni*.

distinct populations. One of these, O. plenus browni, distinguished by the partial or total absence of the hind wing fascia, is apparently almost restricted to the montane grassland areas dominated by Themeda spp., which are also the habitat of O. interruptus, although it does penetrate into areas dominated by Hyparrhenia spp. to the north and by Eragrostis spp. to the west on lower ground. Rattray (1960) quotes the view of an earlier worker, Acocks, who considered that these areas were also originally dominated by Themeda spp. which have been selectively removed by overgrazing. The montane habitat of this subspecies is entirely contained within that of O. plenus dilutus which reaches the south coast around Port Elizabeth. Further west, in Southern Cape Province an isolated population of O. plenus plenus has become adapted to the very distinct winter rainfall area of the western Karoo of Namaqualand. The seasonality of rainfall distribution in South Africa is shown in Fig.154 (after Adamson, 1938). The figures represent the percentage of the total rainfall falling in the southern summer (October to March). The unusual climate of the region supports a complex plant community with many succulents and a large proportion of endemic genera, including the dominant grass Ehrarta calycina. It is probable that the tendency of specimens from this population to have finer pronotal markings is indicative of evolutionary divergence resulting from relative geographical isolation and partial asynchrony of the breeding season caused by the rainfall regime.

Oedaleus flavus, like O. plenus, occurs to north and south of the Brachystegia belt (Fig.155), but the northern population extends northwards across the Equator into Kenya and Somalia whereas O. plenus apparently does not. Also unlike O. plenus, O. flavus occurs as one subspecies, somaliensis, in the northern Acacia savannah zone, and as another subspecies, flavus, in the south where it occupies a habitat similar to that of O. nigrofasciatus even penetrating into the Macchia

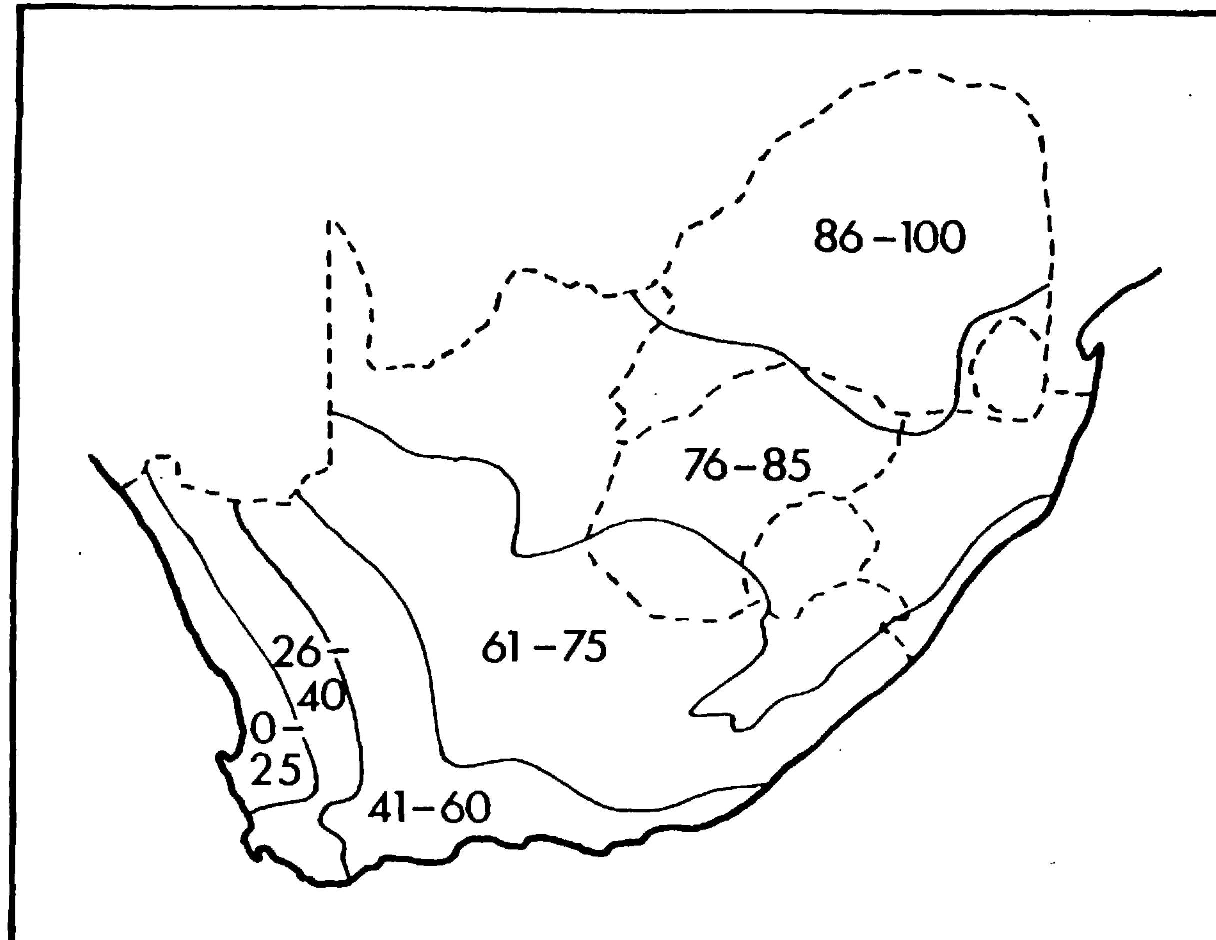


Fig. 154. Map of South Africa showing the percentage of total precipitation falling during the southern summer (October-March) (after Adamson, 1938).

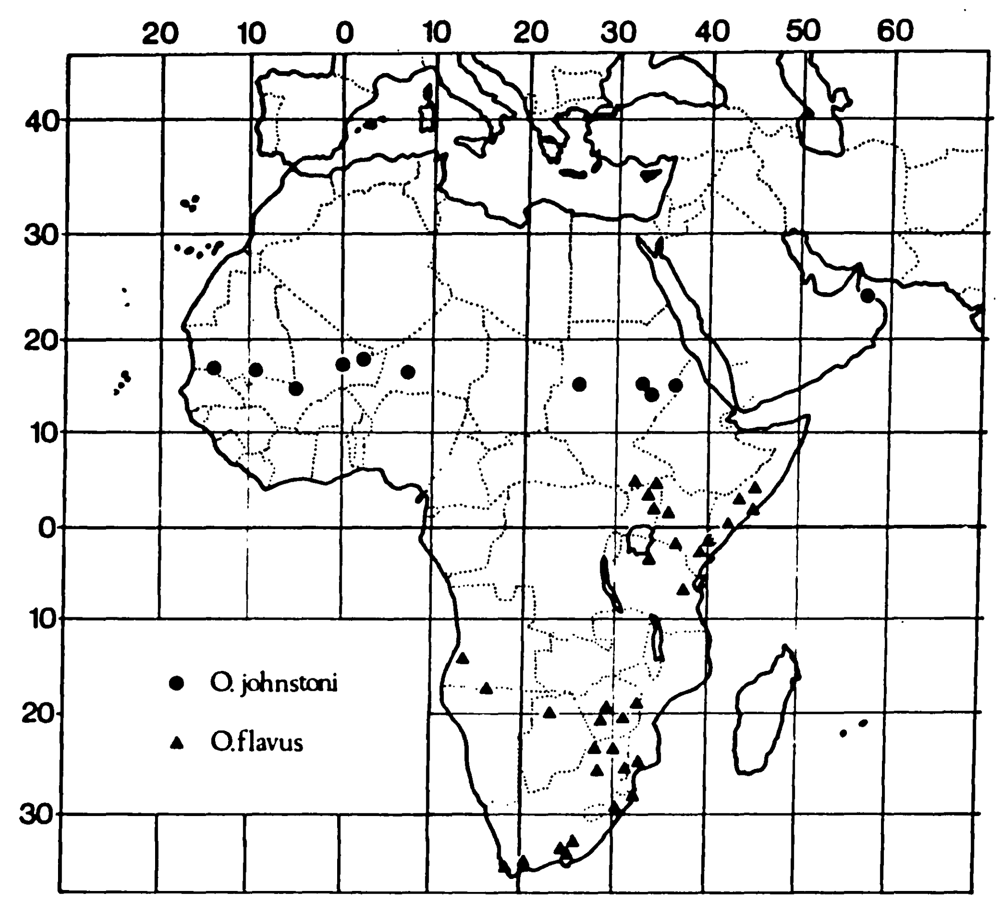


Fig. 155. Distribution of Oedaleus species in Africa. Circles, O. johnstoni; triangles, O. flavus.

vegetation of the southern Cape. Evidently this is yet another example of colonisation across the 'Miombo' woodland during a dry period, with subsequent isolation and divergence. The direction of the migration is assumed to be north to south in view of the greater richness of the Oedaleus fauna of east Africa. The simplest model is that of an east African focus with emigrants travelling south into an area where intra-generic competition would initially be less intense since fewer niches would be filled. However it is possible that in some instances movement could have occurred in the reverse direction.

1.2.5 The Oedaleus fauna of the Somali peninsula

The most remarkable zone of speciation in Oedaleus has been the Somali Peninsula. The arid horn of Africa is effectively separated from the latitudinal vegetation belts to the west by the Ethiopian highlands and Lake Turkana. Moreau (1966) lists the area as having more endemic birds than any other lowland non-forest zone in Africa. However Winterbottom (1967) asserts that the South West Arid District has in fact much the larger avifauna, although direct comparison is impossible. Chapin (1923) considered the area as a distinct avifaunal district (the Somali Arid District) and Popov (1959) found this division relevant to the distribution of the aberrant endemic grasshopper genus Sauracris. Both in Sauracris and Oedaleus it is noticeable that the maximum concentration of species occurs in the northern rangelands. This may in part be due to the wide diversity of structure, vegetation, and rainfall which are experienced within a relatively small area. The climatic zones of the Somali peninsula are shown in Fig. 156 (Griffiths, 1972). Zone I, the northern coastal strip, is characterised by winter rains and summer drought, though high humidity is maintained

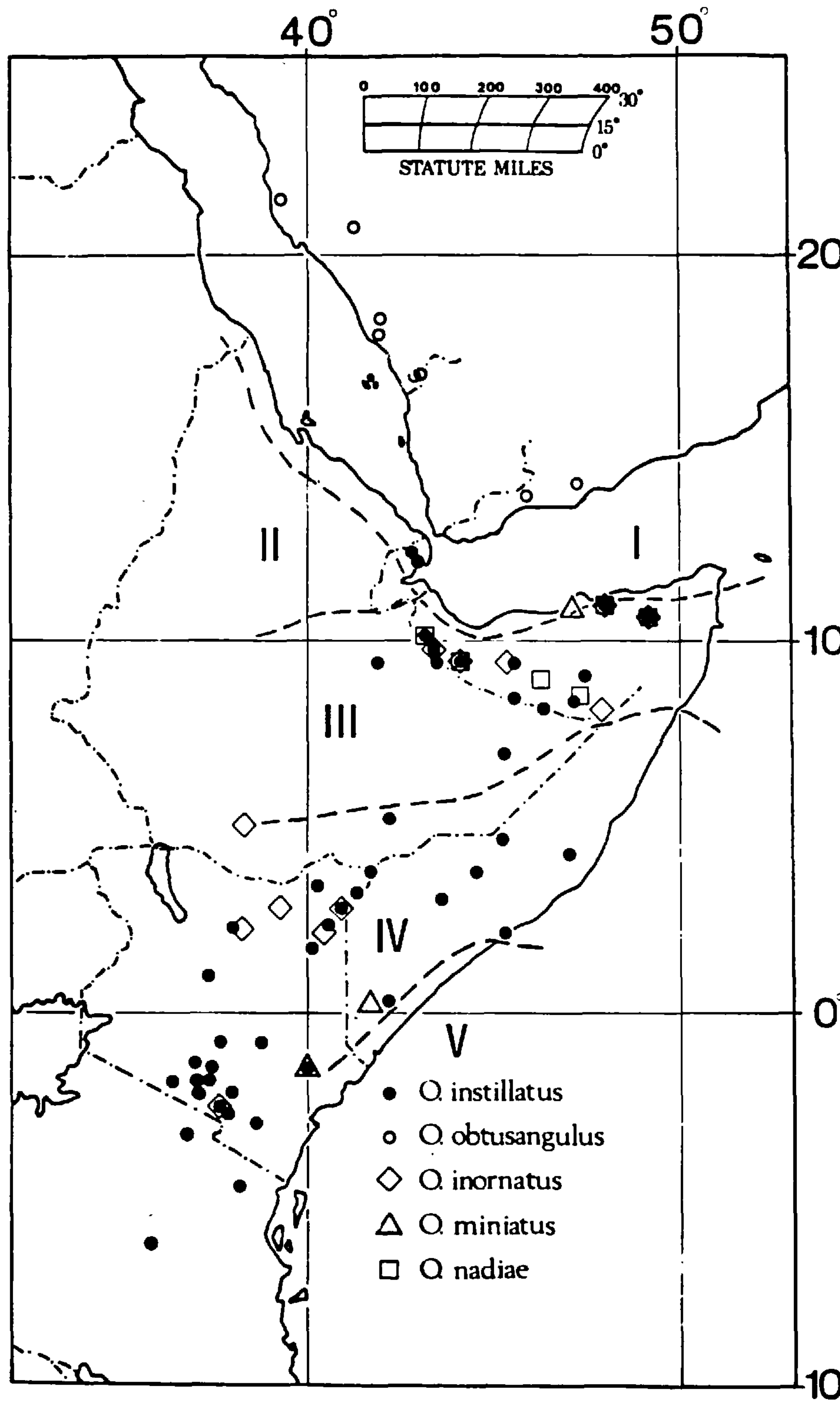


Fig. 156. Distribution of Oedaleus species in eastern Africa and south-western Arabia. Dashed lines with roman numerals, climatic zones (Griffiths, 1972).

by land-sea breeze circulation. Zone II, further west, is little studied in terms of its acridid fauna. It is a summer rainfall area, barely reached by the Intertropical Convergence Zone at its most northerly extension, and very hot and arid. Zone III, south of Zones I and II, which constitutes the main portion of the northern rangelands, has a double rainfall peak in spring and autumn but there is great variability both between stations and from year to year (50-750 mm/yr). In this zone the lowest temperatures are reached in winter (December, January). Hemming (1966) and others have drawn attention to the degradation of this area by overgrazing in recent years. Despite this however, Griffiths (1972) rejects the theory that the overall rainfall has declined during the last century. Further south, Zone IV, covering SE Somalia and the SE border of Ethiopia and NE Kenya, also has a double peaked rainfall but experiences lowest temperatures in summer (July - August). Zone V consists of a SE coastal strip with high rainfall affected by the Indian monsoon.

Oedaleus nadiae is restricted to Zone III, but its known distribution when superimposed on Hemming's Vegetation Map of Somalia (Fig.157) does not suggest any strong habitat preference except for an apparent avoidance of the montane Juniperus forest, as would be expected. The floristic diversity of the six localities from which this species is recorded suggests that the major limitation of its range may be a preference for a winter temperature minimum rather than a summer one.

In all, four species of Oedaleus are endemic to the Somali Peninsula including O. inornatus (Fig.156), a species with a similar range to O. instillatus, and three more extend westwards across the subsaharan latitudinal belt as well, and one species, O. flavus, discussed above, occurs as a separate subspecies in southern Africa. This preponderance of species, coupled with a complete lack of West African endemics and the fact that most of the southern African species are closely related,

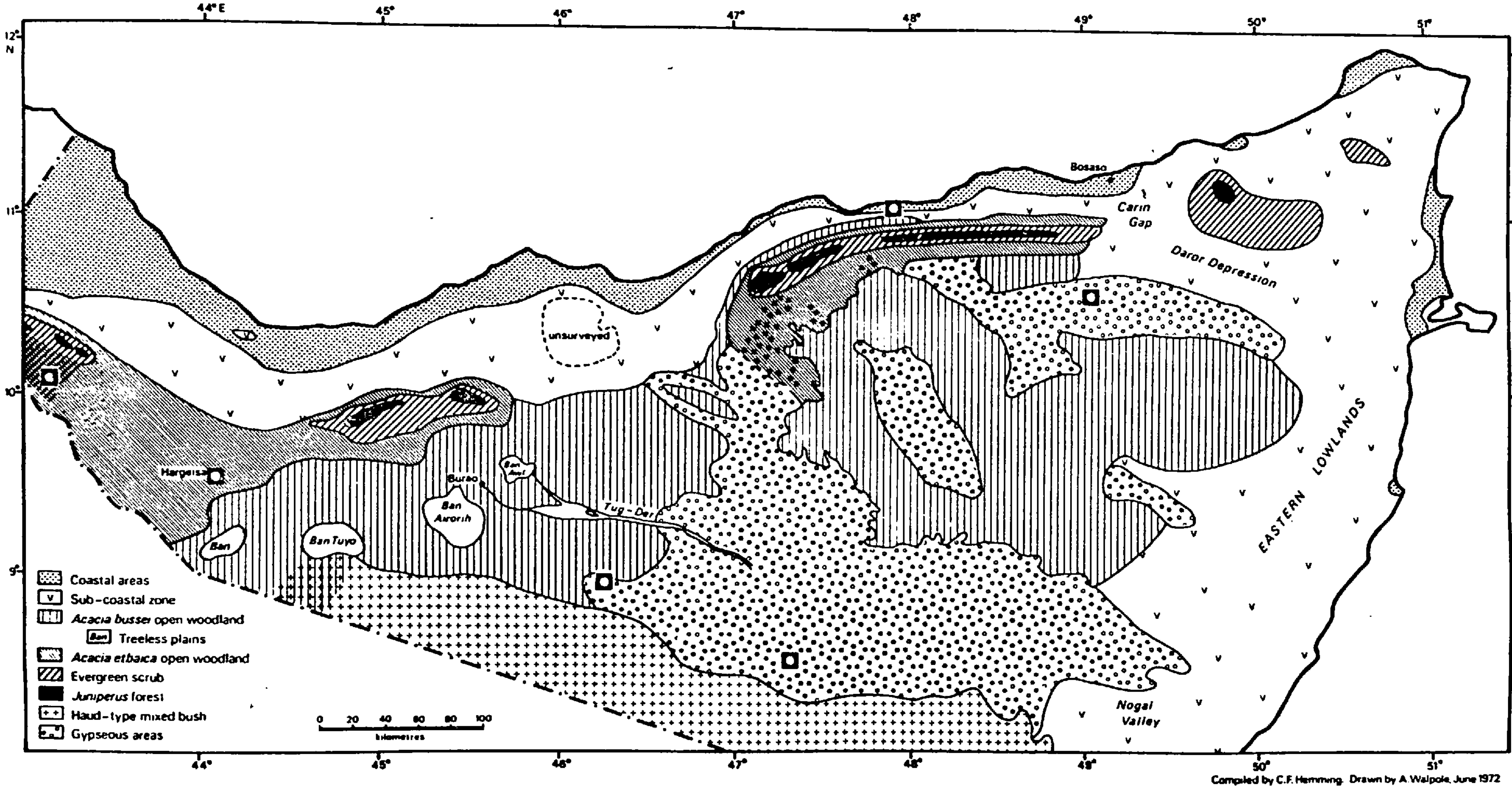


Fig. 157. Vegetation of the northern region of the Somali Republic (after Hemming, 1966) showing the distribution of Oedaleus nadiae sp. n. (black squares with white centres).

suggests that the Somali Peninsula has been the focus of speciation and radiation in the genus. Three members of Group I, one member of Group II, both of Group III, and the two ungrouped species all occur within this area. The species of group II have spread widely. O. instillatus is an East African endemic (Fig.156), but O. obtusangulus (Fig.156) occurs on the far side of the Red Sea in southern Arabia and has a smaller separate population in the mountainous region of Aïr in northern Niger. The remaining member of the group, O. rosescens, discussed below, is endemic to the Indo-Pakistan border area (Fig.158).

1.2.6 The Oedaleus fauna of the sub-saharan latitudinal belt

In his reviews of the Pleistocene in Africa, Moreau (1963, 1966) has shown that the Sahara has undergone far-reaching changes during the last 30,000 years. Plant and animal remains from the Ahaggar Massif 400 miles into the western Sahara indicate that Palaearctic elements were able to reach the centre of the desert during cool periods around 20- 30,000 years ago, and even more recently Mediterranean vegetation apparently reached Aïr and Tibesti and possibly even further south. Ethiopian fauna also spread across the Sahara to north Africa during the late Pleistocene. From this Moreau concludes that at least in the western half of the Sahara there was during a period up until about 5,000 B.P. no effective barrier to movement. From about that time Tibesti developed an Ethiopian flora, partly as a result of the great enlargement of Lake Chad between about 22,000 and 8,500 years ago when it extended for four hundred miles north of its present limit and was as large as the Caspian Sea. East of Aïr, at Adrar Bous, there existed about 8,000 years ago a small lake in an area which is now sand desert. To the west of Aïr, Wadi Azouak, now a dry watercourse, was

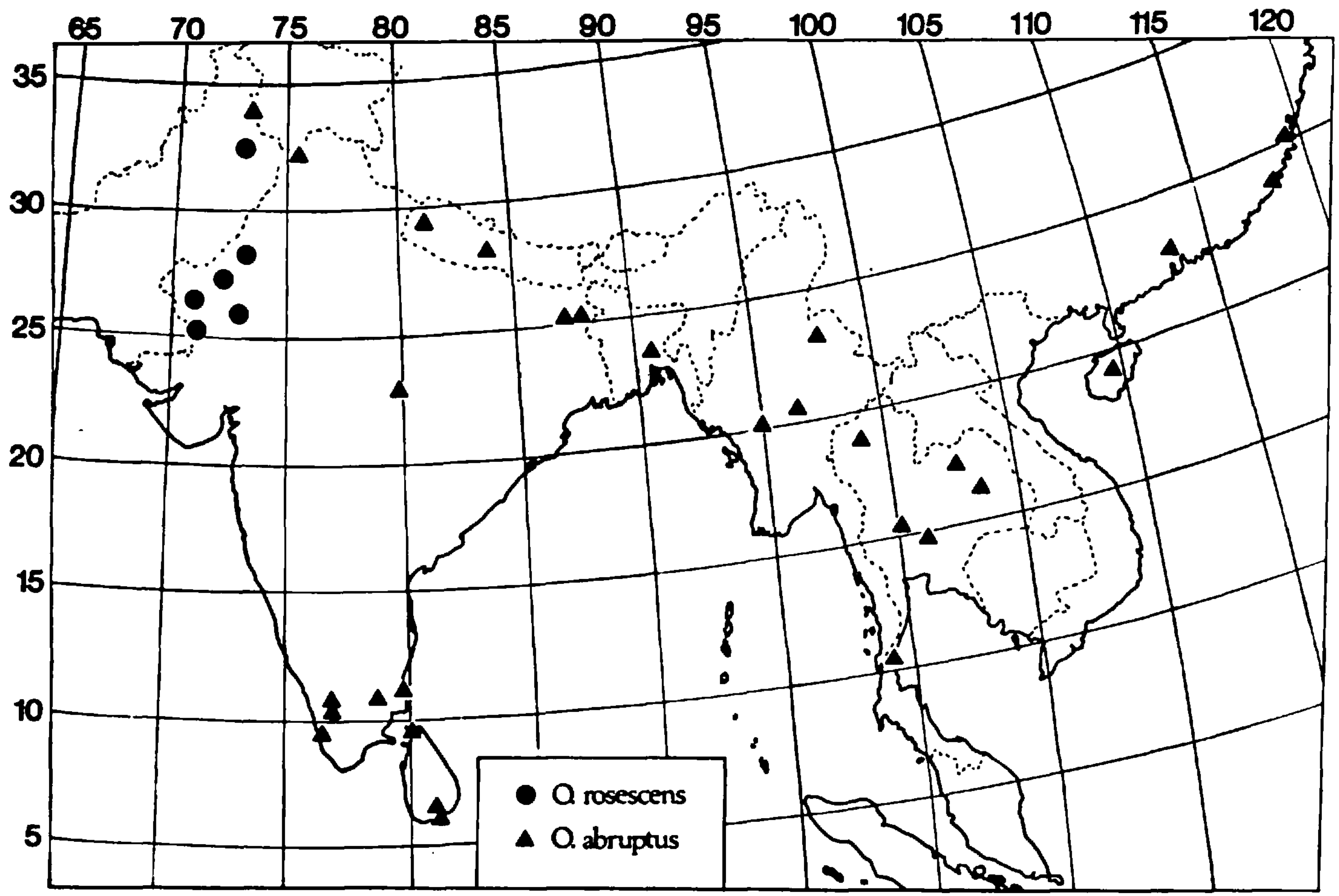


Fig. 158. Distribution of Oedaleus species in Asia. Circles, O. rosescens; triangles, O. abruptus.

flowing around 5,000 years ago, and, further west still, between Taoudeni and Timbuctoo, an inland basin fed by the upper Niger was forming a large lake (L. Arouane) which broke its eastward sill and drained into the lower Niger around 10,000 years ago. From this it may be seen that the western Sahara enjoyed a period of widespread climatic amelioration.

Van Zinderen Bakker (1969) reviewing recent work on the Pleistocene and Holocene lake levels of the Sahara indicates that their relationship to rainfall and temperature is very complex and warns against premature attempts to correlate all the available information into a simplistic model. He summarises available dates for lake deposits into two groups between about 40,000 and 20,000 B.P. and between 12,000 and 3,000 B.P. The earlier period is taken as indicative of the effect of the last glaciation which produced a southward movement of the Mediterranean rain belt and reduced the evaporation rate. The second period is coeval with the period of climatic amelioration after the glaciation which may have allowed the penetration of tropical rain from the south. However the effect of the worldwide brief cold spell at around 5,000 B.P. would have been to cause the tropical rain belt to move southwards again and the succeeding higher temperatures would have completed the desiccation which we see today.

These periods of climatic amelioration in the western Sahara during the last 40,000 years would have allowed the three species of Oedaleus which today have a subsaharan distribution to move northwards into areas which are now completely inhospitable. This may explain the presence of small populations of O. senegalensis in north Africa. O. decorus, the only other species of Oedaleus which occurs north of the Sahara today is also a member of Group I and has become adapted to the winter rainfall Mediterranean zone (Fig.159). If it originated in Africa south of the Sahara it is impossible to establish positively

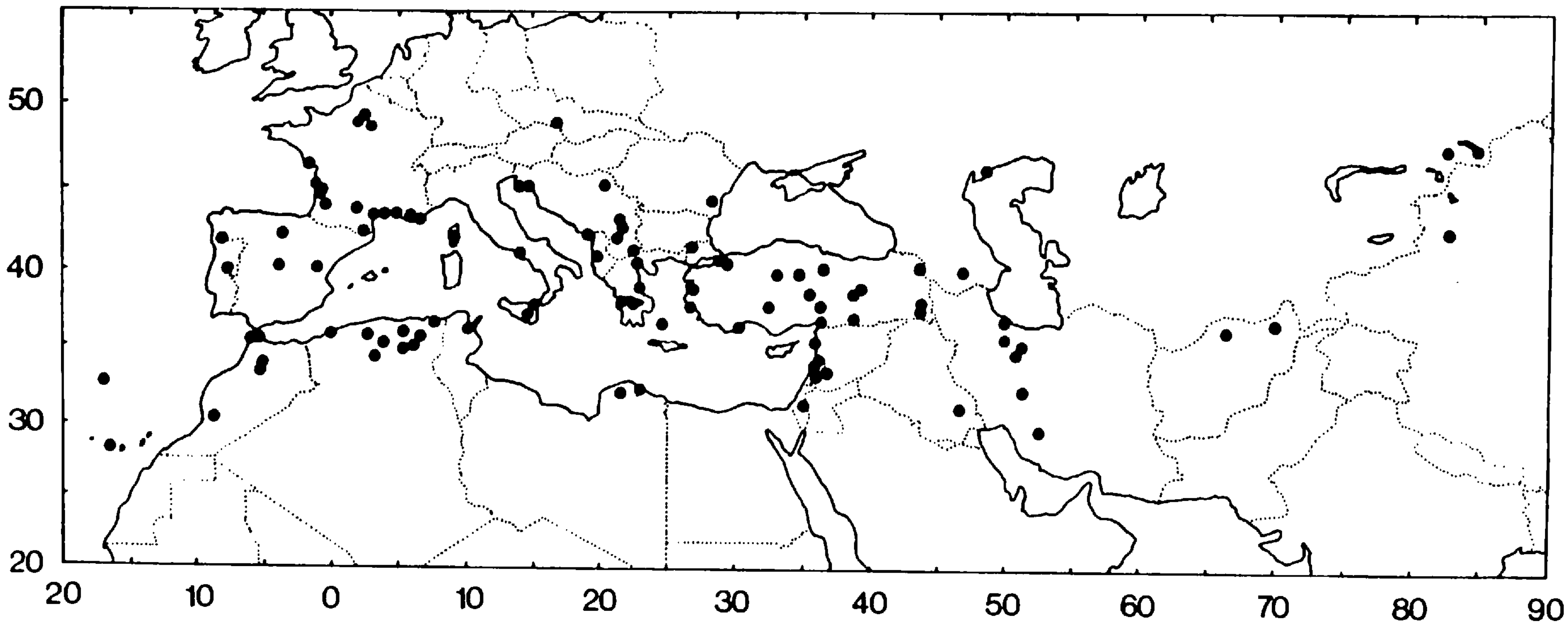


Fig. 159. Distribution of <u>Oedaleus decorus decorus</u> in north Africa, southern Europe, and western Asia.

whether it entered Europe via the Middle East or from north Africa. The present discontinuous distribution of Oedaleus obtusangulus in SW Arabia and Yemen and the Aïr mountains of Niger presumably represents a relic of a much wider continuous distribution during a time of climatic amelioration in the Sahara. This kind of disjunct distribution also occurs in Truxalis longicornis but it is surprising that Aïr should be the only known locality for O. obtusangulus in the Sahara since it only just reaches the lower altitudinal limit of montane conditions whereas Tibesti and Ennedi, or even Ahaggar to the north, are much more substantial mountain refuges. It seems likely that the absence of O. obtusangulus from these areas is more apparent than real and that further populations will come to light. The lack of any discernible differences in morphology between the West African and Arabian populations indicates that this is a very recent disjunction.

While conditions in the Sahara itself were improved during the periods described above, paradoxically desert conditions moved southwards leaving a line of dead dunes 300 miles south of the present limit of moving sand (Fig. 160). It is known that this would have occurred around 20,000 B.P. at the height of the last glaciation, when the Mediterranean rainbelt moved towards the equator (Hamilton, 1976). As a corollary of this advance of the desert, all the vegetation zones to the south must have shifted a corresponding distance and the forest would have been reduced to isolated patches.

These dramatic fluctuations of climatic conditions south of the Sahara doubtless account for the poor representation of grassland acridid species, including Oedaleus, when compared with eastern and southern Africa. The parallel arrangement of vegetation types from Senegal to Ethiopia has given rise to a corresponding distribution of Oedaleus species, of which the most northerly is O. johnstoni. This species is sporadically distributed across the subdesert steppe and

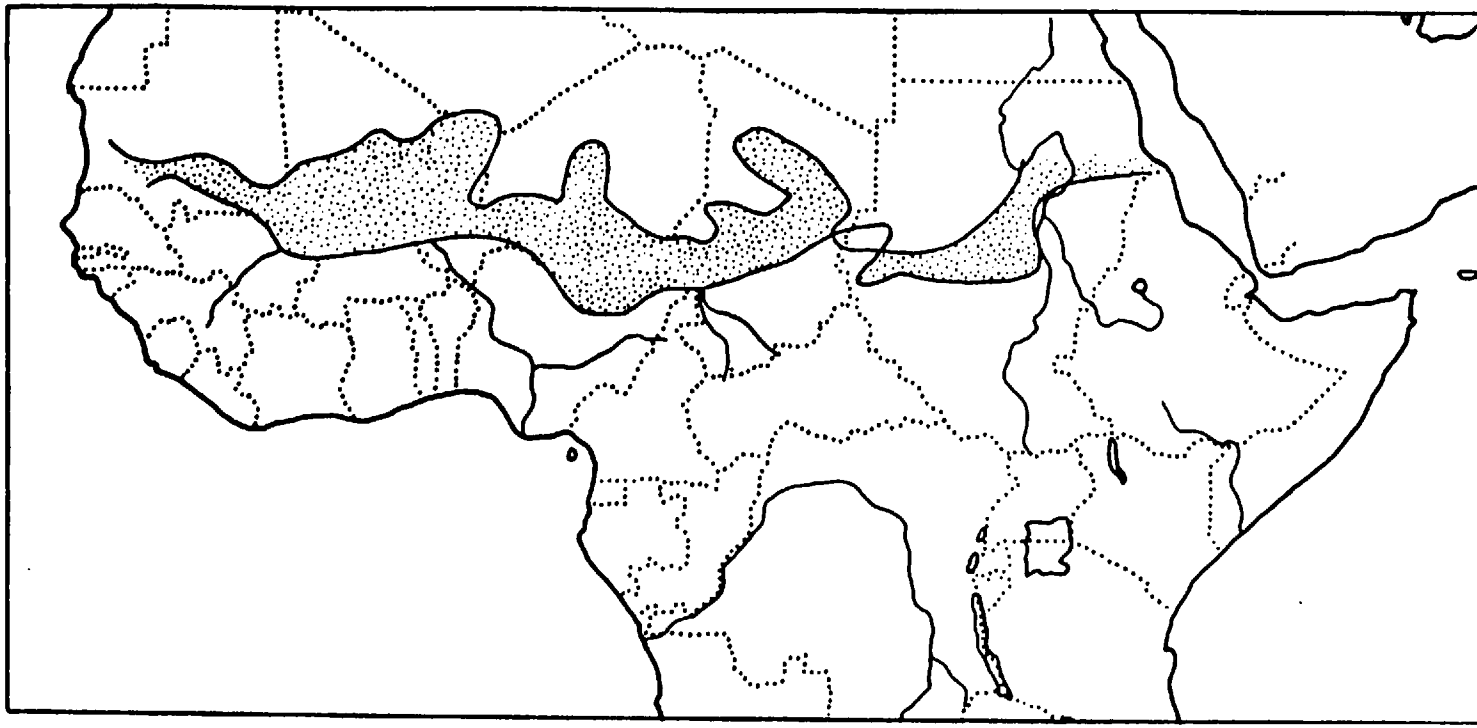


Fig. 160. The evidence for the southward advance of the Sahara during the late Pleistocene (after Hamilton, 1976). Stippled area, belt of fixed dunes.

Sahel savannah (Fig.155) on silt and clay soils in wadis and on clay plains. In view of the mobility of the species, the unconfirmed record from Oman seems quite credible.

Further south (Fig.161) _O. senegalensis_ forms a broader, overlapping band across the Sahel and into the Somali peninsula. West of L. Chad the southern limit of this species corresponds closely with the belt of dead sand dunes mentioned above (Fig. 160). Isolated populations of _O. senegalensis_ exist on both the Canary Is. and the Cape Verde Is. The Cape Verde population has given rise to a melanic form which is described and discussed elsewhere (Ritchie, 1978). It is however of interest that according to Moreau (1966) the present day aridity of the islands has been exacerbated by human degradation of the original endemic vegetation since the discovery of the islands around 1460 AD. This has now been reduced to inaccessible patches on cliff ledges. _O. senegalensis_ may thus be a relatively recent invader though the eastern islands which are low and sandy have probably always been more suitable for the species than the rocky western islands. Outside Africa _O. senegalensis_ occurs around the fringes of the Arabian desert and northwards into the western U.S.S.R. and eastwards through Iran to India. An attempt has been made (Batten, 1969) to relate its distribution to the area between the mean annual isohyets of 10 and 40 inches. However _O. senegalensis_ is found in Arabia where the rainfall is less than 10 inches, and in India where it is in excess of 40 inches per annum.

The southernmost subsaharan range is that of _O. nigeriensis_ (Fig.162) which occupies a variety of vegetation types from the Sahel savannah through the _Isoberlinia_ wooded savannah to the forest-savannah mosaic (Keay, 1959). In East Africa the species occurs in the moist woodland and savannah, particularly in Uganda, and south of the Equator it is found throughout the _Brachystegia_ woodland, penetrating as far as southern Zambia. At this point, around 15° S, the mopane

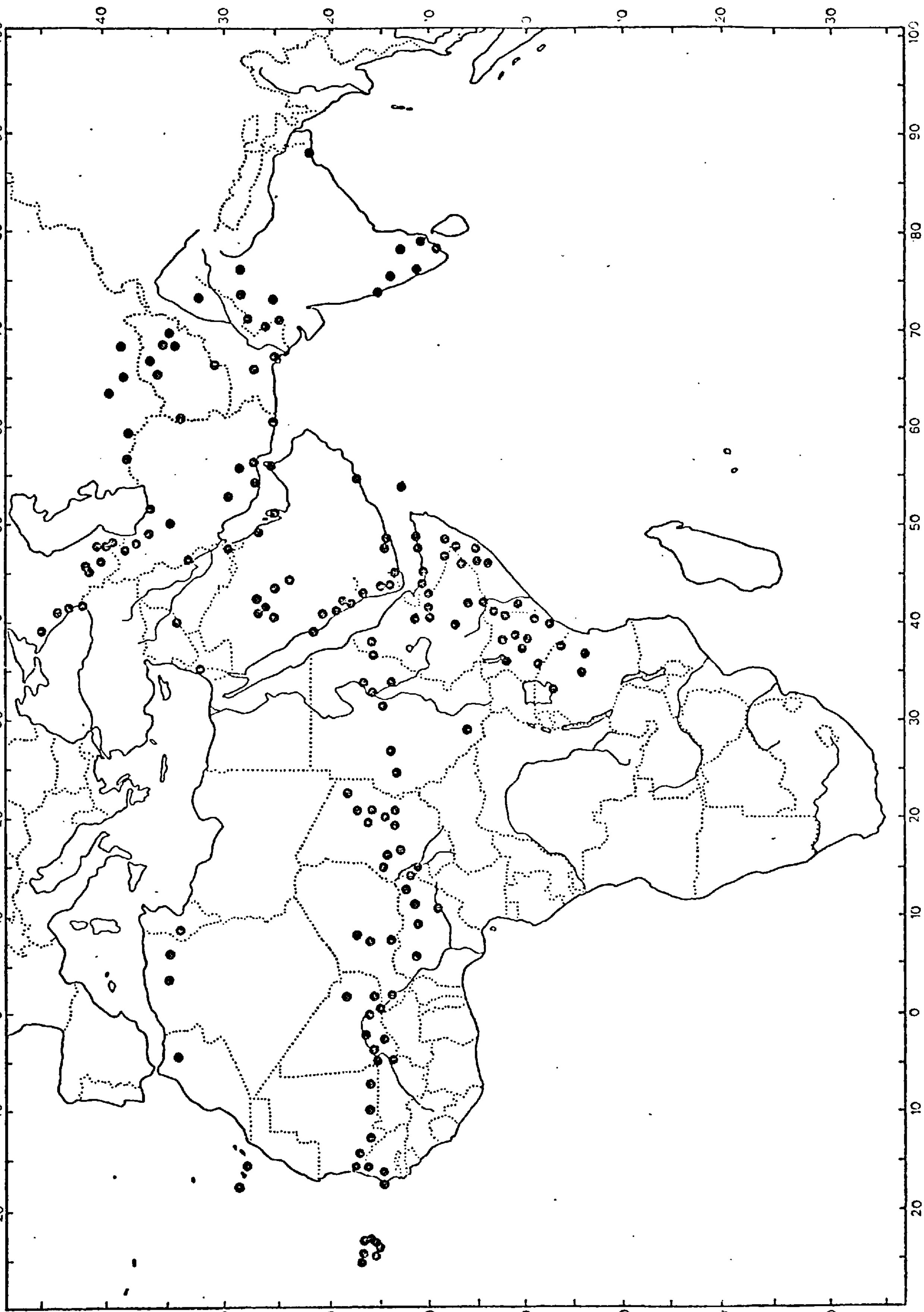


Fig. 161. Distribution of Oedaleus senegalensis in Africa and W Asia.

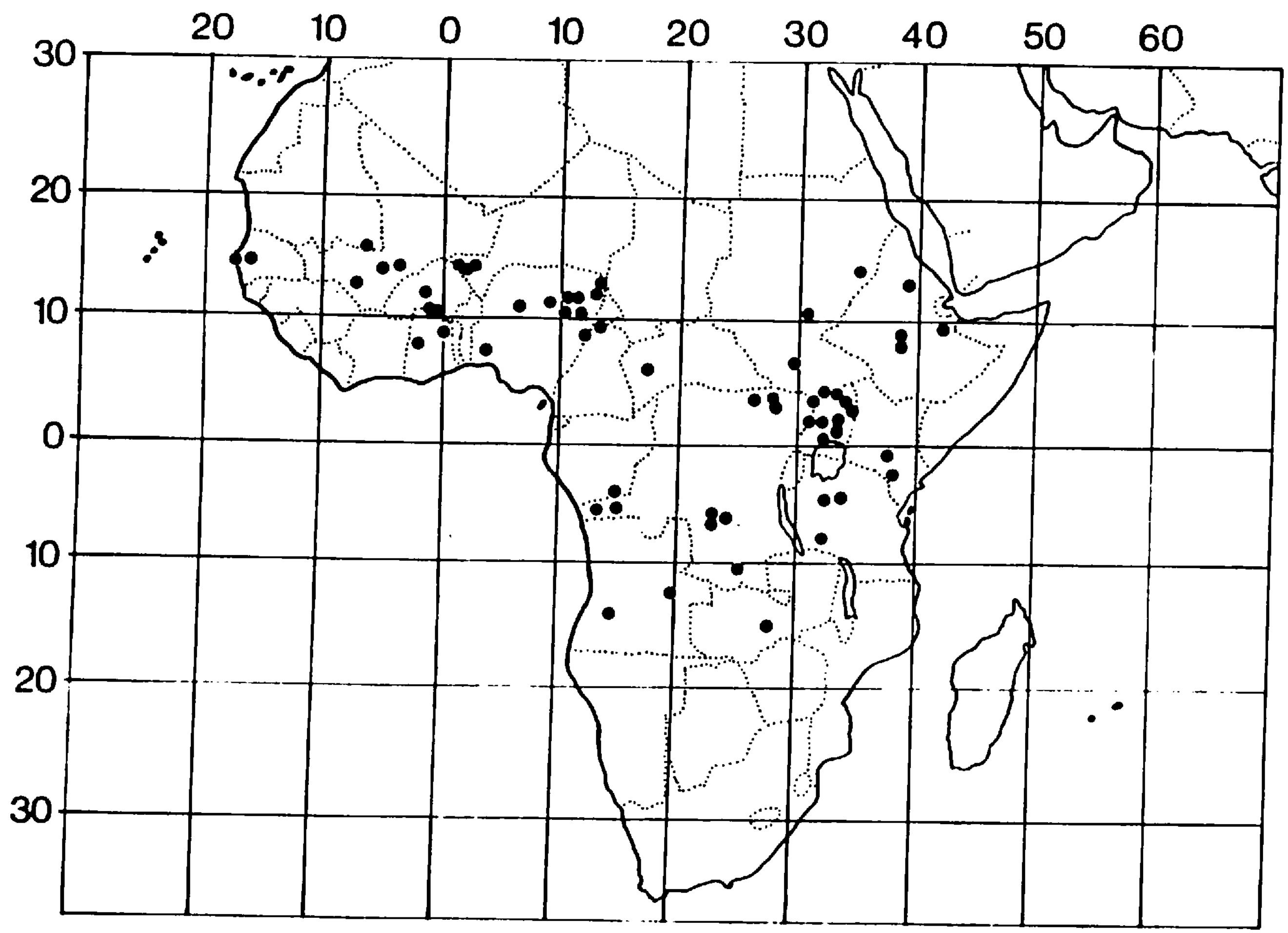


Fig. 162. Distribution of Oedaleus nigeriensis in Africa.

wooded savannah recommences and O. nigeriensis is replaced by O. carvalhoi.

1.2.7 The non-african Oedaleus fauna

The species of Oedaleus found outside Africa are, as stated earlier, either identical with, or closely related on morphological grounds to those of Africa. Madagascar possesses one very widespread endemic species, O. virgula (Fig.163) of which there is one old specimen labelled as from Zanzibar. This record is remarkable if it is genuine since the two islands are well separated and O. virgula is not known from Grand Comoro which lies between. Instead O. nigeriensis occurs on this island but not on Zanzibar which is much closer to the mainland of Africa and was only separated from it around 10,000 years ago (Moreau, 1966). There is one other old specimen of O. virgula labelled as from the Cape, but this can almost certainly be attributed to mislabelling. Very recently Dr. N. Waloff has discovered this species on the island of Aldabra, indistinguishable from the Madagascar population. It may well occur on other islands also.

In mainland Asia there are four endemic species of Oedaleus. O. rosescens, a member of Group II mentioned above, was previously known only from the desert area of N.W. Rajasthan and the Salt Range of N.E. Pakistan, on the border of another desert area, but it has recently been collected west of the mouths of the Indus at Landhi, near Karachi (Fig.158). The habitat of this species is probably similar to that of O. instillatus, a related species in East Africa, though possibly more arid. Further east Oedaleus abruptus (Fig.158), a small species in Group I, has a wide range in the tropical grasslands of southern Asia in lowland areas south of the Himalayas. This species was recently introduced into the island of Oahu in the Hawaian islands, presumably on United States aircraft

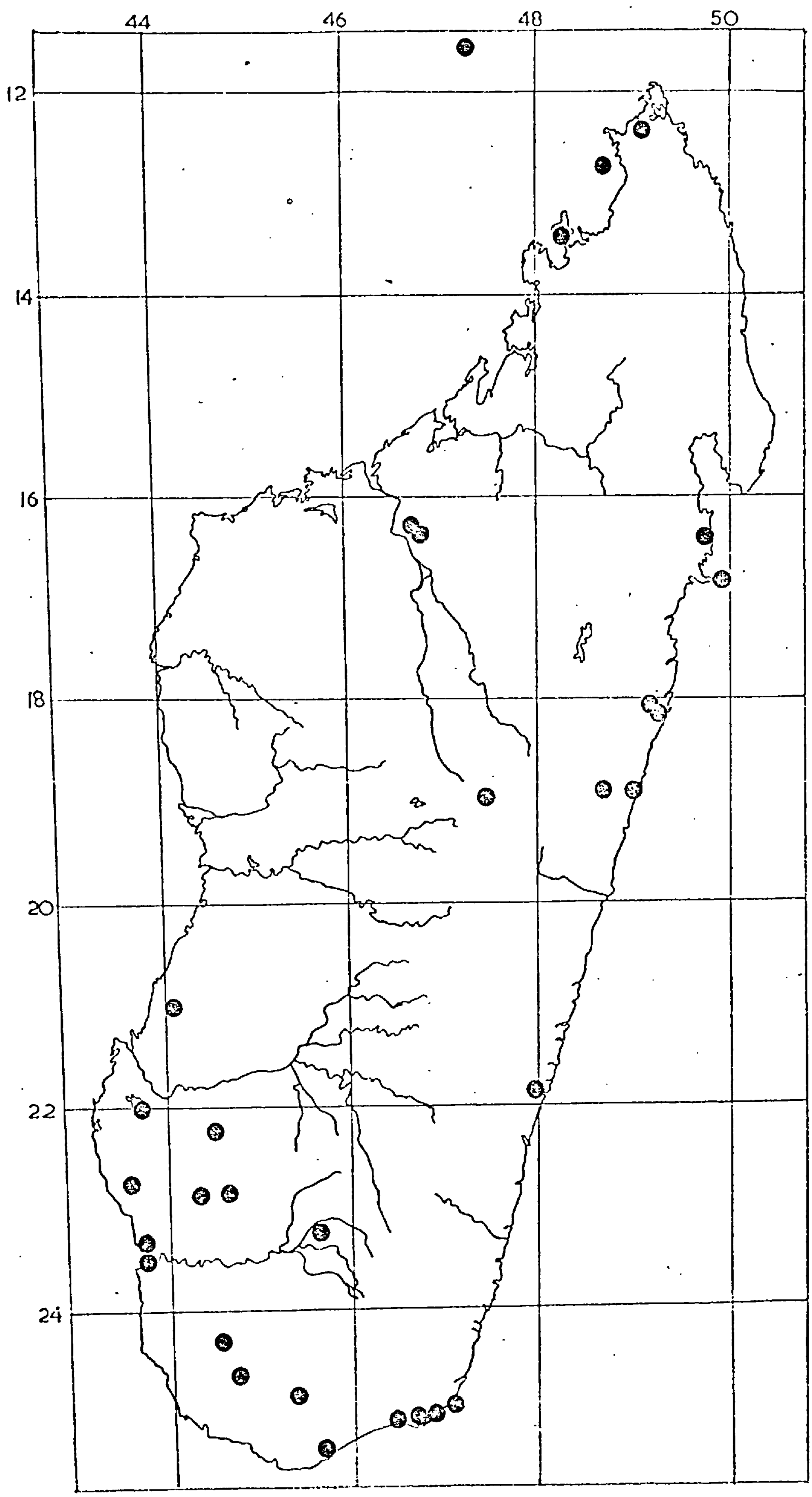


Fig. 163. Distribution of Oedaleus virgula in Madagascar.

returning from S.E. Asia to Hickam Air Force Base, Honolulu (U.S.D.A., 1968). Despite eradication attempts the species has now spread to Kauai island more than 100 miles to the west (U.S.D.A., 1976). To the east of the Himalayas Oedaleus infernalis occurs widely (Fig. 164) in southern and eastern China and into Korea and the extreme south east tip of the U.S.S.R., in areas with an annual rainfall of between 20 and 60 inches. This species also occurs in the southern half of Japan, but in Taiwan it is replaced by Oedaleus formosanus, a little-known related species which appears to be restricted to montane areas (Fig. 164). North of the Himalayas Oedaleus decorus asiaticus (Fig. 164) is distributed in the western Sayan Range and the Transbaikal region of the southern U.S.S.R., and in Mongolia, with a south eastward extension into Hopeh and Shantung provinces of China. Much of the range of this subspecies is montane and winter conditions, particularly at higher latitudes, must be very severe.

The furthest point reached by Oedaleus is the continent of Australia where one species, O. australis, occurs widely in the eastern half of the continent (Fig. 165) apparently independent of vegetation type or altitude but correlated to some extent with areas having an annual rainfall in excess of 10 inches. In the Northern Territory it is probable that the species extends further west than is known at present, but the human population density is low and the area is less well collected than the eastern half of the continent. The absence of O. australis from the south western corner of Western Australia suggests that the species has arrived since the height of the last glaciation when there was a corridor along the south coast between the desert and the sea, formed by the fall in sea level which took place in the Great Australian Bight. This is known to have provided a means of access for non-desert animals to reach the area at that time which have since evolved in isolation from the populations to the east of the desert (W. Bailey,

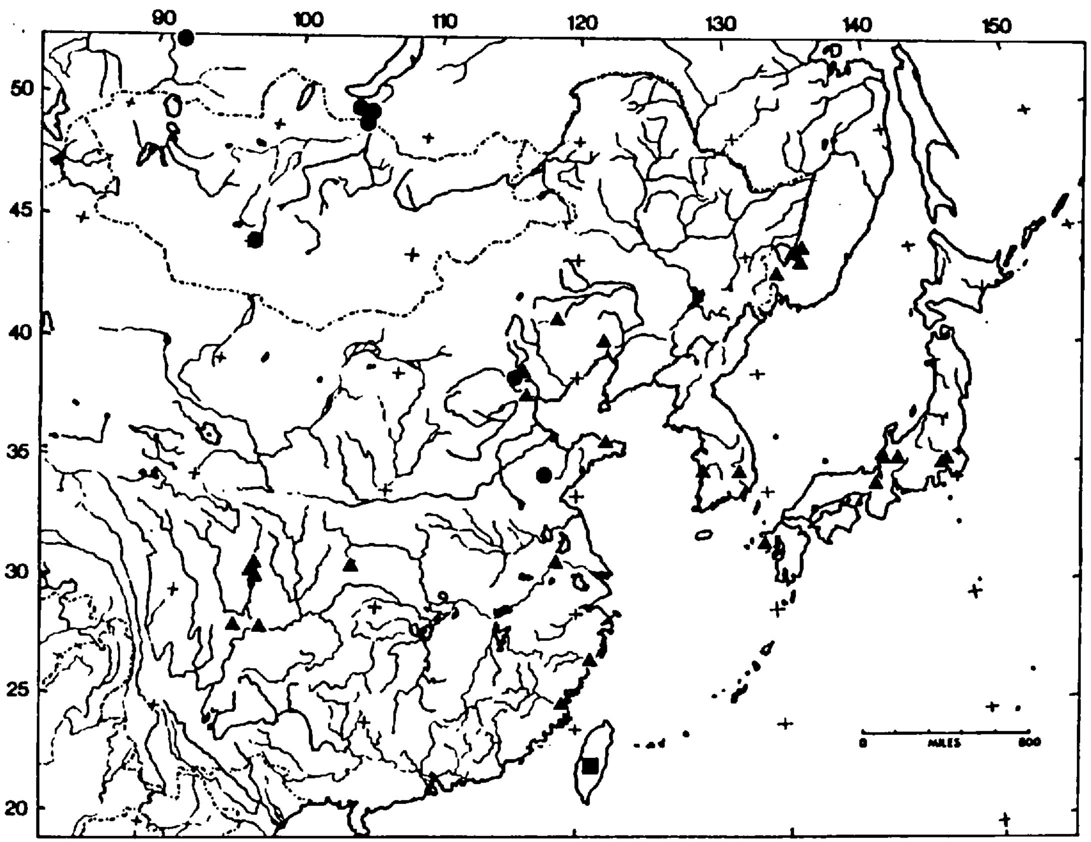


Fig. 164. Distribution of Oedaleus species in eastern Asia. Circles, O. decorus asiaticus; triangles, O. infernalis; squares, O. formosanus.

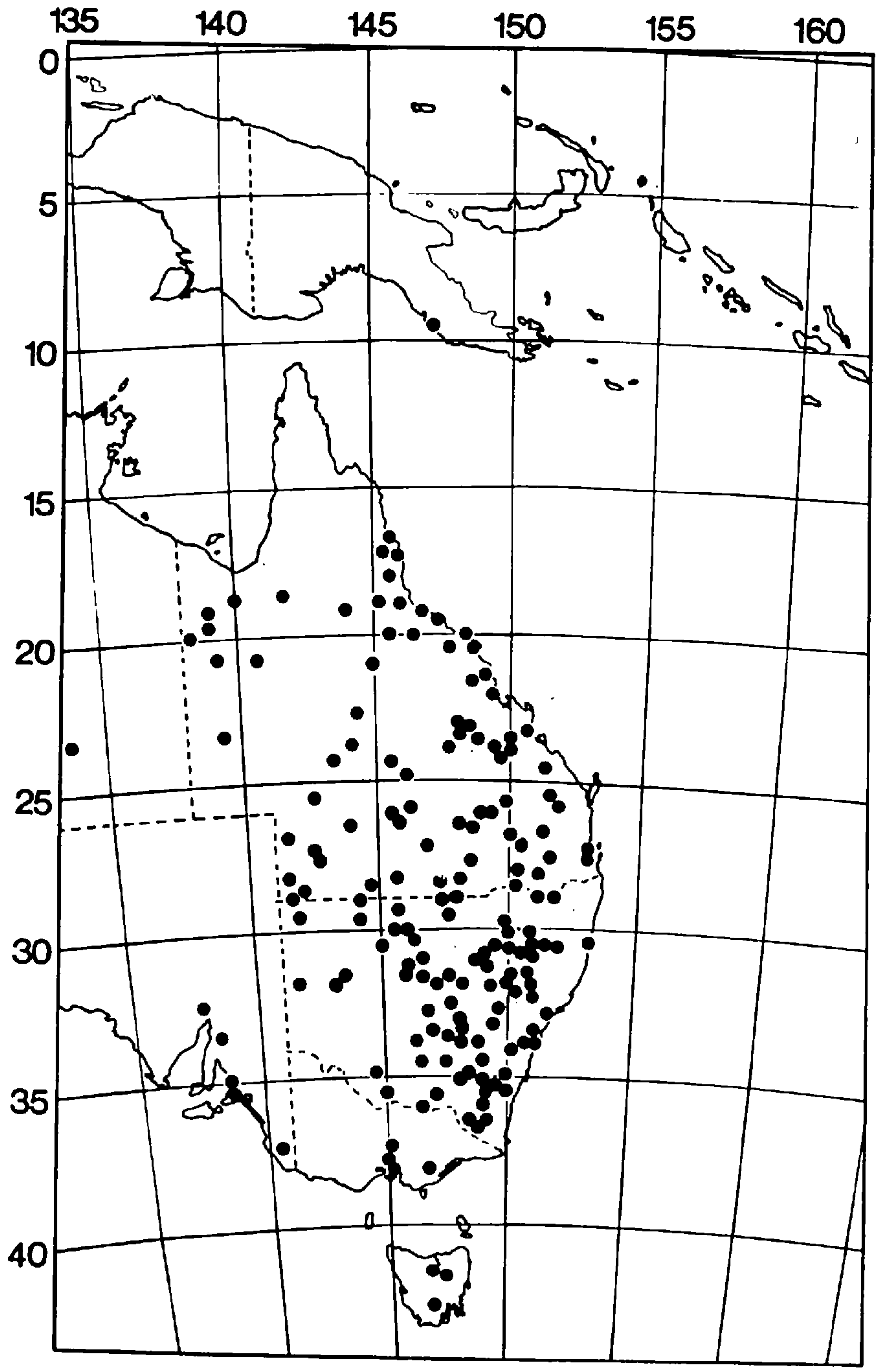


Fig. 165. Distribution of Oedaleus australis in Australasia.

pers. comm.). The single record of O. australis from Port Moresby, New Guinea, is a possible indication of the route by which O. australis may have reached Australia. However Key (pers. comm.) suggests that this may be a recent introduction. Parts of the south coast of New Guinea are quite dry but at present no other suitable sites for O. australis exist. Presumably New Guinea and the Indonesian Archipelago must have been the bridge by which Oedaleus reached Australia, but this could only have been possible at a time when these islands experienced a much drier climate than at present. Whyte (1968) brings forward the lowering of sea level at glacial maxima and the consequent increase of land surface as a possible desiccating factor. However the decline in precipitation occasioned by the glaciation itself seems a more probable cause of the spread of drought-adapted biota through areas like Malaya, Sumatra, Borneo, and New Guinea which are today mainly covered by rain forest. According to Whyte south New Guinea and Australia have many xerophytic plants which are identical to those of mainland Asia and their immigration is therefore believed to be recent. An alternative but less likely explanation of the presence of Oedaleus australis on the far side of a barrier of humid forest would be that it evolved from a form which was initially tolerant of high humidity but became more xerophilous after invading Australia. However, against this suggestion stands the complete absence of any species of Oedaleus anywhere between Thailand and New Guinea today. Instead this region has been the setting for a minor radiation of Gastrimargus species, a group which throughout its range is consistently more tolerant of humid habitats than Oedaleus.

1.2.8 Problems of analysis of distribution patterns

In discussing the distribution of a large (by the standards of the Acridoidea) genus of mobile savannah grasshoppers there are several difficulties. Firstly, there are relatively few other large genera with similar ecology which have recently undergone revision. La Greca (1970) has shown how ideas of the distribution of the Mantodea have been radically altered after comprehensive revision of the taxonomy of the group. Secondly many species of acridids are of rather infrequent occurrence despite wide ranges, and thirdly many distribution maps are based upon an inadequate coverage of the areas treated simply because collections have not been made. Representation of the genus Oedaleus in collections is probably above average because of the tendency to high population levels in many species and their concentration in the marginal agricultural areas of the Old World tropics and subtropics where locust control organisations have worked extensively.

1.2.9 East african origins of Oedaleus

In the above analysis, it has been inferred (p. 153) that Oedaleus is of East African origin, and that this is an outcome of the relative climatic stability of the area during the Pleistocene, its partial isolation both then and now, and its present ecological diversity. This is a familiar pattern of distribution since there are at least 114 genera of African grasshoppers which have some representation in East Africa. Of these 42 are endemic to the area, and 26 of those are monotypic genera. This is a very conservative estimate based on Johnston (1956, 1968) without including genera known from Tanzania unless they are also recorded from further north. Genera known from the islands off the coast of Africa are also excluded in the same way. No attempt has been made to supplement Johnston's information from more recent published or museum sources. Such a survey, to be accurate, would require the revision of all the genera of African grasshoppers. For the purposes of this study it may safely be assumed that there are more described genera represented in East Africa than the figures quoted suggest. There are also undescribed genera from Somalia in the British Museum (Natural History) which would swell the list still further.

As indicated above (p.166), the Oedaleus fauna of West Africa is much poorer than that of East Africa and entirely lacks endemic species. This is a reflection of the comparatively rather low degree of endemism among subsaharan savannah grasshoppers in general. It is however surprising that although Oedaleus senegalensis is found on both sides of the Ethiopian Highlands O. instillatus only occurs to the east although it is a widely distributed, mobile, xerophilous species. Quite possibly the rather more uniform topography and vegetation of the subsaharan latitudinal zones do not offer sufficient habitats for more than the three which are found there. In addition, despite the fluctuations of climate already mentioned, the mountains of Ethiopia and the deserts on the Eritraean coast and around Lake Turkana (L. Rudolph) must have constituted formidable barriers to any westward expansion by the East African biota. Monod (1971) has noted a parallel case of poor subsaharan representation in the genus Commiphora, one of the characteristic plants of Keay's (1959) category "wooded steppe with abundant Acacia and Commiphora". Compared to a total of about 80 East African species West Africa has only five. Monod also notes the surprising absence of the gnu and the zebra from the West African savannah.

1.2.10 The Brachystegia woodland barrier and 'trans-equatorial' speciation in Oedaleus

Another biogeographical feature demonstrated by Oedaleus within Africa is the division of the genus into northern and southern subspecies or species at the equator. This kind of distribution pattern is very common in acridids and Jago (1973) has formulated a hypothesis to account for it. According to this theory savannah grasshoppers having an adult diapause initiated by decreasing daylength north of the Equator are out of step with those on the southern side because the daylength and rainfall regimes are six months out of phase. Hence speciation can occur since sexually mature adults on either side of the Equator never meet. The hypothesis is based upon the known mechanism of photoperiodic diapause-induction in Nomadacris and Anacridium as studied in the laboratory, (Norris, 1959, 1965a, 1965b). However, as Tauber and Tauber have said in their recent review of insect seasonality (1976): "... to establish when reproduction will begin in the field it is generally necessary to know when diapause ends in nature [my underlining]. However answers to this problem are usually not well substantiated even for species whose diapause has been studied". Much field and laboratory work has been done with Nomadacris from the Rukwa valley, south of the equator, and a little on material from the Niger flood plain, north of the equator. In both areas onset of diapause coincides with changing photoperiod (Uvarov, 1977: 305), and theoretically there would be no time overlap in the breeding period to permit interbreeding. However termination of diapause in Nomadacris may well be effected by temperature change or rainfall (Robertson, 1958), and it is possible that a trans-equatorial migrant would be able to synchronise with the resident population at whatever stage was appropriate. In any event the species appears to have a continuous range from Somalia to South Africa without any discernible morphological hiatus at the equator so it cannot at present be considered as offering material support to a belief in an "Equatorial Species Dynamo".

Another factor which tends to weaken the general applicability of a specifically trans-equatorial mechanism is the prevalence of egg rather than adult diapause in Acridids. For example thirteen out of the fifty one species of Sudanese Acridoidea investigated by Joyce (1952) survive the dry season in the egg stage. In species such as these the initiation of diapause may be in response to changing day length, but this response gradually weakens in preparation for post-diapause development (Tauber and Tauber, 1976), and once again the actual trigger for development to recommence may simply be rainfall. In Oedaleus senegalensis in India there is evidence that rainfall between six months and one year after laying is sufficient to break diapause (Venkatesh et al., 1971). The occurrence of intercalary hatching in December 1961 in the Cape Verde Is., in response to unusually heavy rain (Saraiva, 1962; Batten, 1969) may indicate that eggs can hatch soon after laying, even at the end of the season when they would normally diapause. Clearly, if photoperiod does influence egg diapause in O. senegalensis, the influence is on its induction and may be weak and of short duration. A trans-equatorial migrant of this species would presumably have no difficulty in adjusting to the new seasonal timing. However, it is not clear whether the delayed hatching of the eggs of Oedaleus is a true diapause or merely a quiescence resulting from lack of moisture.

Jago (1973) has pointed out that Locusta in Africa cannot exist at high population densities after invading areas south of the equator. However this species appears unable to maintain high densities anywhere else either, apart from the main outbreak area in the flood plain of the Niger. There are in fact many species which do succeed in spanning the equator apparently without alteration (e.g. Dnopherula cruciata, Humbe tenuicornis, Trilophidia conturbata) though there is always the possibility of unrecognised cryptic speciation. The most well-studied example of this phenomenon concerns Eyprepocnemis plorans. This species was divided by Dirsh (1958) into several 'subspecies' of which ornatipes and meridionalis are found to the north and south of the equator respectively. John and Lewis (1965) demonstrated meiotic breakdown in hybrids between these subspecies, indicating that speciation had occurred. No F2 generation hybrids could be produced. There is however no direct evidence that this was directly attributable to trans-equatorial effects. E. p. ornatipes is apparently not found nearer to the equator than Northern Kenya, while E. p. meridionalis in the south penetrates northwards as far as 3^{o}S on the west but only about 7^{o}S in the east of Tanzania. Remarkably, the intervening area is occupied by a hybrid not between these two species or subspecies, but between E. p. meridionalis and E. p. plorans, the Mediterranean form. Clearly this is a rather complex situation, but one feature of it, the diagonal northern boundary of the E. p. meridionalis zone just south of the equator in N. Tanzania, recurs time and time again in the distribution of African acridids and is particularly noticeable in Oedaleus. Examples of northern species which show a discontinuity at this point are O. senegalensis, O. flavus somaliensis, O. instillatus. All these cross the Equator but are apparently unable to advance across the Brachystegia woodland zone, within which the only species of Oedaleus found is O. nigeriensis.

In Aiolopus simulatrix, a member of a related genus revised by Hollis (1968), there is a good example of subspeciation exactly at the northern boundary between the savannah and woodland. On the savannah side of the boundary occurs Aiolopus simulatrix simulatrix, and on the woodland side to the south is found A. s. femoralis. Some acridid species, including Oedaleus plenus plenus and Aiolopus meruensis, occur both north and south of the barrier apparently unaltered, but are never found within the woodland itself. Other species are split into sub-species or species pairs either at the savannah/woodland boundary or across the width of the woodland barrier itself. The major examples of these effects have been described above (p. 158). Key (1959) has pointed out the importance for grasshoppers of "ecotones and mosaic habitats in which the scale of the patchwork is adjusted to the vagility of the species". In Acorypha, a genus of grasshoppers of rather low vagility, speciation has occurred in response to quite small scale geographical features. This has perhaps been assisted by ecological specialisation and the variability of genital morphology allowing pre-mating isolation of newly diverged forms. Only in one species, A. glaucopsis, is there a clear separation at the savannah/woodland boundary, regarded by Jago (1973) as a delayed response to the equator. Oedaleus and Aiolopus on the other hand are both xerophilous genera of high vagility requiring as a rule wide separation to prevent continual reinvasion of disjunct populations. This is particularly true in view of the low level of interspecific variation both in ecology and in genital morphology. The suddenness of specific and subspecific discontinuities and the number of species in which they may be observed, are strong evidence in favour of the view that speciation among the more xerophilous savannah grasshoppers occurs not at the equator but on the northern and southern boundaries of the Brachystegia woodland which constitutes a barrier of no less than 500 miles at its narrowest point, and effectively much wider, particularly when the Southern Highlands of Tanzania are added to the problems encountered by migrant insects.

1.2.11 The woodland barrier and the 'arid corridor': biogeographical evidence from other groups.

The evidence for the importance of the Brachystegia woodland barrier in the evolution of the Acrididae discussed above is strongly reinforced by recent biogeographical studies of other groups of animals and plants. The affinities between the biota of the arid and semi-arid regions of south western and north eastern Africa have been noticed by many biologists and in recent years several of them have suggested that there must have been a former link between the two areas. For example Monod (1971) has shown that of 556 genera of flowering plants occurring in the Sahel 354 (63%) also occur in the southern savannah. Balinsky (1962) has indicated the existence at the present day of an 'arid corridor' joining these regions which could be defined in terms of a rainfall of less than 10 mm per month during at least three consecutive months (fig.166). The disjunct distribution patterns of large numbers of plants and animals suggest that, for them at least, the arid corridor is no longer effectively open and that the belt of Brachystegia woodland now constitutes a complete barrier between the more arid regions north and south. Monod (1971) found that out of 84 genera of flowering plants analysed 50 had disjunct north/south distributions. 40 species of plants and 2 species of coprophilous fungi were found to occur in the northern and southern arid zones but nowhere in between, and Lebrun (1971) has described four more cases of flowering plants with the same disjunct range. De Winter (1971) noted that in the Poaceae alone there were 17 species with discontinuous distributions in the northern and southern arid areas.

Discussing the resemblances of the bird fauna of north-east and south-west Africa, Winterbottom (1967) has estimated that there are 205 species in the S.W. arid zone and 133 in the former British Somaliland and the Gulf of Aden. Of these about 30 species are held in common either as the same or different subspecies, species pairs, or close relatives. From this analysis Winterbottom reached the following conclusions: 1. the necessity of a past connection between the arid faunal areas of Chapin (Fig.167). 2. the different degrees of differentiation between northern and southern populations suggest that there has been more than one period when the corridor was open.

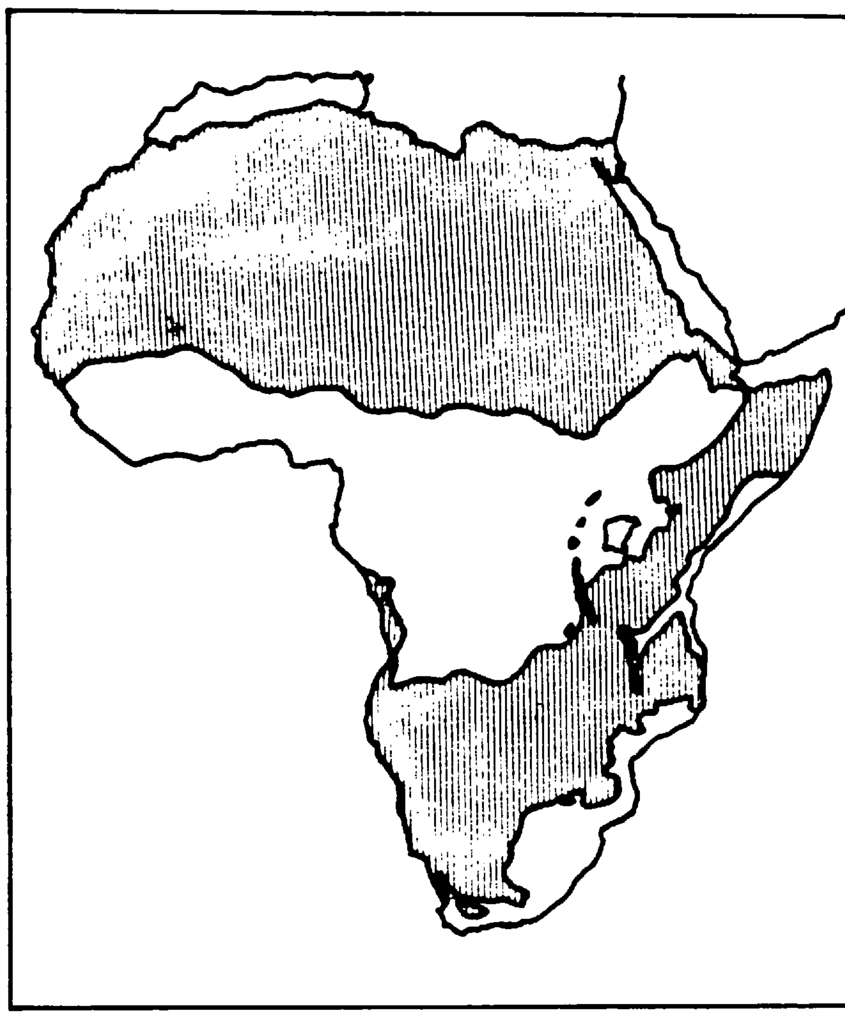


Fig. 166. Distribution in Africa of arid regions having less than 10 mm of rainfall per month during at least three consecutive months (after Balinsky, 1962).

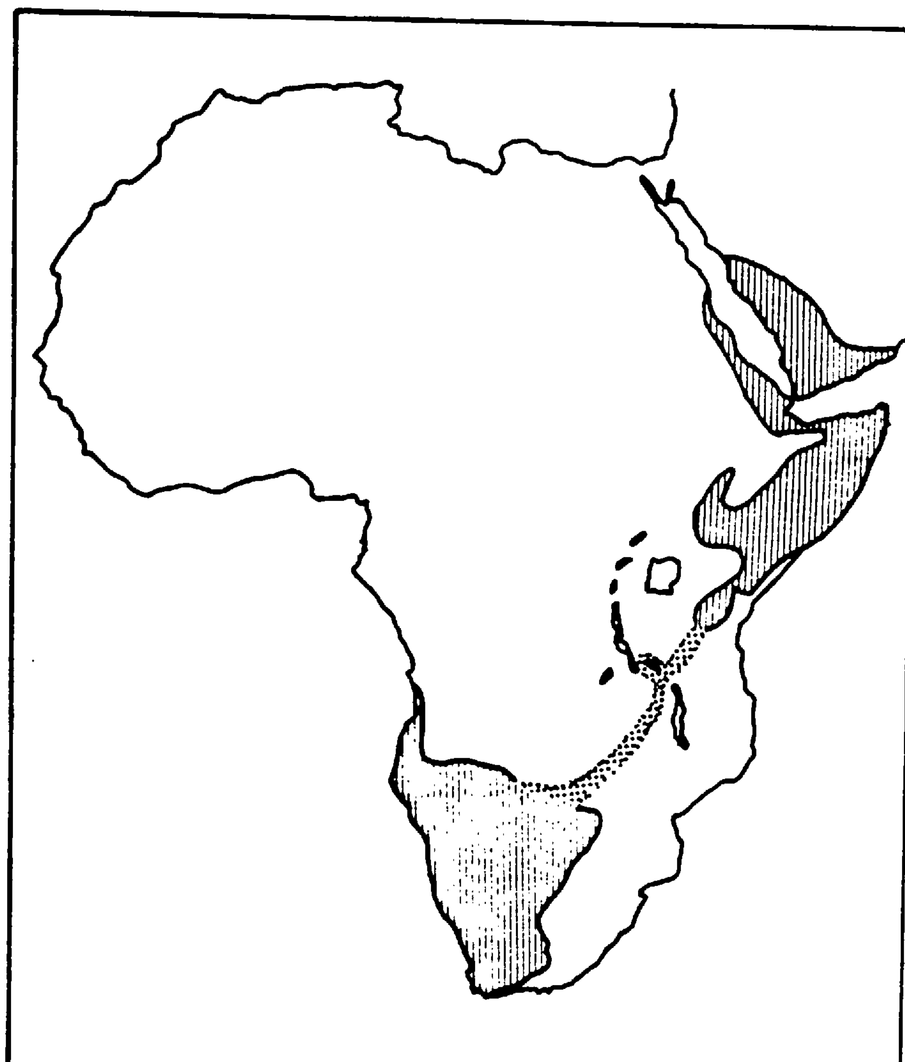


Fig. 167. Outline map of Africa showing Somali Arid and South West Arid Districts (vertical lines) and the suggested past corridor between them (dots) (after Winterbottom, 1967).

3. the high degree of endemism in the two areas suggests that the link between them has been of brief duration or incomplete, or both. He makes the suggestion that the link would have followed the Luangwa valley which at present carries more open vegetation north-eastwards far into the Brachystegia zone. Even today several southern bird species penetrate northwards along this valley to within 150 miles of the dry wooded steppe of NE Tanzania which advances south along the valley of the Great Ruaha river.

Among mammals also there are striking examples of disjunct distribution which suggest the existence of a former connection between the northern and southern arid zones. Roberts (1937, 1937a) noted the discontinuous ranges of the dik-dik, Madoqua kirki, which has a south-western subspecies damarensis (Monod, 1971), and of the oryx, which forms a species pair with Oryx gazella in the south-west and O. beisa in the north-east (Meester, 1965). Meester has also noted further examples including the bat-eared fox, Otocyon megalotis, occurring in both arid regions, and the gerbil which has two closely related species in the two areas. Bigalke (1968) has estimated that the Somali peninsula has about 15 endemic mammals and notes the occurrence of a distinct species of hartebeest, Alcelaphus lichtensteinii in the Brachystegia zone separating different subspecies of A. buselaphus in the north-eastern and south- western arid areas. As further evidence of a past corridor Verdcourt (1969) has stated that the gerenuk, "a typical Somali thornbush antelope extending to N. Tanganyika" has been found fossil at Broken Hill in Zambia, an area presently surrounded by Brachystegia woodland.

Bigalke (1968) considers the observed overlap of some woodland mammals into arid areas as encroachment. However, they could also be regarded as relicts of former woodland extensions. For example Davis (1962) has noted that several southern African species of Muridae which avoid arid areas reach as far north into the savannah as the Tana river watershed in southern Kenya, a level known to zoogeographers as 'Sclater's Line'. Kingdon (1971) suggests that a past extension of the Congo forest eastwards from the north of L. Victoria to Sclater's Line was responsible for the racial divisions of hartebeeste and savannah monkeys (Cercopithecus) to the north-east and south-west. Even under present day conditions one may see from the vegetation map of Africa (Keay, 1959) that there is a considerable barrier to movement of lowland savannah biota across this mosaic of lakes, montane forest, and moist woodland. An additional isolating factor already mentioned above (p. 184) in relation to latitudinal movements, but equally important in impeding north-south mobility, is the desert and subdesert extending south-eastwards from L. Turkana. If it is certain that forest and woodland have on occasions formed an effective barrier under extreme pluvial conditions, it is at least probable that under conditions of increased aridity the Turkana desert would have enlarged suffiniently to impede the migration of less xerophilous biota.

Among entomologists the faunal links between the northern and southern arid zones have apparently received relatively little attention. Koch (1960) has noted the similarities between the Tenebrionid beetle faunas of the Namib desert and the deserts of northern and eastern Africa and even Asia at the tribal level. The extensive and often sympatric speciation in the Namib and the very high degree of specific endemism indicate an ancient union of this area with other deserts in Africa and Asia. However, this could only have resulted from an earlier, more sustained, and more extensive period of aridity than that being postulated here as responsible for the reunion of semi-arid rather than true desert biota. In the Rhopalocera Carcasson (1964) has shown that north-east/south-west speciation is rare since butterflies are essentially insects of forest and woodland which have not extensively colonised the more open vegetation zones. However, there are minor centres of speciation within the Brachystegia woodland and in the north-east arid zone. By contrast to the Tenebrionidae, the butterflies have no centre of radiation within the south-west arid zone. There are however disjunct north/south distributions in the genera Dixaea and Colotis. Carcasson notes that even those species of Colotis which are tolerant of woodland have undergone speciation as a result of a past eastward extension of the forest.

This brief review of recent literature indicates a growing awareness of the rôle of the Brachystegia woodland barrier in the evolution of the savannahs and steppes of Africa, and the past existence on one or more occasions of an arid corridor between the north-eastern and south-western semiarid zones. In addition to this biogeographical evidence there is a growing body of palaeoecological data to assist in reconstructing the changes in the climate and vegetation of Africa during the late quaternary. A useful summary has been given by Van Zinderen Bakker (1976) whose theoretical reconstruction of the vegetation of subsaharan Africa has been mentioned earlier (p. 156 & Fig. 151). In this review (p. 174) Van Zinderen Bakker concludes that during "dry glacial times ... the 'arid corridor' ... would have been open". However, in an earlier paper (1969: 139) he had suggested that "present-day rainfall maps show that a corridor ... probably existed during periods with a high temperature". He added that pollen analyses at Kalambo Falls at the southern end of L. Tanganyika show that "conditions could have been hot and dry in the gap between the Ufipa Plateau and the Malawi Mountains during one of the warm interstadials or during the postglacial temperature optimum". Hamilton (1976) puts the case for the fragmentation of the Congo forest during at least the period of the last glacial maximum between 25,000 and 12,000 B.P. and suggests that the forest may not previously have been continuous across the Congo basin until as far back as 75,000 B.P. During some part of this period the East african arid corridor was presumably open at least partially or intermittently. In an earlier review of the subject Moreau (1966) had put forward the theory that montane forest would have descended from about 1500 m to 500 m at the last glacial maximum, isolating lowland savannah biota in widely separated refuges, but this has since been rejected as unrealistic (Van Zinderen Bakker, 1975).

1.2.12 Conclusions

From the above it will be apparent that the exact timing and duration of any past breaches in the woodland barrier, and the degree of contact between north and south that they afforded, are still matters for discussion. What now seems certain however is that the Brachystegia is an effective isolating mechanism at the present time, and that it has been breached by a corridor of more open vegetation one or more times in the past. The effect this has had on the flora and fauna of Africa is becoming steadily clearer. In the Acridoidea the cyclical separation and reunion of the eastern and southern savannahs explains much of the observed speciation and subspeciation in xerophilic genera. In view of the subtlety of the morphological changes which often accompany this evolutionary process there is a need for thorough revision of savannah genera with more attention to biogeographical considerations. The possibility that cryptic speciation may occur in disjunct populations of acridids highlights the importance of cytogenetic studies like those of John & Lewis on Eyprepocnemis plorans as a necessary back-up to morphological methods. The more precise understanding of the taxonomic status of grasshopper populations which could be gained by such studies would be of practical service in the control of pest species by indicating whether biological data which have been gained, for example, from northern populations of a species are likely to have only limited application to southern populations.

PART TWO

TAXONOMIC AND BIOGEOGRAPHICAL STUDIES OF THE GENUS *GASTRIMARGUS* SAUSSURE

2.1 TAXONOMY OF THE GENUS *GASTRIMARGUS*

2.1.1 Introduction: taxonomic background and methods.

2.1.1.1 History of the genus *Gastrimargus* and scope of revision

Saussure (1884) originally described *Gastrimargus* as a subgenus of *Oedaleus*, characterised by its stouter general shape, longer pronotum, and certain supposed differences in the reticulation of the tegmina. The first species he described in his new subgenus was *G. verticalis*, but he did not formally designate it as the type species. Kirby (1910) synonymised *G. verticalis* with *G. virescens* and designated *virescens* as the type species of *Gastrimargus*. This designation is unaffected by the fact that *G. virescens* had already been recognised as a junior synonym of *G. marmoratus* (Saussure, 1884), whereas *G. verticalis* was and is a valid species. Despite later attempts to substitute *G. verticalis* (Sjöstedt, 1928; Johnston, 1956), *G. virescens* remains the valid type species of *Gastrimargus*.

Kirby (1910) also raised *Gastrimargus* to full generic status, without however giving any reason for doing so. From the beginning there was confusion over the identity of some species, and their correct generic assignment was sometimes in doubt, *Oedaleus virgula* being placed in *Gastrimargus* (as *G. madecassus* Saussure, 1884) in error. The first revision of the genus, by Sjöstedt (1928), tended to confuse rather than to clarify the position. He described numerous species, varieties (understood here and by previous authors in the sense of subspecies), and forms. An indication of the scale of the problem is given by the synonymy of *G. determinatus procerus* (p. 278), which Sjöstedt described no less than six times under various names in the course of his revision.

Over the last half century a few new taxa have been described, and some new synonymy has been reported (Dirsh, 1961, 1966, 1970), but no general study of the genus has been undertaken. Descamps (1972) included *Gastrimargus* among the small group of old world oedipodine grasshopper genera most in need of revision. At the commencement of this study thirty two species and five subspecies were recognised. In this work sixteen species and five subspecies are synonymised, four species are reduced to subspecies, two species and two subspecies are recalled from synonymy, and four new species and one new subspecies are described. A total of twenty three species and seven subspecies are now recognised for which keys and diagnoses are provided below. Because of the small numbers of available specimens of some species and the extensive geographical variation within some species groups, the present study must remain preliminary. For this reason some new races described here have not been given formal latin subspecies names.

2.1.1.2 Economic importance of _Gastrimargus_

Members of the genus _Gastrimargus_ are a conspicuous component of the tropical grassland ecosystems of Africa, Asia, and Australasia, where, because of their numbers they are sometimes considered injurious to pasture. Although there have as yet been no quantitative studies of their effects, the possible rôle of these and other grasshoppers as competitors of grazing stock is likely to assume increasing importance in tropical rangeland management.

Three species of _Gastrimargus_, _G. africanus_ (Saussure) in Africa, _G. marmoratus_ (Thunberg) in SE Asia, and _G. musicus_ (Fabricius) in Australia are minor pests of agriculture. Of these, only _G. musicus_ forms swarms and shows behavioural and morphological phase transformation (Common, 1948). The species is said to be favoured by overgrazing and deforestation which provide bare ground for laying, and short and long grasses for feeding and roosting (Uvarov, 1977). In Malaysia _G. marmoratus_ is often found in association with Lalang (_Imperata arundinacea_), an aggressive colonist in forest areas cleared for crops. In such areas G. marmoratus is able to move from the wild vegetation into the rice, maize, or other crop which is being grown.

With the continuing destruction of rain forest, and its replacement by vegetation types suitable for Gastrimargus species, it is likely that their importance as pests will grow. There is therefore a need for accurate identification of the species and a reliable knowledge of their ranges. References to economic importance are included in the text where appropriate, under species headings.

2.1.1.3 Methods and terminology

In this preliminary study characters for identification and separation of species were derived from the external morphology and colour patterns of both sexes, especially the hind wing, and the internal genitalia of the males. The terminology employed is the same as for Oedaleus (Part 1, pp. 17-18). Sjöstedt (1928) used the term 'cotypus' in the sense of the modern paratype, while others used it in the sense of syntype. Sjöstedt's cotypes are therefore referred to as paratypes whenever they are mentioned. In the genitalia figures (Figs 1-110), the phallic complex is consistently shown in both dorsal and lateral views with the epiphallic membrane and epiphallus removed. For brevity this information is not repeated in the figure legends. The scale line in each of the figures represents 1 mm. For each species the right half of the epiphallus is figured first in dorsal view and then in postero-ventral view to exhibit the degree of development of the lophi which is unclear in dorsal view.

As with Oedaleus (Part 1, p. 17), material examined (Appendix 2) has been limited to recording primary type data and listing the number of other specimens examined. A full list is deposited in COPR library.

2.1.1.4 Depositories

MNHU Berlin - Museum für Naturkunde der Humboldt-Universität zu Berlin

IRSNB Brussels - Institut Royal des Sciences Naturelles de Belgique

DEI Eberswalde - Deutsches Entomologisches Institut, Eberswalde

MHN Geneva - Muséum d'Histoire Naturelle, Geneva

MCSN Genoa - Muséo Civico di Storia Naturale, Genoa

ZM Hamburg - Zoologisches Institut und Zoologisches Museum, Universität Hamburg

RNH Leiden - Rijksmuseum Van Natuurlijke Historie, Leiden

ZI Leningrad - Zoological Institute, Academy of Sciences of the USSR

BMNH London - British Museum (Natural History), London

NM Maastricht - Natuurhistorisch Museum, Maastricht

MNHN Paris - Muséum National d'Histoire Naturelle, Paris

ANS Philadelphia - Academy of Natural Sciences, Philadelphia

DATS Pretoria - Department of Agricultural Technical Services, Pretoria

NR Stockholm - Naturhistoriska Rijksmuseum, Stockholm

MRAC Tervuren - Musée Royal de l'Afrique Centrale, Tervuren

ZIUU Uppsala - Zoologiska Institutionen, Uppsala Universitet

2.1.2 Gastrimargus Saussure, 1884

Oedaleus (Gastrimargus) Saussure 1884: 109,110

Gastrimargus Saussure; Kirby, 1910:226

Type-species Gryllus virescens Thunberg, 1815, by subsequent designation (Kirby, 1910: 226).

2.1.3 Description and affinities of the genus Gastrimargus.

Medium size (total length 20 - 45 mm male, 24 - 64 mm female). Integument finely or moderately rugose and pitted. Antennae filiform, 0.8-1.25 times combined length of head and pronotum; flagellum with 22 -27 segments. Fastigium of vertex concave, flat, or convex; raised marginal carinae distinct or indistinct, medial carina present or absent; fastigium narrowing to about half maximum width anteriorly, foveolae obsolete, or if present, triangular; frons in profile oblique or vertical, convex; frontal ridge with or without variable longitudinal sulcus, smooth, sometimes widening at median ocellus, widening evenly and obsolescent towards clypeus. Eyes oval, 1.2-1.5 times as deep as wide. Pronotum low to high tectiform with median carina from weakly raised to high blade-like (in G. mirabilis), intersected or not intersected by posterior sulcus; dorsum of pronotum sometimes with scattering of raised round warts; hind margin from rounded obtusangular (gregarious phase of G. musicus) to sharply acutangular (G. mirabilis); mesosternal interspace trapezoidal or rectangular, wider than long, narrower or wider anteriorly than metasternal; metasternal interspace usually forming a closed elongate lozenge-shaped area (but with narrow anterior opening to metasternum in G. willemsei). Tegmen and wings fully developed or slightly abbreviated, in male exceeding hind knees by variable amount, in female sometimes not reaching hind knees but never by more than one third of hind femur length; intercalary vein of medial area of tegmen usually well-developed and serrate, at least in males (unserrated in *G. acutangulus*); hind wing unspecialised. Hind femur normal, of variable thickness, lacking specialised features; hind tibia as long as femur, with 11-14 inner and outer spines, inner apical spurs about 1.5 times length of outer spurs; tarsi unspecialised, arolium 0.3-0.6 times claw length. Male supraanal plate shield-shaped, rounded triangular; male cercus subconical to finger-shaped, 2-2.75 times its basal width; sungenital plate subconical with rounded apex. Genitalia typically oedipodine, similar to *Oedaleus*. Aedeagus (paired apical penis valves) short, variably projecting from short enclosing cingular rami, and bearing a subapical ventral process of variable size; epiphallus bridge-shaped with bilobate lophi, outer lobes often acutely projecting. Ovipositor of variable length, not markedly elongated; ventral valves variable in shape and degree of sclerotisation, usually with simple acute apex (bifurcated in *G. willemsei*); basivalvular sclerites rugose or smooth.

General colouration: brown with green / brown polymorphism variably expressed as lighter brown or green markings on frons, vertex, genae, pronotum, hind femora, and anal area of tegmen (dorsal surface when folded); pale oblique band on genae continued onto pronotal shoulders, sometimes partly or completely obscuring x-marking, and occasionally forming a light border to dorsum of pronotum; x-marking when visible cream, light brown, or light green, with anterior and posterior arms joined separately on each side of median carina; anterior or posterior arms or both may be obsolete. Tegmen usually opaque brown in basal half or two thirds, green in anal area of green morphs, with two or three transverse pale bands extending variable distance from costal margin, situated one eighth, one quarter, and one half along from base, sometimes somewhat more distally placed; bands sometimes reduced or, occasionally obsolete; remainder of tegmen clearing towards apex with dark speckling. Hind wing with or without fascia; basal area pale blue, pale greenish yellow, pale yellow, or bright sulphur yellow. Hind femur usually with two or three oblique transverse bands externally, coinciding with darker areas between pale bands of folded tegmen, producing camouflage effect; bands may be reduced or obsolete, with or without residual spotting on upper and lower carinulae; internal surface with or without transverse band sometimes coalescing to form solid brown or black zone in basal half of medial area; internal ventral surface red, black, blue, or straw-coloured; hind knees brown to black, hind tibiae yellow, orange, red, brown, purplish, or straw-coloured.

The genus Gastrimargus is classed among the Oedipodinae by virtue of its serrated intercalary vein and banded hind wings (absent in extreme forms of G. rothschildi and G. determinatus). It is allied to Locusta, Oedaleus (as already stated, Part 1, p. 15), Humbe, and Oreacris, but may be differentiated from these and other genera of Oedipodinae by the following combination of characters:

1. Pronotum with median carina raised, arcuate, not deeply excised by posterior sulcus (as in Pycnocrania, Oreacris).
2. Pronotal pattern, when visible, consisting of light x-marking with anterior and posterior arms joined (separate in Oedaleus).
3. Tegmina with serrated intercalary vein, but without specialised stridulatory cross-veins (as in Heteropternis or Homoeopternis).
4. Hind femur lacking expanded upper or lower marginal area (as in Oedipoda or Pycnodictya)
5. Genitalia with aedeagus short, never elongated (as in Locusta).

The species of the genus form a close-knit group, more closely allied even than those of Oedaleus. The recognition of distinct 'species groups' based on common characters is therefore problematic. Affinities between species are discussed under the species concerned.

2.1.4 Keys to the species of the genus Gastrimargus

2.1.4.1 Key to African species of Gastrimargus

1. Hind wing bright blue basally (eastern and southern Africa) ... ... *G. acutangulus* (Stål)

-. Hind wing basally colourless, pale yellow, or bright yellow, rarely pale greenish blue, never bright blue 2

2.(1) Tegmen length less than 20 mm ♂, 22 mm ♀, not or barely reaching hind knees in female 3

-. Tegmen length more than 20.5 mm ♂, 25 mm ♀, always exceeding hind knees in female 5

3.(2) Pronotal x-marking with anterior arms distinctly curved, posterior arms not, or rarely faintly visible (Plate 30); posterior margin of pronotum rectangular to obtusangular; epiphallic lophi with relatively large, protrusive, and divergent outer lobes; posterior projection elongated and acute (Figs 100, 101); aedeagal valves strongly projecting, with large bulbous subapical ventral processes (Figs 98,99); ventral ovipositor valves short, 1.2 times perpendicular basal width (Ivory Coast, Ghana, Zaire) ... ... *G. ochraceus* Sjöstedt

-. Pronotal x-marking with anterior arms straight, no more pronounced than posterior arms (Plates 9-12); hind margin of pronotum acutangular; epiphallic lophi with outer lobes small, not protrusive or divergent (Figs 39,40,43,44); aedeagal valves weakly projecting, with small subapical ventral processes (Figs 37,38,41,42); ventral ovipositor valves longer, 1.45 times perpendicular basal width 4

4.(3) Pronotal x-marking, when present, with straight posterior arms; hind margin of pronotum rounded acutangular (Plates 9,10); lateral and ventral surfaces of thorax hairy; external upper and lower carinulae and medial area of hind femur with row of irregular brown speckles; tegmen length / pronotum length ratio 3.3 ♂, 2.4–2.7 ♀ (Ethiopia) G. hyla Sjöstedt

–. Pronotal x-marking with recurved posterior arms; pronotal hind margin sharply acutangular, at least in males (Plates 11,12); thorax not hairy; external surface of hind femur unspeckled, with longitudinal dark stripe of variable thickness in upper half of medial area; tegmen length / pronotum length ratio 2.4–3.2 ♂, 1.4–1.9 ♀ (Ethiopia) G. rothschildi Bolivar

5.(2) Dorsum of pronotum extremely elongated, more than 2.5 times length of lateral lobe; hind margin narrowly acutangular, forming an angle of less than 45° (Plate 27); median carina high arcuate, blade-like, never intersected by posterior sulcus; hind femur narrow, elongated, length / depth ratio 5.1–5.7 ♂, 4.9–5.7 ♀; hind wing with complete fascia (Angola, Zaire, Zambia, Uganda) ... ... G. mirabilis Uvarov

–. Dorsum of pronotum shorter, less than twice length of lateral lobe; hind margin forming an angle of more than 45°; median carina never blade-like, sometimes intersected by posterior sulcus; hind femur thicker, length / depth ratio usually less than 5 ♂♀, if more, then hind wing fascia very incomplete or absent 6

6.(5) Hind wing with well-defined continuous dark band and bright yellow basal area 7

–. Hind wing with fascia continuous, interrupted, or absent, but basal area never bright yellow 8

7.(6) Tegmen length / pronotum length ratio 3.2–3.7 ♂, 2.9–3.6 ♀; inner and outer surfaces of hind femur with rows of irregular black specks on upper and lower carinulae; pronotal x-marking variable, but usually distinct (Plate 21); aedeagal valves strongly projecting, with large, bulbous subapical ventral processes (Figs 64,65) (Zimbabwe, S. Africa) ... ... *G. crassicollis* (Saussure)

-. Tegmen length/pronotum length ratio 3.9 - 4.6 ♂, 3.8 - 4.6 ♀; hind femur without dark specks on carinulae; pronotal x-marking, especially posterior arms, usually indistinct (Plates 1,2); aedeagal valves weakly projecting, with weak subapical ventral process (Figs 1,2) (Subsaharan Africa) ... ... *G. africanus africanus* (Saussure)

8.(6) Ventral surface and interior ventral carina of hind femur red; ventral ovipositor valves short, less than 1.25 times their perpendicular basal width (Angola) *G. insolens* sp. n.

-. Ventral surface and interior ventral carina of hind femur black, blue-black, blue-grey, or straw-coloured, never red; ventral ovipositor valves longer, more than 1.25 times their perpendicular basal width 9

9.(8) Ventral surface of hind femur blue-grey to blue-black ... 10

-. Ventral surface of hind femur straw-coloured 13

10.(9) Pronotum dorsally smooth, without warts (Plate 22); median carina low arcuate (South Africa) *G. drakensbergensis* sp. n. ♂♂ only (♀♀ have hind femur ventral surface straw-coloured, not blue-black)

-. Pronotum dorsally rugose, with numerous small globose warts; median carina high arcuate 11

11.(10) Female pronotum length less than 11.6 mm, tegmen length less than 28 mm; male with strong complete wing fascia and apical half of wing strongly infumate (Plate 23); outer lobes of epiphallic lophi forming a small circular bump (Figs 74, 75) (Zaire, Angola) ... ... *G. obscurus* sp. n.

-. Female pronotum length more than 12 mm, tegmen length more than 34 mm; male either with weak complete wing fascia and apical half of wing weakly infumate, or with strong fascia and apical half of wing clear (Plates 25,26); outer lobes of epiphallic lophi laterally elongated, forming a lozenge-shaped bump (Figs 78, 79, 82, 83) 12

12.(11) Hind wing fascia distinct, apical half of wing clear (Plate 25); main wing veins usually tinted with pale blue basally; subapical ventral process of aedeagus bulbous, more strongly projecting (Figs 76,77); outer edge of ventral ovipositor valves distinctly excavated (Fig. 80) (Eastern South Africa) G. wahlbergii (Stål)

-. Hind wing fascia indistinct, apical half of wing indistinctly infumate (Plate 26); wing veins never tinted with pale blue; subapical ventral process of aedeagus less strongly projecting (Figs 81, 82); outer edge of ventral ovipositor valves smoothly curved, almost straight (Fig. 84) (Angola, Zambia) ... ... G. angolensis Sjöstedt

13.(9) Hind wing without fascia (Plate 20) (E and S Africa) ... ... G. determinatus vitripennis (Saussure)

-. Hind wing with partial or complete fascia 14

14.(13) Hind wing fascia complete, apical half of wing infumate (Plate 14) (Tanzania) ... G. verticalis mpwapwae sp. n. ♂♂ only

-. Hind wing fascia complete or incomplete, apical half of wing never infumate 15

15.(14) Hind wing fascia not extending further anteriorly than 1A 16

-. Hind wing fascia extending to anterior margin of wing, narrowly interrupted between Cu2 and 1A (Plates 16, 22) 17

16.(15) Hind wing fascia not reaching hind margin of wing in females; tegmen short, 21-25 mm ♂, 32-40 mm ♀; tegminal pattern distinct, with pale transverse bands strongly marked (Eastern and Southern

Africa) ... ... *G. verticalis* (Saussure) ♀♀ & some ♂♂

-. Hind wing fascia reaching hind margin of wing posteriorly in both sexes (Plate 19); tegmen longer, 25-34 mm ♂, 42-48 mm ♀; tegminal pattern pale and indistinct, light transverse bands weakly marked (Plate 19) (W & Central Africa to Uganda) ... ... *G. determinatus procerus* (Gerstäcker)

17.(15) Anterior arms of pronotal x-marking meeting posterior arms at an angle of 90-120°; metazona with indistinct pale striae extending obliquely outwards and backwards on each side of median carina to hind margin (Plate 16); ventral ovipositor valves with outer edge excavated (Fig. 56) (Central Africa) *G. miombo* sp. n.

-. Anterior arms of pronotal x-marking meeting posterior arms at an angle of more than 125°; metazona without pale striae; ventral ovipositor valves with outer edge almost straight ... 18

18.(17) Males 19

-. Females 20

19.(18) Size smaller: tegmen usually less than 25 mm; pronotal x-marking with very thin arms; hind wing band strongly incurved towards anal margin of wing, distinct as far as 6A (Plate 13); aedeagus only moderately protruding from cingular rami (Figs 45, 47) (Eastern & Southern Africa) *G. verticalis verticalis* (Saussure)

-. Size larger: tegmen more than 25 mm; pronotal x-marking with thicker arms; hind wing band weakly incurved towards anal margin of wing, fading beyond 5A (Plate 17); aedeagus strongly projecting from cingular rami (Figs 57, 58) (Cape Province) ... ... *G. determinatus determinatus* (Walker)

20.(18) Smaller insects: tegmen length lessthan 31 mm; hind wing with distinct broad fascia reaching anal margin of wing and incurving towards inner edge (Plate 22) (S Africa) *G. drakensbergensis* sp. n.

–. Larger insects: tegmen length more than 36 mm; hind wing with fascia not reaching anal margin of wing, and only weakly incurved towards inner edge, fading beyond 5A (Plate 18) (Cape Province) ... ... *G. determinatus determinatus* (Walker)

2.1.4.2 Key to non-African species of Gastrimargus

1. Hind wing with basal area pale blue (Timor) ... ... G. subfasciatus (de Haan)

-. Hind wing basal area never blue (bases of major wing veins occasionally faintly tinged with pale blue; see couplet 10) 2

2.(1) Hind wing without fascia (Arabia) ... ... G. determinatus arabicus Uvarov

-. Hind wing with partial or complete fascia 3

3.(2) Apical half of wing beyond fascia infumate, becoming as dark as fascia at tip of wing (Plate 32) 4

-. Apical half of wing clear, wing tip sometimes infumate .. 6

4.(3) Head small, femur length / head width ratio more than 3.6 ♂, 3.4 ♀ (Plate 32); hind wing basal area bright sulphur yellow (New Caledonia) ... ... G. sarasini (Saussure)

-. Head larger, femur length / head width ratio less than 3.6 ♂, 3.3 ♀; hind wing basal area pale yellow, pale greenish yellow, or colourless 5

5.(4) Hind wing with some darkened cross-veins in basal area (Plate 31); metasternal interspace with narrow anterior medial opening, continuous with metasternum; epiphallus with lophi protruding backwards beyond posterior projections, outer lobes of lophi elongated, incurved (Figs 104,105); ventral ovipositor valves long and apically bifurcated (Fig. 106); (New Guinea) .. .. G. willemsei sp. n.

-. Hind wing without darkened cross-veins in basal area (Plate 3); metasternal interspace closed; epiphallus with lophi not protruding backwards beyond posterior projections; outer lobe subtriangular, not incurved (Figs 10,11) (Himalayas) ...

... ... G. nubilus Uvarov

6.(3) Internal ventral surface of hind femur red (except G. musicus in Solomon Is) 7

-. Internal ventral surface of hind femur straw to blue-black, never red 8

7.(6) Small species, tegmen length less than 25 mm ♂, 32 mm ♀; hind wing basally pale yellow; fascia narrowly interrupted between Cu2 and 1A, with posterior portion thinning at its anterior end and curving inwards towards wing base along 2A (Plate 4) (Lesser Sunda Is) ... ... G. lombokensis Sjöstedt

-. Larger species, tegmen length usually more than 25 mm ♂, 32 mm ♀ (females sometimes smaller in Solomon Is); hind wing basally bright sulphur yellow (except in E New Guinea and Solomon Is where paler); fascia broad throughout, not incurved towards wing base along 2A (Plate 6) (Australia, Tasmania, New Guinea, Solomon Is) ... ... G. musicus (Fabricius)

8.(6) Internal ventral surface of hind femur blue-grey to blue-black (Arabia, Madagascar, India) G. africanus (Saussure)

-. Internal ventral surface of hind femur straw-coloured ... 9

9.(8) Hind wing fascia thin and indistinct, variably interrupted between M and 2A, sometimes between costal margin and 3A (Plate 8) (Réunion) G. immaculatus (Chopard)

-. Hind wing fascia distinct, complete 10

10.(9) Hind wing fascia, especially in female, with dark pigment diffusing outwards along 3A and subsequent veins towards wing tip (Plate 7); main wing veins usually faintly tinged with pale blue basally; hind femur with external upper marginal and sometimes medial areas immaculate, unicolourous light brown or green; internal surface straw-coloured, with small brown patch in basal half of medial area only (SE Asia: Assam to W New Guinea) ... ... G. marmoratus (Thunberg)

–. Hind wing fascia not diffusing outwards along wing veins; bases of wing veins not blue-tinged; hind femora usually with oblique transverse dark bands on external medial and upper marginal areas; internal medial area entirely black in basal two thirds, separated from apical transverse black band by sub-apical pale zone 11

11.(10) Male cercus blunt, finger-like, with convexly rounded lower edge; aedeagus strongly projecting (Figs 20-23) (Solomon Is) ... ... G. musicus (Fabricius) (pale race)

–. Male cercus acute, triangular, with concave lower edge; aedeagus weakly projecting (Figs 1-3) (Indo-China, Java, Kangean Is) ... ... G. africanus parvulus Sjöstedt

2.1.4.3 Notes on the keys

A key to the species of Gastrimargus was given by Sjöstedt (1928), but the large number of synonyms which were accorded separate species status and the unreliable characters used to distinguish them rendered the result valueless as a tool for identification.

The two keys provided here cover Africa and the remainder of the old world separately, as in the case of Oedaleus (Part 1, pp. 22-34). The occasional cases of sexual dimorphism are dealt with by keying out sexes separately where necessary (e.g. G. verticalis mpwapwae). A more serious difficulty is posed by the large amount of geographical variation among the members of the G. africanus - musicus group. The loss of wing and hind femur colour characters in specimens of G. africanus parvulus from Indo-China and Java, and G. musicus from the Solomon Is.

leads to a situation where without label data positive identification would, in a small percentage of cases, be impossible. Males can be separated with difficulty (key to non-african species, couplet 11, p. 212), but no reliable characters have been found to separate females. However, in view of the observed clinal variation within the two species determination can be made on the basis of their discontinuous ranges.

Two Gastrimargus specimens from Nigeria, of uncertain identity, possibly G. verticalis, have been omitted from the keys. They are discussed under G. verticalis (p. 268) and the male is shown in plate 15.

Characters from the male genitalia, particularly the length and shape of the aedeagus and the shape of the epiphallic lophi have been used in the keys and diagnoses, but caution is necessary in interpreting small changes in shape of these and other parts of the phallic complex. As in some other genera, there is general uniformity of shape over the genus as a whole but considerable variation within one species or even within one population. There are two major problems of interpretation of the genitalia. Firstly, new material is added to the endocuticle of internal skeletal structures daily throughout all or most of the adult life of grasshoppers (Neville, 1963). Thus, for example, the cingular apodemes (including the zygoma), and the aedeagal apodemes ('basal penis valves' of Dirsh) are continually extending and thickening at their anterior extremities. Up to ten or twelve growth layers can often be seen even by reflected light at fifty times magnification. Older animals therefore tend to have some features much more pronounced than younger ones, while in teneral insects the genitalia may be transparent and delicate, difficult to examine and easily deformed by handling. Secondly, the correct understanding of the epiphallus is complicated by a tendency to be curved or folded to a variable degee. If the epiphallus is considered lying in the position in which it is usually figured, lying on its ventral surface in the plane of the paper, there are three ways in which its apparent shape may vary. Firstly the anterior margin bearing the ancorae may be in the plane of the paper or curve upwards or downwards. Secondly the lateral plates with their anterior and posterior projections may also either lie flat or curve upwards or downwards, affecting the angle and shape of the lophi. Thirdly the bridge may be curved in the plane of the paper to a variable extent, altering the outline of the epiphallus and bringing the lophi closer together or pushing them apart. In view of these points specimens being compared must be examined in identical positions and from several angles. Genitalia drawings can only be used as a guide and should never be regarded as definitive.

2.1.5 Annotated species catalogue of the genus *Gastrimargus*, with synonymy, diagnoses, measurements, and biological notes.

2.1.5.1 Gastrimargus africanus (Saussure, 1888)

(Figs 1-7, 116, 117; Plates 1,2)

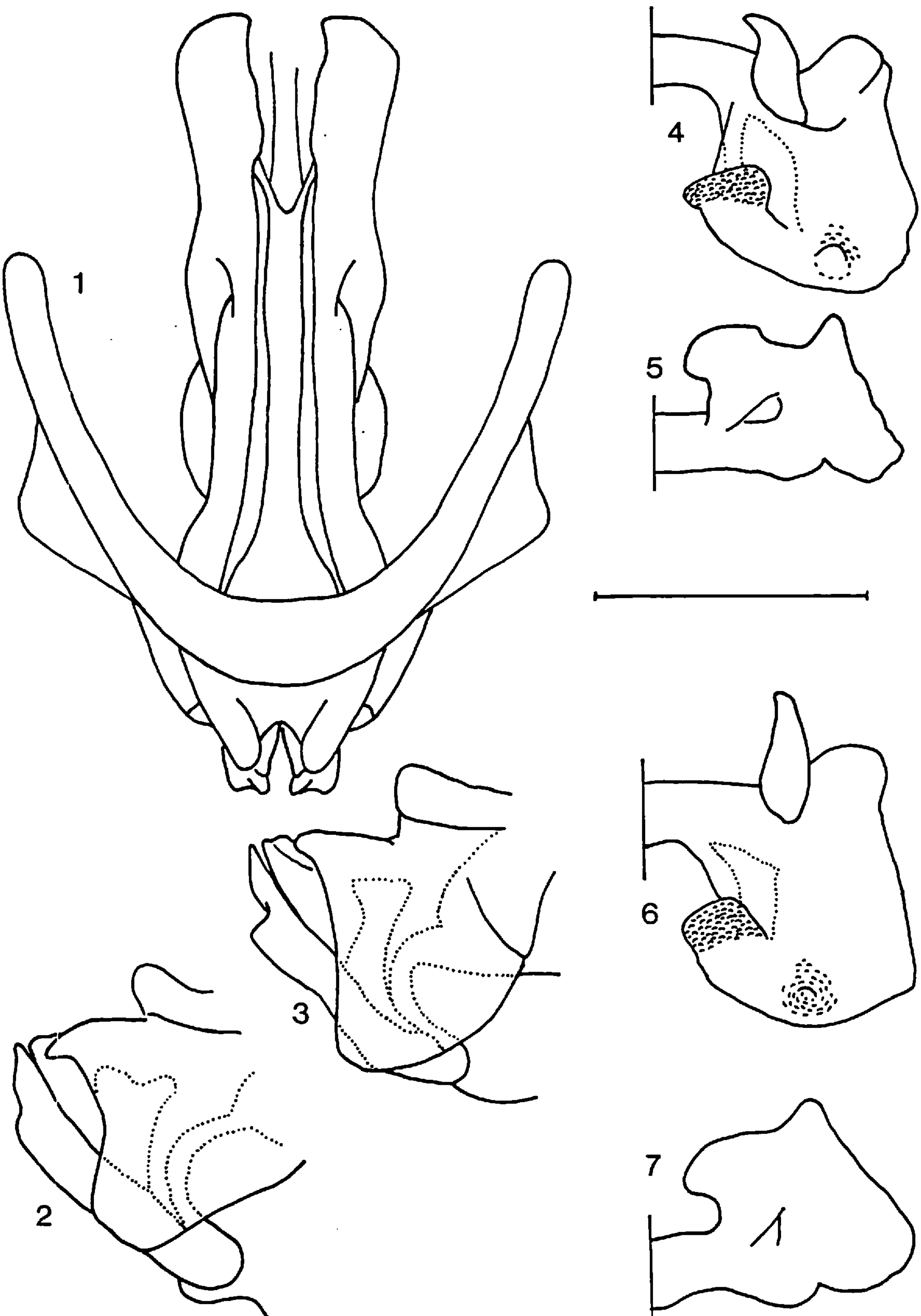
This species is here divided into four subspecies under which the specific synonymy is separately listed.

Diagnosis. Fastigium of vertex concave. Pronotum with median carina moderately arcuate, shallowly intersected by posterior sulcus; hind margin sharply or bluntly acutangular; dorsum smooth. Tegmen surpassing hind knees by one quarter to one half of hind femur length, according to subspecies. Genitalia (Figs 1-7): aedeagus very short, usually with small variable subapical ventral process (more pronounced in G. a. sulphureus, Fig. 3); epiphallus rather variable in outline, with protruding conical outer lobe of lophi slightly divergent to slightly convergent.

Colouration. Dorsum of pronotum with pale x-marking often partly or completely obscured. Tegmen with basal pale transverse band sometimes reduced or absent. Hind wing with complete fascia (Plates 1,2); basal area usually bright yellow (paler and sometimes greenish in subspecies parvulus and sulphureus); apex of wing variably infumate. Hind femur usually with three dark oblique transverse bands externally, sometimes obsolete in green morphs; internal surface with two basal bands forming black zone in medial area, apical band separate; interno-ventral carinula and ventral surface of hind femur blue-grey or blue-black Africa, Madagascar, Arabia, India) to straw-coloured (China, Indo-China, Java). Hind tibiae basally brownish or reddish, subbasally straw, otherwise raspberry red to dull pale reddish (in G. parvulus).

Key to subspecies of G. africanus

1. Hind femur with interior ventral surface suffused with blue-grey to blue black in basal half 2



Figs 1-7. Gastrimargus africanus (Saussure), genitalia. 1, G. a. africanus, phallic complex, dorsal view; 2, same, posterior portion, lateral view; 3, same, G. a. sulphureus; 4, G. a. africanus, epiphallus, right half, dorsal view; 5, same, posterior view; 6, G. a. sulphureus, epiphallus, right half, dorsal view; 7, same, posterior view.

Plate 1. G. africanus africanus (Saussure) ♂

Plate 2. G. africanus sulphureus Bei-Bienko ♂

-. Hind femur ventrally straw-coloured, without blue pigment (E China, Hongkong, Vietnam, Burma, Thailand, Java, Kangean Is) ... ... G. africanus parvulus Sjöstedt

2. Tegmen surpassing hind knees by 1/4 to 1/3 of hind femur length. General colouration sombre; basal pale transverse band of tegmen partially or completely obsolete; hind wing basal area pale yellow or greenish yellow, not bright yellow. Subapical ventral process of aedeagus pronounced in lateral view (Fig. 3) (Pakistan, India (Kashmir, Uttar Pradesh, Punjab), Nepal) ... ... G. africanus sulphureus Bei-Bienko

-. Tegmen surpassing hind knees by 1/3 to 1/2 of hind femur length. General colouration more vivid; pale bands of tegmina distinct; hind wing basal area bright yellow. Subapical ventral process of aedeagus weak in lateral view (Fig. 2) 3

3. Tegmen short, usually less than 27.5 mm ♂, 36 mm ♀; TL / PL ratio less than 3.9 ♂, 4.2 ♀. Metazona of pronotum with posterior arms of x-marking usually visible and with several indistinct pale striae extending obliquely outwards and backwards on each side of median carina (Madagascar) G. africanus madagascariensis Sjöstedt

-. Tegmen longer, usually more than 25 mm ♂, 37 mm ♀; TL / PL ratio more than 3.9 ♂, 3.8 ♀. Metazona of pronotum with x-marking usually effaced and without pale striae.(Africa, Arabia, India) ... ... G. africanus africanus (Saussure)

Gastrimargus africanus africanus (Saussure, 1888)

Oedaleus (Gastrimargus) marmoratus var. africana Saussure, 1888: 39.
LECTOTYPE ♂, SOUTH AFRICA (MHN, Geneva) here designated [examined].

Gastrimargus africanus (Saussure); Kirby, 1910: 227.

Gastrimargus africanus var. zebrata Sjöstedt, 1928: 41. Holotype ♀, TANZANIA (NR, Stockholm) [synonymised by Dirsh, 1966: 426] [examined].

<u>Gastrimargus</u> <u>africanus</u> var. <u>orientalis</u> Sjöstedt, 1928: 41. Holotype ♀, SRI LANKA (MHN, Geneva) [examined]. Syn. n.

Synonymy

<u>G.</u> <u>africanus</u> <u>orientalis</u> Sjöstedt was based on material from India and Ceylon which does not differ morphologically from african specimens and the name is therefore synonymised. Sjöstedt (1928:50) clearly designated one female from Ceylon, deposited in the MHN, Geneva, as the holotype. The female from Darjeeling in the NR, Stockholm labelled 'Typus' cannot therefore be the holotype.

Measurements: Table 1.

<u>Gastrimargus</u> <u>africanus</u> <u>madagascariensis</u> Sjöstedt, 1928

<u>Gastrimargus</u> <u>africanus</u> var. <u>madagascariensis</u> Sjöstedt, 1928:41. Holotype ♀, MADAGASCAR (NR, Stockholm) [incorrectly synonymised by Dirsh, 1963: 273] [examined]. Nom. rev.

Measurements: Table 2.

<u>Gastrimargus</u> <u>africanus</u> <u>sulphureus</u> Bei-Bienko, 1951 comb. et stat. n.

<u>Gastrimargus</u> <u>sulphureus</u> Bei-Bienko, 1951: 580. Holotype ♂, PAKISTAN (ZI, Leningrad) [examined].

[<u>Gastrimargus</u> <u>minor</u> (Saussure); Sjöstedt, 1928: 26. Misidentification, referred to <u>G.</u> <u>sulphureus</u> by Bei-Bienko, 1951: 580.]

Synonymy

Specimens from Simla, India, wrongly determined by Sjöstedt (1928: 26) as <u>Gastrimargus</u> <u>minor</u> belong to this subspecies. <u>G.</u> <u>marmoratus</u> var. <u>minor</u> (Saussure, 1888: 39), described from Mongolia, is a <u>nomen</u> <u>incertae</u> <u>sedis</u> since no species of <u>Gastrimargus</u> is otherwise known from there and the original material of <u>minor</u> is lost. Saussure was familiar

Table 1

Measurements

G. africanus africanus: Tanzania

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	38.23	5.01	7.08	29.18	16.93	3.88	4.37	3.38	4.12	1.73
Range	33.10-43.25	4.50-5.65	6.25-8.10	25.10-32.45	14.20-19.40	3.35-4.25	4.00-4.85	3.09-3.58	3.92-4.54	1.64-1.86
S.D.	2.076	0.270	0.412	1.543	1.104	0.204	0.17	0.128	0.150	0.060
No.	30	30	26	30	30	30	30	30	26	30
♀ Mean	53.36	7.12	9.82	40.56	23.59	5.48	4.31	3.31	4.14	1.71
Range	48.75-58.50	6.60-7.65	9.05-10.90	37.20-44.70	20.65-25.90	4.95-5.89	4.04-4.66	3.07-3.51	3.83-4.58	1.27-1.83
S.D.	2.284	0.270	0.447	1.952	1.291	0.225	0.155	0.120	0.195	0.108
No.	30	30	28	30	30	30	30	30	28	30

Table 2

Measurements

G. africanus madagascariensis: Madagascar

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	32.28	4.56	6.76	24.37	16.42	3.66	4.49	3.60	3.63	1.49
Range	29.10-35.95	4.15-4.95	6.15-7.40	21.80-27.40	15.25-17.90	3.35-3.95	4.19-4.88	3.28-3.76	3.31-3.90	1.41-1.58
S.D.	1.477	0.207	0.312	1.178	0.661	0.170	0.168	0.110	0.164	0.049
No.	29	29	25	29	25	25	25	24	25	24
♀ Mean	43.60	6.33	9.04	32.50	21.58	4.96	4.35	3.40	3.59	1.52
Range	39.50-47.55	5.80-6.90	8.05-10.00	29.35-35.55	18.70-23.40	4.25-5.55	3.86-4.62	3.00-3.70	3.28-4.17	1.38-1.66
S.D.	2.320	0.263	0.542	1.864	1.118	0.269	0.176	0.134	0.175	0.075
No.	33	39	38	36	38	38	38	37	35	34

with Oedaleus infernalis from Mongolia and it is possible that it was this species that he was considering under the name G. marmoratus var. minor.

Measurements: Table 3.

Gastrimargus africanus parvulus Sjöstedt, 1928 comb. et stat. n.

Gastrimargus parvulus Sjöstedt, 1928: 38. Holotype ♀, JAVA (NM, Maastricht) [examined].

Gastrimargus pusillus Sjöstedt, 1928: 38. Holotype ♀, 'Nederl. Indien' (NM, Maastricht) [examined]. Syn. n.

Synonymy

G. parvulus Sjöstedt is the most easterly race of G. africanus and is here retained as a subspecies. Sjöstedt described the green morph as G. parvulus and the brown morph as G. pusillus, a separate species. With the prerogative of first reviser parvulus is regarded as the senior synonym despite the line priority of pusillus (Sjöstedt: 1928: 38), since only G. parvulus has a precise type locality.

Measurements: Tables 4,5.

Material examined (all subspecies): Appendix 2, pp. 379-380.

Distribution (Figs 116,117, and Biogeography section, p. 331 - 336).

G. africanus africanus ranges across most of Africa south of the Sahara, SW Arabia, and India. G. africanus madagascariensis is restricted to Madagascar. G. africanus sulphureus occurs in the mountains of Pakistan, Kashmir, and Nepal, overlapping with the nominate race in the Simla hills of NW India. G. africanus parvulus is found in Indo-China and Java. Additional data for the distribution map were provided by

Table 3

Measurements

G. africanus sulphureus: India, Pakistan, Nepal.

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	30.62	4.59	6.03	22.46	15.29	3.79	4.04	3.34	3.72	1.46
Range	26.80–33.25	4.15–4.90	5.50–6.50	19.10–24.60	13.30–16.45	3.20–4.10	3.85–4.22	3.16–3.47	3.44–4.08	1.24–1.53
S.D.	1.478	0.184	0.329	1.212	0.773	0.216	0.134	0.100	0.191	0.067
No.	17	18	16	18	15	15	15	15	16	15
♀ Mean	42.36	6.73	8.59	30.89	21.78	5.46	4.00	3.24	3.55	1.40
Range	37.20–47.50	6.00–7.90	7.35–9.70	26.70–35.50	19.30–25.05	4.65–6.85	3.40–4.16	3.06–3.38	3.32–4.18	1.30–1.64
S.D.	3.012	0.521	0.711	2.529	1.800	0.578	0.177	0.089	0.225	0.085
No.	12	15	15	13	15	15	15	15	13	13

Table 4

Measurements

G. africanus parvulus: Thailand

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	36.83	5.09	6.94	27.83	17.55	4.09	4.19	3.38	4.01	1.62
Range	32.95–40.00	4.75–5.45	6.20–7.60	24.40–30.00	15.30–18.55	3.65–4.50	3.88–4.64	3.12–3.60	3.54–4.34	1.52–1.73
S.D.	1.710	0.208	0.405	1.333	0.821	0.210	0.162	0.113	0.193	0.053
No.	33	35	33	33	33	33	33	33	31	31
♀ Mean	51.52	7.35	9.48	38.79	23.92	5.83	4.11	3.25	4.09	1.63
Range	47.05–54.70	6.85–7.85	8.95–10.60	35.05–41.80	22.15–26.45	5.40–6.25	3.96–4.40	3.08–3.45	3.67–4.37	1.50–1.73
S.D.	1.825	0.252	0.384	1.697	1.304	0.261	0.147	0.094	0.192	0.069
No.	20	20	19	20	19	19	19	19	19	19

Table 5

Measurements

G. africanus parvulus: Java

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	28.30	4.05	5.47	21.07	13.80	3.25	4.20	3.39	3.85	1.54
Range	28.15–28.40	3.90–4.18	5.40–5.55	20.80–21.35	13.80–13.80	3.25–3.25	4.15–4.25	3.33–3.46	3.85–3.85	1.54–1.55
S.D.	–	–	–	–	–	–	–	–	–	–
No.	2	2	2	2	2	2	2	2	2	2
♀ Mean	42.98	5.93	7.71	31.95	19.38	4.76	4.07	3.25	4.12	1.65
Range	38.85–48.50	5.45–6.95	6.95–8.75	28.30–37.05	17.05–22.55	4.35–5.45	3.79–4.35	2.99–3.50	3.90–4.42	1.59–1.74
S.D.	2.675	0.366	0.505	2.500	1.578	0.318	0.160	0.142	0.154	0.040
No.	12	16	16	14	15	15	15	15	14	13

Table 6

Measurements

G. nubilus: China, Yunnan

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	29.03	4.62	6.10	21.04	15.63	3.50	4.47	3.38	3.48	1.35
Range	26.60–31.35	4.35–4.85	5.55–6.50	19.30–22.60	14.05–17.05	3.20–3.70	4.24–4.68	3.16–3.55	3.33–3.72	1.26–1.43
S.D.	1.200	0.175	0.298	0.841	0.942	0.232	0.128	0.135	0.107	0.048
No.	14	14	9	14	12	12	12	12	9	12
♀ Mean	36.49	6.54	8.19	25.63	20.44	4.97	4.12	3.15	3.19	1.26
Range	28.95–40.35	5.35–7.05	6.70–9.25	20.15–28.70	19.55–22.85	3.65–5.35	3.91–4.35	2.96–3.32	2.99–3.57	1.20–1.34
S.D.	2.711	0.398	0.758	2.060	1.769	0.447	0.139	0.123	0.190	0.043
No.	14	15	11	14	12	12	12	12	10	11

Dr P. Basilewsky (MRAC, Tervuren) and Dr G. Demoulin (IRSNB, Brussels). Localities for the following countries were supplemented from the literature: Chad (Descamps, 1968), Cameroon (Descamps, 1953), Comoro Is (Descamps & Wintrebert, 1969), Senegal (Roy, 1970), Ivory Coast (Gillon, 1974).

Affinities

G. africanus is allied to the african G. crassicollis (p. 283) on the basis of the shared complete fascia and bright yellow basal area of the hind wing and the blue shading of the underside of the hind femur. In Asia G. africanus has close affinities with the montane species, G. nubilus (p. 227), and in Indo-China there is sometimes a close approach in size and general appearance to the larger G. marmoratus (p. 243). The nearly related australian species G. musicus (p. 237) is easily differentiated by the red undersides of the hind femora, but is otherwise very close to G. africanus. G. crassicollis, G. marmoratus, and G. musicus all have a distinctly longer aedeagus than G. africanus.

Biology

G. africanus frequents bare patches in tall grassland, open woodland, and forest clearings (Jago, 1968; Joyce, 1952b; Phipps, 1970). The species is often caught at light, and in Mali is believed to migrate between the Niger flood plain and the drier Sahel savannah (Descamps, 1965). There are normally two generations in drier areas (Descamps, 1953; Robertson & Chapman, 1962) but there may be three in Madagascar (Descamps & Wintrebert, 1966), and continuous breeding in Ghana (Chapman, 1962). The dry season is survived by both egg and adult (Gillon, 1974; Joyce, 1952b; Robertson & Chapman, 1962). The egg stage may last 22 - 24 days during the rains (Golding, 1948; Davey et al., 1959; Descamps, 1965). There are five or six nymphal instars (Davey et al., 1959; Descamps,

1965) lasting 30 - 89 days in all (Davey et al., 1959; Jerath, 1968). Details of the eggs and egg pod were given by Chapman (1961), Descamps & Wintrebert (1966), Katiyar (1960) (as *G. transversus*), and Phipps (1971). Birds, spiders, and *Scelio* spp. have been reported as natural enemies (Descamps & Wintrebert, 1966; Golding, 1948). There are published reports of damage by this species to maize and millet (Descamps, 1954), sorghum (Joyce, 1952), tobacco (Zacher, 1921) and some other plants.

Discussion

The measurements of *G. africanus sulphureus* and *G. africanus parvulus* (Tables 3,5) are generally much smaller than those of *G. africanus africanus* (Table 1). Specimens of *G. africanus* from central Thailand are intermediate both in size (Table 4) and colouration between *G. a. parvulus* and the nominate subspecies. They may or may not show some degree of blue pigmentation on the underside of the hind femur and reduction in the intensity of the yellow colour of the hind wing basal area. The shorter wings and darker colour of *G. a. sulphureus* are presumably a response to high altitude. Genitalia differences within this highly variable species will not become clear until more material from a greater range of localities is available for study.

2.1.5.2 Gastrimargus nubilus Uvarov, 1925

(Figs 8-11,117; Plate 3)

Gastrimargus nubilus Uvarov, 1925a: 325. Holotype ♂, CHINA (BMNH) [examined].

Gastrimargus africanus chinensis Willemse, 1933: 15. LECTOTYPE ♂, CHINA (DEI, Eberswalde), here designated [synonymised by Uvarov, 1939:564] [examined].

Diagnosis. Fastigium of vertex flat or slightly concave. Pronotum with median carina arcuate, not intersected by posterior sulcus; dorsum smooth; hind margin acutangular. Tegmen reduced, surpassing folded hind knees by one fifth of hind femur length in male, hardly at all in female. Genitalia (Figs 8-11): similar to G. africanus.

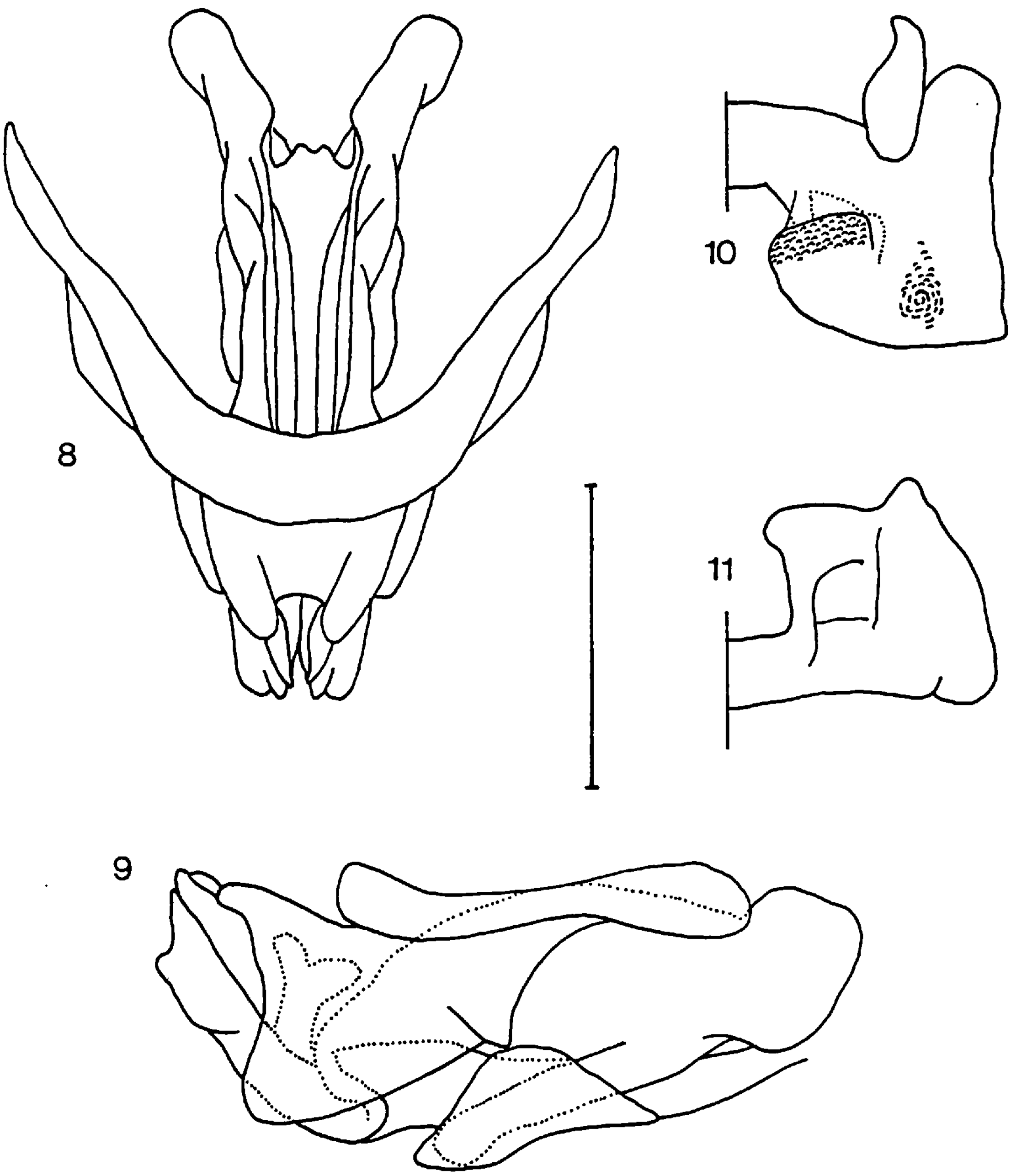
Colouration variable, generally more sombre than G. africanus. Pronotal x-marking often indistinct (Plate 3). Tegmen with pale cross-banding reduced to one or two variable pale patches on costal margin, two and four sevenths along from base (Plate 3). Hind wing with complete fascia (Plate 3) and with apical half of wing beyond fascia infumate (less distinctly in female); basal area of wing pale greenish yellow. Hind femur as in G. africanus africanus, interior ventral surface blue-black. Hind tibiae red.

Measurements: Table 6

Material examined: Appendix 2, p. 380.

Distribution (Fig. 117, and Biogeography section, p. 333).

G. nubilus is a montane species endemic to the mountains of southern China, north of the Burma border.



Figs 8-11. *Gastrimargus nubilus* Uvarov, genitalia. 8, phallic complex, dorsal view; 9, same, lateral view; 10, epiphallus, right half, dorsal view; 11, same, posterior view.

Plate 3. _G._ _nubilus_ Uvarov ♂

Plate 4. _G._ _lombokensis_ Sjöstedt ♂

Affinities

The range of this species overlaps with G. africanus, a species which it closely resembles and from which it has presumably been derived by the process of adaptation to harsh montane conditions. The reduction of tegmen and wing length, loss of the bright yellow basal area of the hind wing, and darkening of the apical half of the wing are all recurring features of this process. Similar characteristics are found in many montane Oedipodinae, as for example in G. willemsei (p. 315).

2.1.5.3 Gastrimargus lombokensis Sjöstedt, 1928
(Figs 12-15, 118; Plate 4)

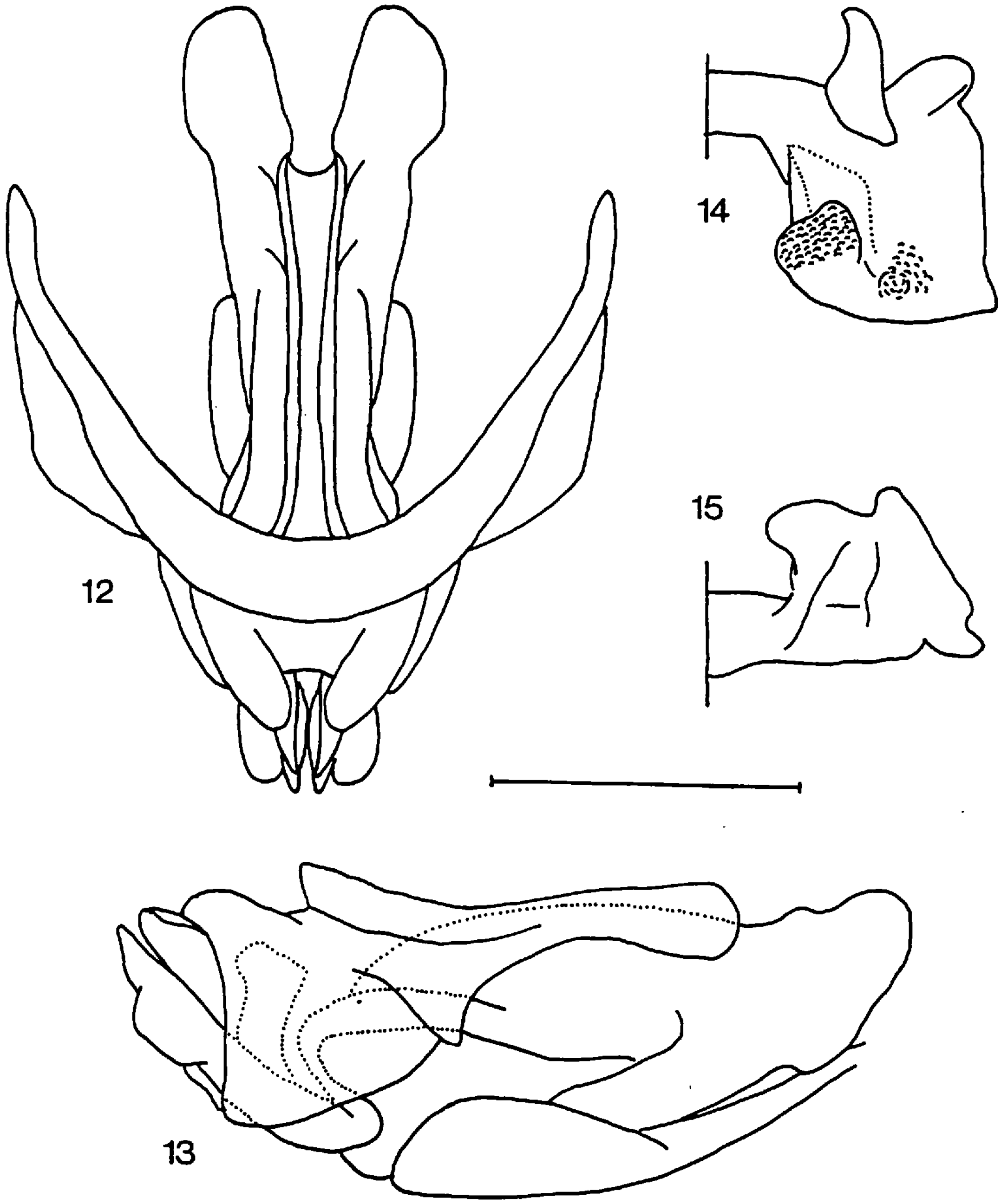
Gastrimargus lombokensis Sjöstedt, 1928: 6, 12. Holotype ♀, LOMBOK I. (MNHU, Berlin) [examined].

Gastrimargus lumbokensis [sic] Sjöstedt, 1928: 42.

Gastrimargus floresensis Sjöstedt, 1928: 43. Holotype ♂, FLORES I. (MNHU, Berlin) [lost]. Syn. n.

Diagnosis. Fastigium of vertex convex. Pronotum as in G. africanus, not intersected by posterior sulcus; hind margin rectangular to slightly acutangular. Tegmen surpassing folded hind knees by about one third of hind femur length. Genitalia (Figs 12-15) similar to G. africanus.

Colouration similar to G. africanus. Hind wing basally pale yellow, and fascia narrowly interrupted between Cu2 and 1A, with anterior end of anal section noticeably incurved towards wing base along 2A (Plate 4). Hind femur as in G. africanus externally; internal surface pale red, sometimes partly obscured by variable dark patch in medial area; dark pigment sometimes absent in green morphs except for rows of black dots on carinulae; ventral surface pale red. Hind tibiae orange-red in male becoming paler on outer sides, duller in female.



Figs 12-15. Gastrimargus lombokensis Sjöstedt, genitalia. 12, phallic complex, dorsal view; 13, same, lateral view; 14, epiphallus, right half, dorsal view; 15, same, posterior view.

Synonymy

Despite the loss of the unique holotype male of _G. floresensis_, the above synonymy is confirmed both by Sjöstedt's description and plate (1928: 43), and by examination of new material from Flores.

Measurements: Table 7

Material examined: Appendix 2, p. 380.

Distribution (Fig. 118, and Biogeography section, p. 336).

Lesser Sunda Is.

Affinities

G. lombokensis occupies a geographical and taxonomic position intermediate between _G. africanus_ in Java and _G. musicus_ in New Guinea. The male genitalia with their rather short aedeagus are closer to those of _G. africanus_ than to _G. musicus_, but the red underside of the hind femur is a character found also in _G. subfasciatus_ on neighbouring Timor and _G. musicus_ in New Guinea and Australia. However the form of the hind wing band is peculiar to this species (Plate 4) suggesting that _G. lombokensis_ was not an intermediate stage in the evolution of _G. musicus_.

Table 7

Measurements

G. lombokensis: Lesser Sunda Is.

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	29.63	4.32	5.89	21.93	14.98	3.47	4.32	3.48	3.75	1.47
Range	26.10–33.50	3.90–4.80	5.10–7.05	19.15–24.85	13.20–16.95	3.10–3.85	4.04–4.65	3.24–3.77	3.17–4.18	1.30–1.58
S.D.	1.847	0.245	0.481	1.442	0.814	0.185	0.160	0.137	0.234	0.098
No.	36	36	36	36	34	34	34	34	36	34
♀ Mean	38.90	6.04	7.77	28.29	19.95	4.72	4.23	3.33	3.65	1.41
Range	33.60–43.30	5.35–6.85	6.35–9.25	22.10–32.00	16.55–22.75	4.25–5.40	3.85–4.53	2.87–3.66	2.68–4.02	1.06–1.52
S.D.	2.490	0.414	0.636	2.162	1.451	0.284	0.161	0.164	0.241	0.080
No.	35	37	37	36	35	35	35	34	36	34

Table 8

Measurements

G. subfasciatus: Timor

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	30.61	4.32	6.15	22.74	14.87	3.52	4.20	3.45	3.70	1.53
Range	28.25–33.65	4.00–5.00	5.55–6.70	21.00–24.65	13.15–16.65	2.65–3.95	3.96–5.25	3.30–3.87	3.45–3.96	1.45–1.65
S.D.	1.700	0.307	0.385	1.270	1.311	0.407	0.406	0.175	0.144	0.060
No.	10	10	10	10	10	9	9	10	10	10
♀ Mean	42.04	6.22	8.39	31.33	19.92	4.93	4.04	3.20	3.77	1.58
Range	37.65–45.10	5.65–6.75	7.00–9.75	27.70–34.50	17.65–21.65	4.45–5.30	3.75–4.39	3.02–3.41	3.16–4.16	1.46–1.78
S.D.	2.087	0.310	0.524	1.784	1.174	0.255	0.172	0.108	0.201	0.088
No.	28	30	28	28	22	22	22	22	26	20

2.1.5.4 Gastrimargus subfasciatus (de Haan, 1842)

(Figs 16–19, 120; Plate 5)

Acridium (Oedipoda) subfasciatum de Haan, 1842: 161. LECTOTYPE ♂, TIMOR (RNH, Leiden) here designated [examined].

Oedaleus (Gastrimargus) subfasciatus (de Haan); Saussure, 1884: 115; 1888: 39 [gives incorrect type locality].

Gastrimargus subfasciatus (de Haan); Willemse, 1928: 14

Diagnosis. Antennae long, in male 1.25 times combined length of head and pronotum. Fastigium of vertex flat or slightly concave. Pronotum with median carina arcuate, not intersected by posterior sulcus; hind margin slightly acutangular. Tegmen surpassing folded hind knees by about one third of hind femur length. Genitalia (Figs 16–19) similar to G. africanus.

Colouration similar to G. africanus. Metazona of pronotum often with dark brown diamond-shaped area in male, reduced in female to two dark bars flanking median carina on inner sides of posterior arms of x-marking; x-marking often indistinct. Tegmen similar to G. africanus. Hind wing basally pale blue; fascia interrupted, restricted to posterior margin of wing, not advancing further than 3A (Plate 5). Hind femur externally as in G. africanus, internally with dark brown patch in basal half of medial area; lower internal carinula and ventral surface of hind femur bright red in male, duller in female. Hind tibiae of male bright orange red on internal lateral surface, paler on outer surface, less pronounced in female.

Measurements: Table 8

Material examined: Appendix 2, p. 380.

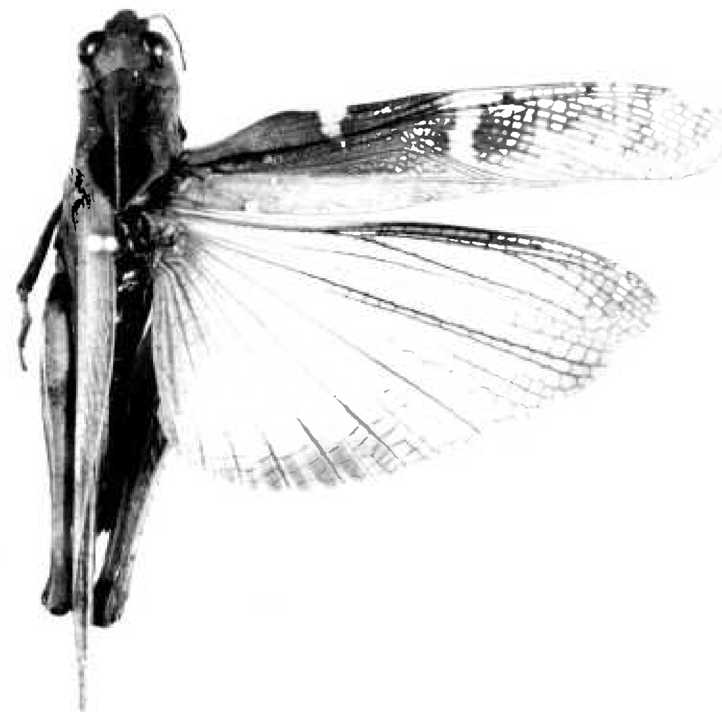
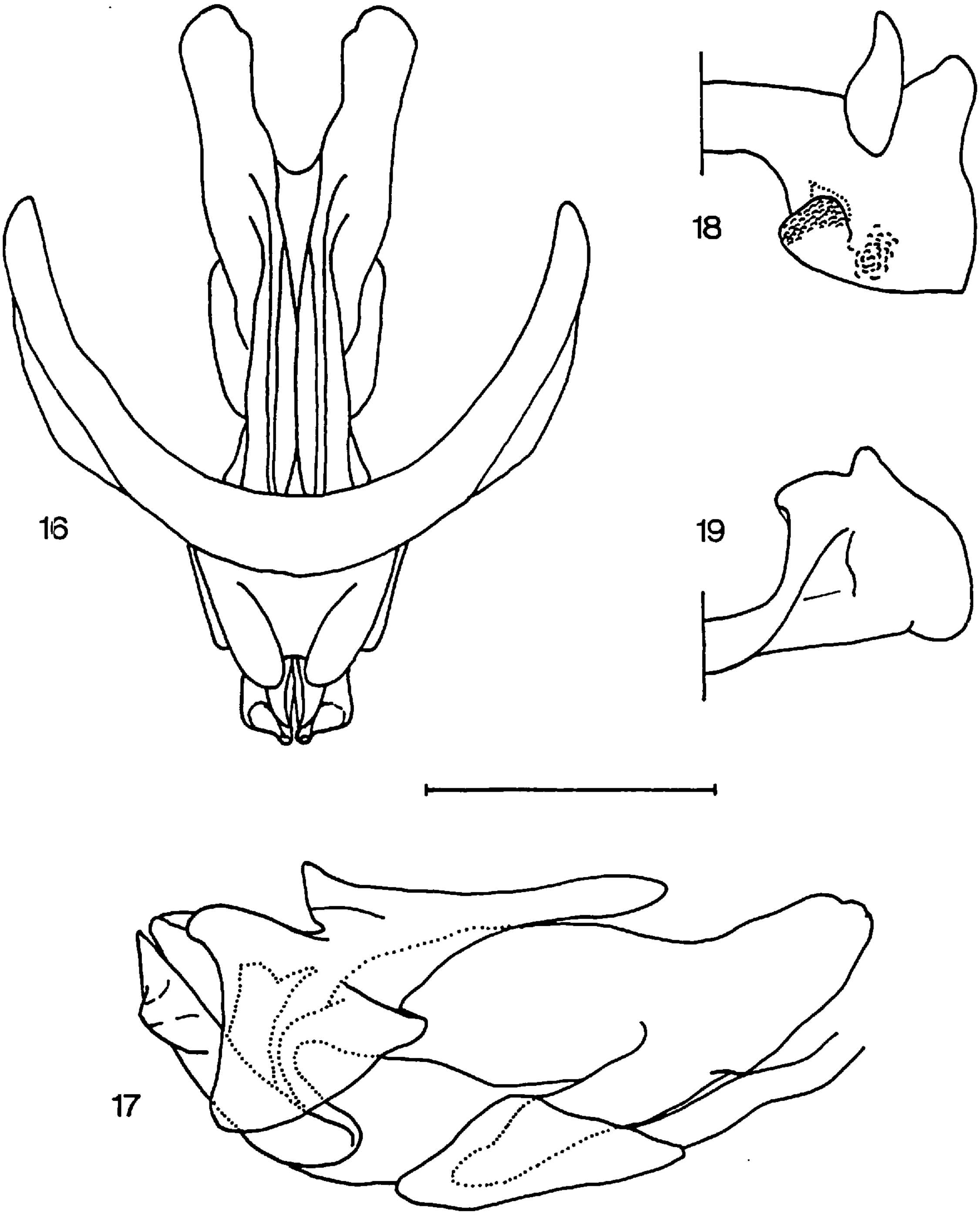


Plate 5. *G. subfasciatus* (de Haan) ♂

Plate 6. *G. musicus* (Fabricius) ♂: New Guinea
'Bright yellow winged race'



Figs 16-19. Gastrimargus subfasciatus (de Haan), genitalia. 16, phallic complex, dorsal view; 17, same, lateral view; 18, epiphallus, right half, dorsal view; 19, same, posterior view.

Distribution: (Fig. 120, and Biogeography section, p. 338).

Affinities

G. subfasciatus is closely allied to G. lombokensis on the basis of its genitalia and general appearance, particularly the red undersides of the hind femora. The greatly reduced hind wing fascia and the pale blue basal area are relatively minor modifications of the condition found in G. lombokensis (see Biogeography section, p. 338), despite the distinctive appearance which they present.

2.1.5.5 Gastrimargus musicus (Fabricius, 1775)
(Figs 20-25, 120; Plate 6)

Gryllus musicus Fabricius, 1775: 290. Holotype ♀, AUSTRALIA (BMNH) [examined].

Acrydium musicum (Fabricius); Olivier, 1791: 222.

Gryllus pictus Leach, 1814: 57 [type(s) presumed lost: synonymy indicated by coloured plate 25 of male (?) in Leach, 1814].

Gryllus stollii Leach, 1814: 137 [unjustified emendation of previous name].

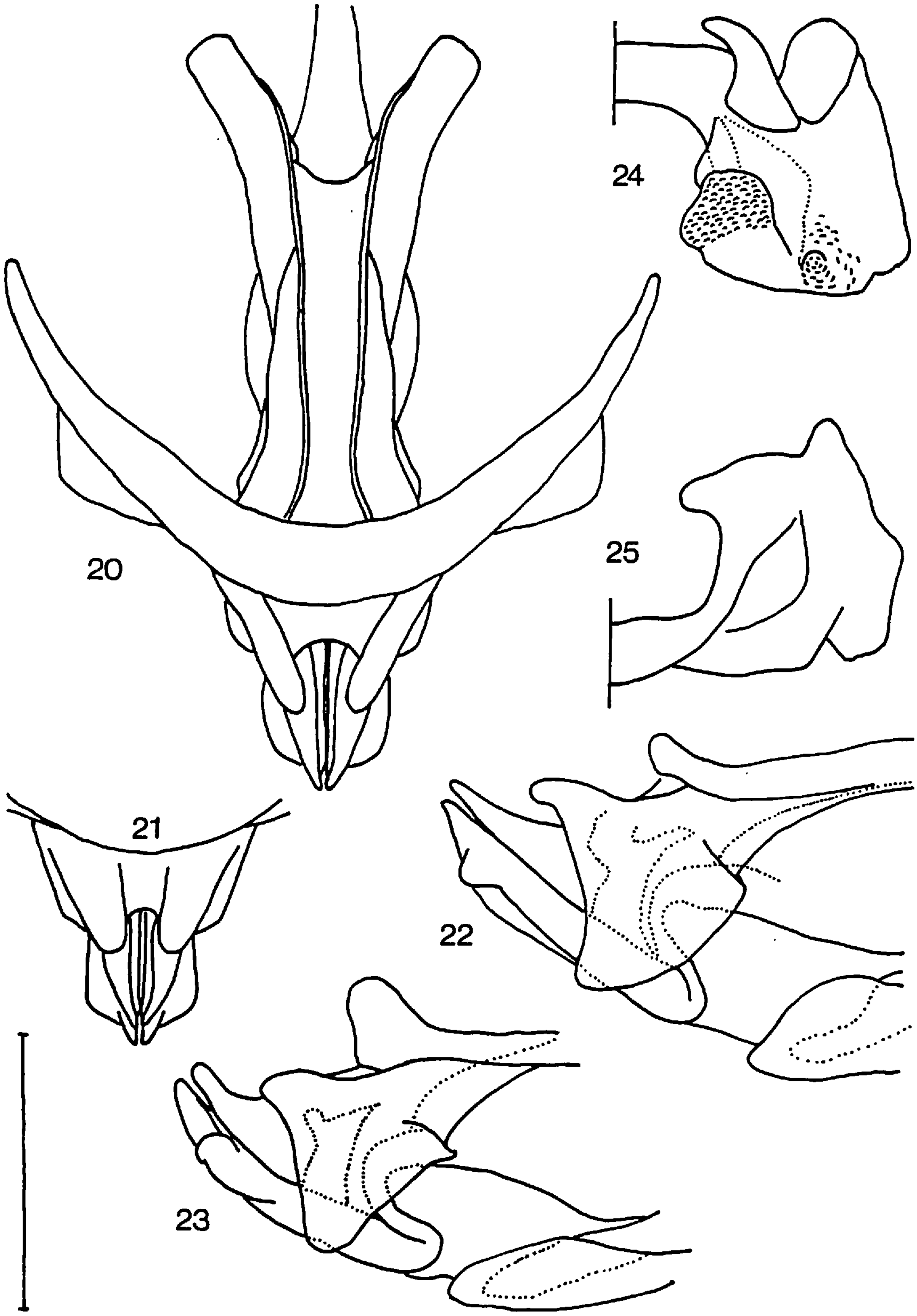
Oedipoda musica (Fabricius); Serville, 1839: 720.

[Locusta danica Linnaeus; Froggatt, 1903: 1104; 1907:41; 1910: 9. Misidentifications.]

Gastrimargus musicus (Fabricius); Kirby, 1910: 227.

Gastrimargus musicus var. kimberleyensis Sjöstedt, 1928: 42. Holotype ♂, AUSTRALIA (NR, Stockholm) [examined]. Syn. n.

Diagnosis. Fastigium of vertex slightly convex, flat, or slightly concave. Pronotum with median carina arcuate, sometimes intersected by



Figs 20-25. *Gastrimargus musicus* (Fabricius), genitalia. 20, phallic complex, dorsal view (Australia); 21, same, posterior portion (Solomon Is); 22, same, lateral view (Australia); 23, same (Solomon Is); 24, epiphallus, right half, dorsal view (Australia); 25, same, posterior view.

posterior sulcus; hind margin acutangular to rectangular, sharply or bluntly angled. Tegmen surpassing folded hind knees by one quarter to one third of hind femur length. Genitalia (Figs 20-25) with strongly projecting aedeagus and variable subapical ventral process, more strongly protruding laterally in pale wing race (E New Guinea and Solomon Is).

Colouration similar to G. africanus. Pronotal x-marking usually indistinct, posterior arms usually obscured. Tegmen with variable cross-banding, usually distinct. Hind wing (Plate 6) with complete fascia, sometimes narrowly interrupted between Cu2 and 1A; basal area bright yellow (Australia, central New Guinea) to pale yellow or almost colourless (E New Guinea, Solomon Is). Hind femur externally with or without oblique cross-banding, internally dark brown in basal half of medial area; internal ventral carinula and ventral surface red, tending to lose colour in New Guinea, usually straw-coloured in Solomon Is. Hind tibiae usually red, sometimes dull brown or straw (especially in Solomon Is).

Measurements: Tables 9 - 11

Material examined: Appendix 2, p. 380.

Distribution: (Fig. 120 , and Biogeography section, p. 341).

G. musicus occurs in Tasmania, Australia, New Guinea, and the Solomon Is.

Affinities

G. musicus is allied to G. africanus on the basis of the yellow hind wing basal area and uninterrupted fascia, as well as the general form and colouration. The red undersides of the hind femora are common to G. lombokensis and G. subfasciatus, but G. musicus has a distinctly longer aedeagus than any of these species and can be differentiated by the characters given in the key (pp. 211-212).

Table 9

Measurements

G. musicus (bright yellow winged race): New Guinea

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	36.27	4.95	7.21	27.56	17.60	3.77	4.63	3.56	3.82	1.56
Range	33.55–38.90	4.55–5.30	6.65–7.90	25.30–29.30	16.20–19.40	3.25–4.10	4.26–4.91	3.43–3.70	3.44–4.08	1.40–1.64
S.D.	1.490	0.227	0.362	1.188	0.902	0.233	0.193	0.079	0.149	0.060
No.	17	19	18	17	19	19	19	19	16	17
♀ Mean	45.12	6.36	8.97	34.16	21.58	4.76	4.53	3.39	3.82	1.59
Range	42.90–47.65	6.05–6.75	8.20–10.30	32.55–36.30	19.75–24.25	4.30–5.25	4.41–4.62	3.22–3.59	3.52–4.02	1.50–1.65
S.D.	1.392	0.254	0.684	1.113	1.363	0.293	0.081	0.149	0.179	0.049
No.	7	7	7	7	7	7	7	7	7	7

Table 10

Measurements

G. musicus (pale yellow winged race): New Guinea

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	37.23	5.29	7.40	28.00	17.78	4.11	4.32	3.36	3.79	1.58
Range	34.10–41.45	4.55–5.95	6.60–8.30	25.90–31.55	15.55–20.50	3.65–4.55	4.00–4.67	3.18–3.62	3.42–4.16	1.46 1.72
S.D.	1.810	0.355	0.451	1.324	1.180	0.218	0.157	0.089	0.153	0.068
No.	37	37	37	37	37	37	37	37	37	37
♀ Mean	46.13	7.03	9.46	34.87	22.16	5.02	4.39	3.15	3.69	1.58
Range	34.55–50.30	6.20–7.65	8.85–10.50	32.35–37.75	18.75–25.35	4.15–5.80	3.65–4.92	2.89–3.57	3.34–3.95	1.48–1.77
S.D.	3.456	0.311	0.420	1.651	1.615	0.384	0.358	0.167	0.151	0.076
No.	19	21	21	19	20	20	20	20	19	19

Table 11

Measurements

G. musicus (pale race): Solomon Is.

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	37.83	5.35	7.33	28.54	18.12	4.17	4.35	3.39	3.90	1.58
Range	33.75–41.40	5.05–5.60	6.60–8.05	27.00–31.40	16.65–19.20	3.80–4.65	4.07–4.58	3.23–3.56	3.64–4.21	1.50–1.68
S.D.	1.782	0.153	0.412	1.453	0.834	0.261	0.160	0.106	0.136	0.053
No.	14	14	14	14	14	14	14	14	14	14
♀ Mean	48.19	7.01	9.21	36.06	22.48	5.20	4.33	3.21	3.90	1.60
Range	43.35–55.10	6.45–8.00	8.00–10.75	31.80–42.35	19.25–26.2	4.20–6.15	4.04–4.67	2.92–3.40	3.57–4.37	1.53–1.84
S.D.	2.943	0.380	0.593	2.336	1.457	0.391	0.202	0.100	0.171	0.073
No.	24	25	25	24	25	25	25	25	24	24

Table 12

Measurements

G. marmoratus: Thailand

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	39.46	5.19	8.19	29.68	20.27	4.14	4.89	3.90	3.63	1.47
Range	34.30–43.90	4.55–6.00	6.80–9.25	25.65–32.95	16.85–23.75	3.60–4.55	4.15–5.22	3.51–4.20	3.26–3.96	1.34–1.59
S.D.	2.619	0.396	0.759	1.960	2.010	0.305	0.247	0.160	0.174	0.071
No.	22	22	19	22	21	21	21	21	19	21
♀ Mean	57.42	7.65	11.63	43.02	28.62	6.02	4.76	3.74	3.72	1.50
Range	55.00–61.20	7.00–8.25	10.60–13.05	39.55–46.20	26.65–31.85	5.55–6.80	4.44–5.02	3.59–3.94	3.38–3.92	1.39–1.60
S.D.	2.057	0.388	0.805	1.919	1.701	0.363	0.222	0.108	0.185	0.057
No.	10	12	10	11	12	12	12	12	9	11

Biology

G. musicus frequents tall grass with patches of bare ground, with or without trees (Common, 1948). There are normally two generations in central Queensland and one on the New South Wales tablelands. In suitable conditions eggs may hatch 17 days after laying, though they can remain viable for up to ten months. The nymphal stages are completed in 39 - 48 days. Hatching occurs in September-November and January - March (Common, 1948; Key, 1938) and adults are found from October to May. Eggs are laid in firm bare soil, and egg fields may cover 1-10 acres at densities of up to 270 pods per square foot (Common, 1948; Mungomery, 1944). Details of egg pod and eggs are given by Common (1948). Swarms occur periodically in Queensland and move southward and coastward. Individuals from swarms show phase changes in behaviour and morphology, having longer wings and less pronounced sexual dimorphism than solitary insects (Common, 1948). The species is preyed upon by numerous insects and many birds (Carrick, 1959; Common, 1948; Mungomery, 1945; Fuller, 1938; Uvarov, 1928). There are numerous reports of occasional damage by swarms to pasture and a variety of crops (Common, 1948), especially sugarcane. In Queensland in 1962 *G. musicus* was calculated to have caused losses of 4756 tons to this crop (Wilson et al., 1963). It has been suggested however that even spectacular defoliation may ultimately have little effect on yields (King et al., 1953). All the available information on this species relates to Australian populations. There are no data from New Guinea or the Solomon Is.

Discussion

The mainland form of *G. musicus* is characterised by the bright yellow basal area of the hind wing and the red ventral surface of the hind femur. The population in central New Guinea, across the straits from Cape York is identical to the mainland form, but further east there is a noticeable loss of depth of the yellow colour of the hind wing and some reduction in the red colour of the hind femur. This population is intermediate between the mainland form and the extreme condition of the Solomon Is race which exhibits almost complete loss of colour in both the wing and the hind femur. Comparing the morphometrics of the three forms (Tables 9-11) there are relatively minor differences, but there is a slight trend of increasing size from central New Guinea eastwards to Guadalcanal as judged by both tegmen length and femur length. The formal taxonomic status of the eastern populations is best left undecided until larger samples are available for study, preferably with the back-up of comparative genetical studies.

2.1.5.6 Gastrimargus marmoratus (Thunberg, 1815)

(Figs 26-32, 119; Plate 7)

Gryllus marmoratus Thunberg, 1815: 232. LECTOTYPE ♀, 'Cap.' [incorrectly labelled: actual locality unknown] (ZIUU, Uppsala) here designated [examined].

Gryllus transversus Thunberg, 1815: 232. LECTOTYPE ♀, CHINA (ZIUU, Uppsala) here designated [synonymised by Stål, 1873: 124] [examined].

Gryllus virescens Thunberg, 1815: 245. Holotype ♂, no locality data (ZIUU, Uppsala) [synonymised by Stål, 1873: 124] [examined].

Gryllus assimilis Thunberg, 1815: 246. Holotype ♂, no locality data (ZIUU, Uppsala) [synonymised by Stål, 1873: 124] [examined].

Pachytylus (Oedaleus) marmoratus (Thunberg); Stål, 1873: 123.

Oedaleus (Gastrimargus) marmoratus (Thunberg); Saussure, 1884: 112.

Oedaleus (Gastrimargus) marmoratus Stirps sundaicus Saussure, 1884: 113. LECTOTYPE ♀, SUMATRA (MHN, Geneva) here designated [synonymised by Sjöstedt, 1928: 34] [examined].

Oedaleus (Gastrimargus) marmoratus var. sundaicus Saussure; Saussure, 1888: 39 [emendation of the above, erroneously including material from the Congo].

Oedaleus (Gastrimargus) marmoratus var. grandis Saussure, 1888: 39. Holotype ♀, CHINA (NR, Stockholm) [synonymised with var. sundaicus by Kirby, 1910:228] [examined].

Gastrimargus virescens (Thunberg); Kirby, 1910: 226.

Gastrimargus assimilis (Thunberg); Kirby, 1910: 226.

Gastrimargus marmoratus (Thunberg); Kirby, 1910: 226.

Gastrimargus transversus (Thunberg); Kirby, 1910: 227.

Gastrimargus sundaicus (Saussure); Kirby, 1910: 228.

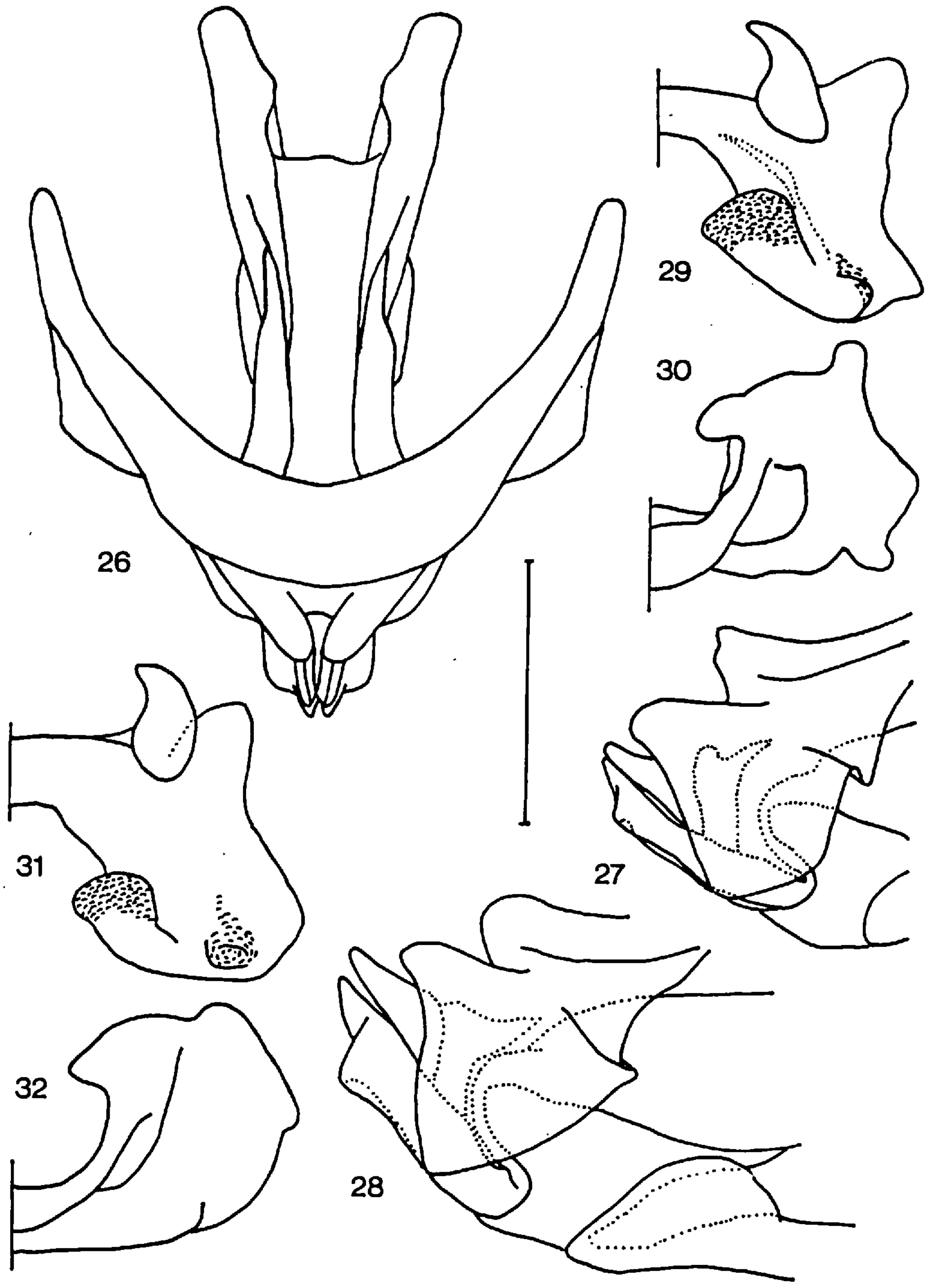
Gastrimargus marmoratus var. transversa (Thunberg); Sjöstedt, 1928: 37.

Gastrimargus marmoratus var. grandis (Saussure); Sjöstedt, 1928: 37.

Gastrimargus marmoratus var. grandis forma rectinotum Sjöstedt, 1928: 37 [unavailable infrasubspecific name].

Diagnosis. Fastigium of vertex slightly convex. Pronotum with median carina arcuate, sometimes intersected by posterior sulcus; hind margin sharply acutangular. Tegmen surpassing folded hind knees by one quarter to two fifths of hind femur length. Genitalia (Figs 26-32) variable, similar to G. africanus, but with aedeagus more strongly projecting.

Colouration variable. Pronotal x-marking with posterior arms usually indistinct or absent. Transverse bands on tegmen sometimes reduced. Hind wing fascia (Plate 7) complete, with some diffusion of dark pigment towards wing apex along third and subsequent anal veins, more marked in female; basal area of wing pale yellow with pale blue tinge on bases of veins; apex lightly infumate. Hind femora externally with variable oblique transverse banding, often absent except for rows of black dots on upper and lower carinulae; internal surface with dots on carinulae and indistinct brown patch in basal half of medial area



Figs 26-32. Gastrimargus marmoratus (Thunberg), genitalia. 26, phallic complex, dorsal view (New Guinea); 27, same, posterior portion, lateral view (Borneo); 28, same (New Guinea); 29, epiphallus, right half, dorsal view (Borneo); 30, same, posterior view; 31, same, dorsal view (New Guinea); 32, same, posterior view.

Plate 7. G. marmoratus (Thunberg) ♂

Plate 8. G. immaculatus (Chopard) ♂

only; ventral surface straw-coloured. Hind tibiae light red.

Synonymy

G. marmoratus stirps _sundaicus_ was based on female specimens of the brown morph of _G. marmoratus_ from Sumatra. These exhibit light and dark brown mottling or streaking on the dorsum of the pronotum. This type of colouration occurs widely and is of no geographical or racial significance. The type locality 'Cap.' (Cape of Good Hope) for _G. marmoratus_ is a labelling error first noted by Stål (1873) which probably arose during Thunberg's extensive travels, first to the Cape and then to east Asia. From Thunberg's descriptions of _G. virescens_ and _G. assimilis_ there is some suggestion that the two type specimens may have been subsequently switched. In Thunberg's description of _G. assimilis_ (1815) he states that it is '_simillimus G. virescenti sed duplo fere minor_', i.e. half the size of _G. virescens_. In fact, as noted by Sjöstedt (1928: 35), the specimen now labelled as _G. virescens_ is the smaller, but a confusion of labels cannot be proved and is not now of taxonomic importance. An interesting historical note is that Thunberg's _Gastrimargus_ specimens, with the exception of the lectotype of _G. marmoratus_ and the holotype of _G. assimilis_ which have both been repinned, are mounted on contemporary eighteenth century needles rather than pins.

Measurements: Tables 12, 13

Material examined: Appendix 2, p. 380

Distribution (Fig. 119, and Biogeography section, p. 338).

G. marmoratus is widely distributed in SE Asia from Assam NE to Japan, SW to Sumatra, and SE to the Vogelkop peninsula of New Guinea. Records from India other than Assam (e.g. Katiyar, 1960) should be referred to _G. africanus_.

Table 13

Measurements

G. marmoratus: Malaysia

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	35.89	4.71	7.51	26.91	17.79	3.67	4.75	3.77	3.60	1.51
Range	31.40–39.65	4.15–5.15	6.50–8.75	23.60–30.20	15.35–20.20	3.25–4.00	4.92–5.32	3.45–4.03	3.25–4.27	1.40–1.59
S.D.	2.053	0.252	0.523	1.627	1.220	0.207	0.540	0.136	0.196	0.047
No.	33	33	30	33	30	30	30	30	30	30
♀ Mean	53.48	7.08	11.07	40.49	26.67	5.63	4.74	3.77	3.66	1.52
Range	49.65–56.70	6.40–7.45	10.25–12.15	43.20–37.65	24.05–28.40	5.15–6.10	4.37–5.12	3.49–3.95	3.41–3.93	1.47–1.64
S.D.	2.320	0.263	0.638	1.800	1.268	0.309	0.202	0.128	0.119	0.044
No.	14	16	16	15	15	15	15	15	15	14

Table 14

Measurements

G. immaculatus: Réunion

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	26.00	3.95	5.28	18.95	12.98	3.26	3.98	3.28	3.59	1.46
Range	23.15–29.20	3.70–4.25	4.55–5.95	16.50–21.75	11.75–14.30	2.95–3.60	3.60–4.25	3.02–3.47	3.29–3.85	1.34–1.54
S.D.	1.473	0.196	0.343	1.195	0.715	0.189	0.166	0.112	0.164	0.050
No.	23	23	23	23	23	23	23	23	23	23
♀ Mean	35.87	5.82	7.63	25.61	17.49	4.63	3.79	3.01	3.36	1.47
Range	33.80–37.65	5.35–6.25	6.55–8.10	24.20–27.10	15.95–18.85	5.05–4.10	3.51–4.10	2.70–3.22	3.13–3.76	1.39–1.63
S.D.	1.100	0.223	0.374	0.841	0.894	0.237	0.177	0.128	0.161	0.064
No.	19	20	20	19	20	20	20	19	20	19

Affinities

G. marmoratus is related to G. africanus from which it differs principally by the longer wings and hind femora, the more pointed pronotal hind margin, the pale basal area of the hind wing, and the absence of blue pigment on the underside of the hind femur. In E China and Burma where G. africanus loses the bright yellow hind wing colour and blue underside of the hind femur, there is need of care to distinguish the two species.

Biology

G. marmoratus frequents tall grassland, old cultivations, and grazing land, often with Lalang (Imperata arundinacea Cyr.) (Miller, 1932, 1934; Tinkham, 1935b, Roffey, in press). It is also found around rice paddy, and on shrubs (Tsyplenkov, 1970). There is little information available on the life cycle in nature. In Taiwan there are two generations, with overwintering normally as eggs, rarely as nymphs. There are six nymphal instars occupying 54 - 102 days in total (Sonan & Fukuda, 1926). There are records of damage to maize, rice, sorghum, citrus, sugar cane, cocoa, and oil palm (Roffey, in press). Adults are preyed on by Sphex (Prionyx) subfuscatus (Dahl) (Piel, 1935), and eggs and nymphs are attacked by the fungus Metarrhizium sp. (Wood, 1968).

2.1.5.7 <u>Gastrimargus immaculatus</u> (Chopard, 1957)
(Figs 33-36, 116; Plate 8)

<u>Oedaleus immaculatus</u> Chopard, 1957: 51. Holotype ♂, REUNION I. (MNHN, Paris) [examined].

<u>Gastrimargus immaculatus</u> (Chopard); Têtefort & Wintrebert, 1965: 650.

Diagnosis. Fastigium convex. Pronotum with median carina low arcuate or flat, not intersected by posterior sulcus; posterior margin blunt acutangular or rectangular. Tegmen surpassing folded hind knees by one third of hind femur length. Genitalia (Figs 33-36) similar to <u>G. africanus</u>; aedeagus very short, epiphallus with convergent outer lophi.

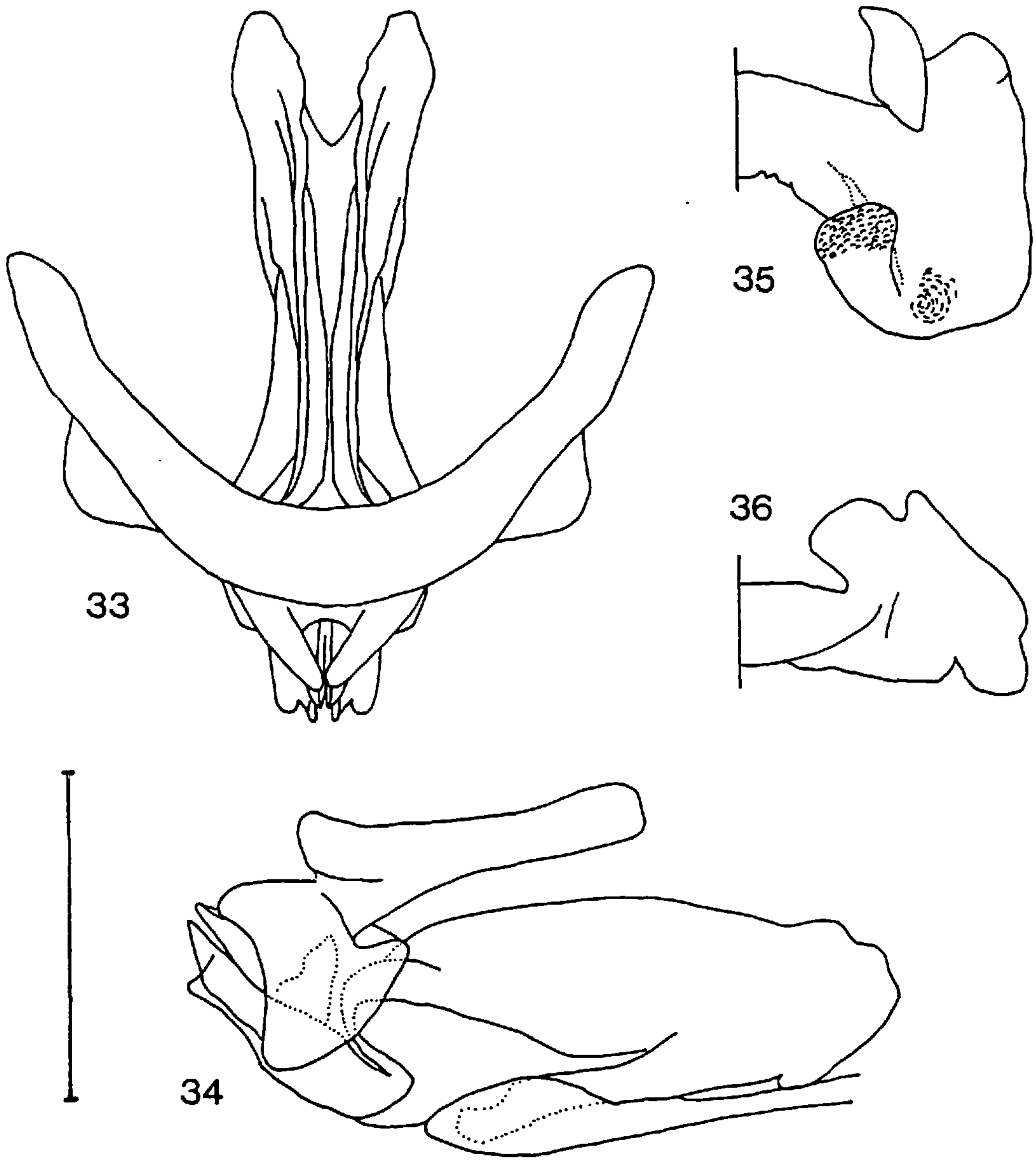
Colouration similar to <u>G. africanus</u>. Pronotal x-marking sometimes obsolete in green morphs. Tegmen opaque brown, clearing in apical half, usually lacking pale transverse bands (Plate 8). Hind wing basal area very pale yellow, fascia (Plate 8) variable, sometimes indistinct or absent between costal margin and 3A, usually interrupted between M and 2A in males; in female fascia restricted to anal area posterior to 3A or absent. Hind femur externally as in <u>G. africanus</u>; internal surface dark brown in basal half of medial area only; ventral surface straw-coloured. Hind tibia orange red.

Measurements: Table 14

Material examined: Appendix 2, p. 381.

Distribution (Fig. 116, and Biogeography section, p. 333).

La Réunion.



Figs 33-36. Gastrimargus immaculatus (Chopard), genitalia. 33, phallic complex, dorsal view; 34, same, lateral view; 35, epiphallus, right half, dorsal view; 36, same, posterior view.

Affinities

G. immaculatus is allied to G. africanus and its relatives on the basis of the male genitalia. It has however lost the bright yellow colour of the hind wing basal area and the blue underside of the hind femur. In this respect it resembles G. marmoratus, but there is further reduction in the hind wing fascia and the species is much smaller than any of its near relatives (see measurements Table 14).

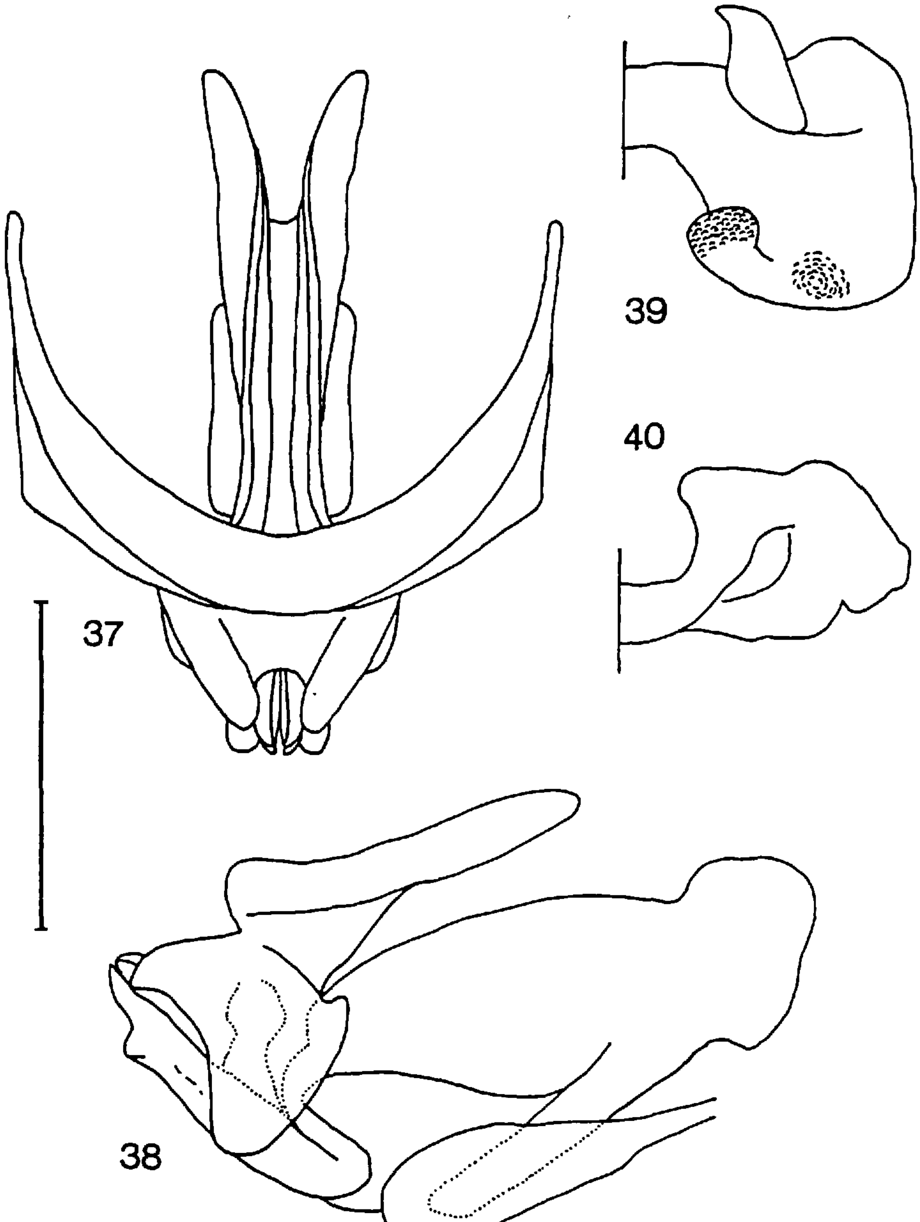
2.1.5.8 Gastrimargus hyla Sjöstedt, 1928
(Figs 37-40; Plates 9,10)

Gastrimargus hyla Sjöstedt, 1928: 28. Holotype ♀, ETHIOPIA (MNHN, Paris) [examined].

Gastrimargus abessinicus Sjöstedt, 1928: 28. Holotype ♀, ETHIOPIA (MNHN, Paris) [examined]. Syn. n.

Diagnosis. Fastigium of vertex flat or slightly concave. Pronotum laterally rugose; median carina low arcuate, intersected by posterior sulcus; hind margin blunt acutangular. Lateral and ventral surfaces of thorax sparsely hairy. Tegmen surpassing folded hind knees by two fifths of hind femur length in male, barely reaching hind knees in female. Tegmen length / pronotum length ratio 3.26 ♂, 2.38-2.67 ♀. Genitalia (Figs 37-40) similar to G. rothschildi (Figs 41-44), but aedeagus with smaller subapical ventral process.

Colouration brown or green. Pronotal x-marking thin, pale, with short, straight posterior arms (Plate 10), not recurved; pronotal pattern may be obsolete in green morphs. Tegmen with cross bands obsolete. Hind wing fascia (Plate 10) indistinct in male, narrowly interrupted by all major veins but otherwise complete, much fainter in female; basal area



Figs 37-40. Gastrimargus hyla Sjöstedt, genitalia. 37, phallic complex, dorsal view; 38, same, lateral view; 39, epiphallus, right half, dorsal view; 40, same, posterior view.

Plate 9. G. hyla Sjöstedt ♂

Plate 10. G. hyla Sjöstedt ♀

pale yellow. Hind femur externally with irregular dark brown dots along upper and lower carinulae and in medial area; internal medial and ventral areas unicolourous blue-black except for subapical pale ring above knee in male; blue-black replaced by maroon in female except for carinulae. Hind tibiae red.

Synonymy

Sjöstedt (1928) repeatedly fell into the error of describing the green and brown morphs of the same species as separate taxa. In this instance G. abessinicus is merely the brown morph of G. hyla.

Measurements: Table 15

Material examined: Appendix 2 , p. 381.

Distribution

All the known specimens of G. hyla were collected from an unknown locality or localities in Ethiopia by members of the ill-fated Bonchamps expedition to Fachoda (Michel, 1900). The general similarity of G. hyla to G. abessinicus and in particular the short wings of the female suggest that the species probably occupies a montane habitat like that of G. abessinicus. The expedition travelled WSW from Harer in the east to the White Nile at its junction with the Sobat. Michel (1900: 90) recorded that the expedition's insect collections were already considerable by the time they had reached the junction of the Kesem and Awash rivers. One possible locality for the specimens of G. hyla is the eastern part of the Ahmar mountains near Harer, where the expedition spent some time. Another possible site is offered by the mountains along the road from Addis Ababa to Nekemte. It is known that a small collection of birds was made at 'Léka' in the 'Rogué mountains'. This evidently refers to the range just east of Nekemte. The expedition also passed through the

Table 15

Measurements

G. hyla: Ethiopia, locality unknown

Specimen	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
G. abessinicus Holotype ♀	29.80	5.70	7.95	20.25	16.45	4.30	3.83	2.89	2.55	1.23
G. abessinicus Paratype ♀	30.00	5.85	8.35	19.90	17.10	4.30	3.98	2.92	2.38	1.16
G. hyla Holotype ♀	30.65	5.75	8.05	21.45	17.15	4.40	3.90	2.98	2.67	1.25
Undescribed Unique ♂	24.30	3.45	5.45	17.75	11.70	3.00	3.90	3.39	3.26	1.52

Table 16

Measurements

G. rothschildi: Ethiopia, Balé Province ('Blue-leg' race)

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	22.49	3.48	6.03	16.26	12.54	2.93	4.28	3.60	2.71	1.30
Range	20.30–24.80	3.15–3.75	5.20–6.70	14.15–17.85	11.30–13.85	2.55–3.20	4.03–4.77	3.39–3.94	2.46–3.18	1.16–1.38
S.D.	1.250	0.147	0.414	0.977	0.728	0.157	0.195	0.130	0.188	0.056
No.	20	20	20	20	20	20	20	20	20	20
♀ Mean	26.59	5.90	10.18	16.58	17.61	4.79	3.68	2.99	1.64	0.94
Range	24.65–29.10	5.30–6.35	8.80–11.80	15.15–18.40	16.20–19.85	4.20–5.40	3.41–3.98	2.83–3.15	1.48–1.83	0.88–1.03
S.D.	1.380	0.288	0.765	1.003	0.956	0.329	0.159	0.092	0.113	0.046
No.	17	17	17	17	17	17	17	17	17	17

mountainous area of the Menagesha National Forest, known to them as Mt. Toké. More recent collecting in Ethiopia has so far failed to rediscover this species and its whereabouts remains a mystery.

Affinities

This species is allied to G. rothschildi on the basis of the genitalia and the reduction of the female tegmen length and hind wing fascia. The differences are outlined in the key (p. 205). The male of G. hyla is described for the first time, by courtesy of Dr M Donskoff (MNHN, Paris).

2.1.5.9 Gastrimargus rothschildi Bolivar, 1922
(Figs 41-44, 114; Plates 11,12)

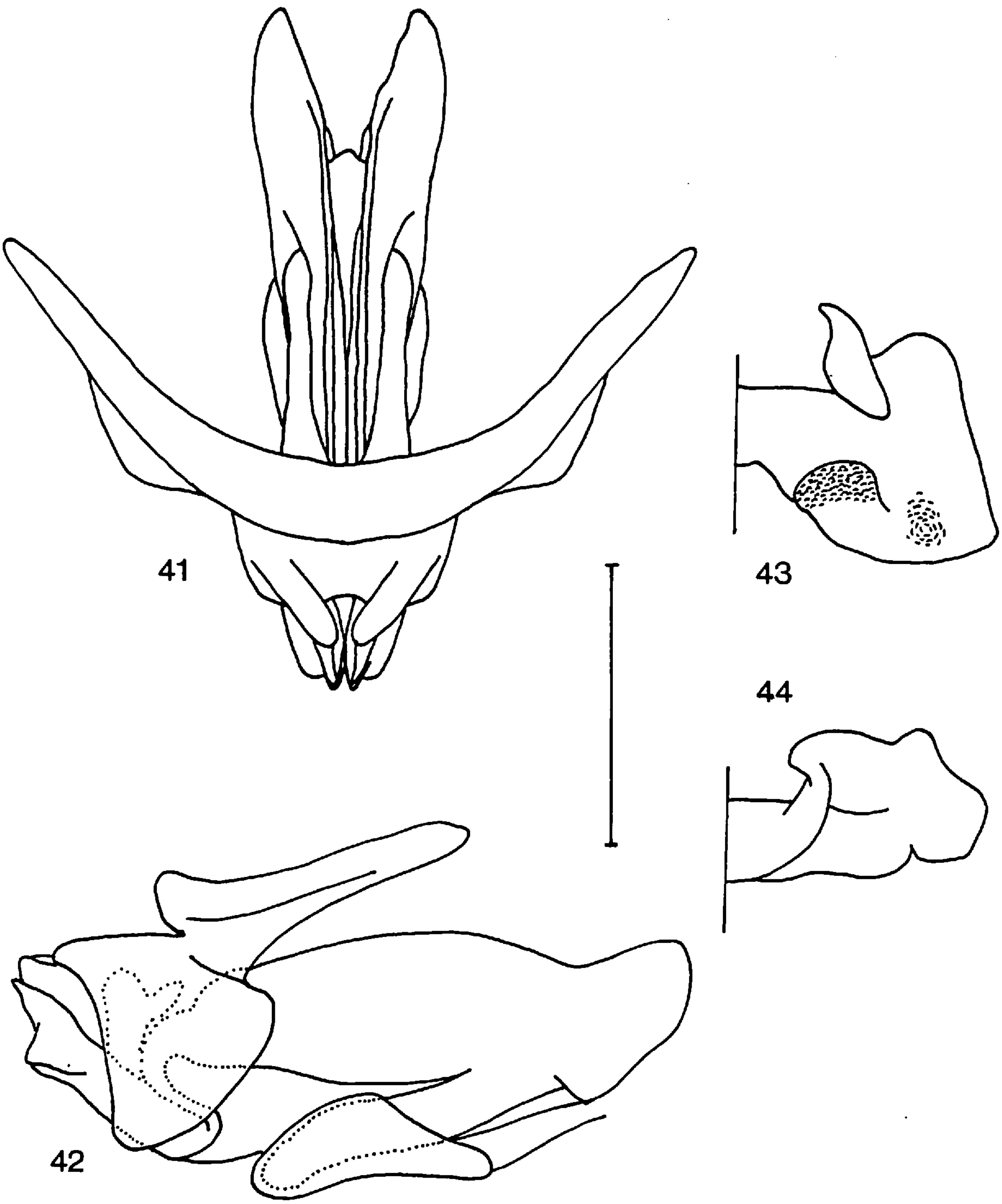
Gastrimargus Rothschildi [sic] Bolivar, 1922: 175. Holotype ♀, ETHIOPIA (MNHN, Paris) [examined].

Gastrimargus cristagalli Sjöstedt, 1928: 46. Holotype ♀, ETHIOPIA (BMNH) [examined]. Syn. n.

Gastrimargus rothschildi montanus Uvarov, 1934: 607. Holotype ♂, ETHIOPIA (BMNH) [examined]. Syn. n.

Diagnosis. Antennal flagellum short, thick, with bead-like segmentation; segments 8-9 barely longer than wide. Fastigium of vertex convex. Pronotum with median carina low arcuate, not intersected by posterior sulcus; posterior margin narrowly acutangular. Tegmen surpassing hind knee by one twelfth to one quarter of hind femur length in male, not reaching hind knees in female. Tegmen length / pronotum length ratio 2.46 -3.18 ♂, 1.48-1.83 ♀. Genitalia (Figs 41-44) similar to G. verticalis, but smaller and more delicate; aedeagus more weakly protruding.

Colouration vivid green with variable dark maroon markings. Pronotal x-marking thin, similar to G. verticalis, posterior arms elongated and incurved posteriorly (Plate 12). Tegmen in male predominantly dark



Figs 41-44. Gastrimargus rothschildi Bolivar, genitalia . 41, phallic complex, dorsal view; 42, same, lateral view; 43, epiphallus, right half, dorsal view; 44, same, posterior view.

Plate 11. _G_. _rothschildi_ Bolivar ♂

Plate 12. _G_. _rothschildi_ Bolivar ♀

maroon in basal two thirds, lighter brown in apical third and clearer, with two or three variable pale blotches or bands; female tegmen with maroon areas reduced to five or six blotches or bands on a green background. Hind wing unfasciated or with faint traces only; basal area pale yellow. Hind femur externally with longitudinal dark purple or maroon stripe extending to variable thickness below dorsal carinula, sometimes obsolete (for internal surface see key to geographical races below). Hind tibia basally dark brown, otherwise red.

Key to geographical races of *Gastrimargus rothschildi*

1. Internal ventral carina and internal medial area of hind femur dull straw-coloured, at least partially tinged with blue-grey, blue-black, or mauve, never bright red ... ... 'Blue-leg' nominate race

-. Internal ventral carina and lower half of internal medial area of hind femur bright yellow straw-coloured, sometimes tinged with bright red, never mauve or blue ... ... 'Yellow-leg' race

Synonymy

G. rothschildi exhibits considerable variation in size, wing length, and colouration within any given population, in addition to the geographical variation in certain characters outlined above in the key. The newly synonymised taxa vary in size and patterning within the range of the 'blue-leg' race.

Measurements: Table 16

Material examined: Appendix 2, p. 381.

Distribution (Fig. 114 , and Biogeography section, p. 327).

G. rothschildi is restricted to montane Ethiopia. The nominate 'blue-leg' race occupies the two mountain areas on the east side of the great rift valley south of Asela, separated by the Wabi Shebele river, and also occurs in the Simien National Park area NE of the L. Tana to the west of the rift, where it is separated from the southern population by more than 150 miles. In the intervening area the 'yellow-leg' race extends on the west side of the rift valley roughly from Sodo in the south to the Abay (Blue Nile) gorge north of Goha Tsion in the north. It is not known whether either race is to be found north of the Blue Nile in the Mangestu mountains. The Abay may well bound the distribution of the species in the north as the Omo river valley does in the west. Both races generally occur above the 2000 m contour (shown as a thin continuous line on the distribution map, Fig. 114). I am grateful to Dr N.D. Jago for drawing my attention to the occurrence of variation in hind femur colouration in this species.

Affinities

G. rothschildi is allied to G. verticalis, ethiopian material of which exhibits a trend towards complete loss of the hind wing fascia (culminating in 'G. aethiopicus' Bolivar, p. 266). Longer winged females of rothschildi may be difficult to distinguish from those of G. verticalis to which they bear a close resemblance, except for their darker tegminal pattern and higher TL/PL ratio (see Tables 16,17). The males are more easily distinguished from those of G. verticalis by their smaller size and the absence of any distinct hind wing fascia. It seems probable that this species is a high-altitude derivative of G. verticalis (see p. 327). It would be interesting to investigate the two ecology and genetics of the two races of G. rothschildi and the local population of G. verticalis more closely. At present it is not possible to determine how the two 'blue-leg' populations came to be separated by an intervening area occupied by the 'yellow-leg' race. The relationship with G. hyla, another ethiopian species, is discussed above (p. 257).

2.1.5.10 Gastrimargus verticalis (Saussure, 1884)

(Figs 45-51, 113; Plates 13,14)

This species is here divided into two subspecies under which the specific synonymy is separately listed.

Gastrimargus verticalis verticalis (Saussure, 1884)

Oedaleus (Gastrimargus) verticalis Saussure, 1884: 111. LECTOTYPE ♀, SOUTH AFRICA (MHN, Geneva) here designated [incorrectly synonymised with G. determinatus by Kirby, 1902: 71] [examined]. Nom. rev.

Gastrimargus verticalis var. Burr, 1900: 39.

Gastrimargus aethiopicus Bolivar, 1922: 175. Holotype ♀, ETHIOPIA (MNHN, Paris) [examined]. Syn. n.

Gastrimargus longipes Sjöstedt, 1928: 21. Holotype ♀, SOUTH AFRICA (NR, Stockholm) [examined]. Syn. n.

Gastrimargus longipes var. recta Sjöstedt, 1928: 22. Holotype ♀, [not cotype as labelled] ZANZIBAR (NR, Stockholm) [examined]. Syn. n.

Gastrimargus longipes var. decliva Sjöstedt, 1928: 22. Holotype ♀, TANZANIA (BMNH) [examined]. Syn. n.

Gastrimargus brevipes Sjöstedt, 1928: 22. Holotype ♀, TANZANIA (NR, Stockholm) [synonymised with G. verticalis by Dirsh, 1966: 428] [examined].

Gastrimargus brevipes var. elgonensis Sjöstedt, 1928:23. Holotype ♀, KENYA/UGANDA (NR, Stockholm) [synonymised with G. verticalis by Dirsh, 1966: 428] [examined].

Gastrimargus brevipes var. abessina Sjöstedt, 1928: 23. Holotype ♂, ETHIOPIA (MNHU, Berlin) [synonymised with G. verticalis by Dirsh, 1966: 428].

Gastrimargus verticalis var. fusca Burr; Johnston, 1956: 570 [incorrect emendation of Burr's unnamed var., synonymised with G. verticalis by Dirsh, 1966: 428; original material lost].

Diagnosis. Fastigium of vertex convex. Pronotum with median carina arcuate, not intersected by posterior sulcus; hind margin acutangular. Tegmen surpassing folded hind knees by about one eighth of hind femur length. Genitalia (Figs 45-51) with aedeagus moderately strongly protruding; epiphallus with lateral plate widening posteriorly, outer lophi small, rounded, straight or slightly divergent.

Colouration. Pronotal x-marking with fine lines on dark background. Tegmen with two pale cross bands, basal band sometimes reduced or absent. Hind wing basally pale yellow; fascia (Plate 13) complete in male, reaching and following hind margin of wing, interrupted between Cu2 and 1A, and sometimes, especially in Ethiopia, obsolete from costal margin to Cu2; fascia reduced in female, occasionally almost obsolete, especially in Ethiopia, ceasing to reach hind margin, thin, sometimes not reaching beyond Cu2 anteriorly. Hind femur externally with faint traces of transverse banding in medial area; upper carinula with row of black dots. Internal surface with medial area brown in basal half, upper and lower carinulae with row of dots; ventral surface straw-coloured. Hind tibiae pink or red in male, light brown in female.

Synonymy

The four newly synonymised species are all based on female holotypes exhibiting the wide range of variation shown by this species. The profile of the pronotal median carina and the degree of expression of the hind

Plate 13. G. verticalis verticalis (Saussure) ♂

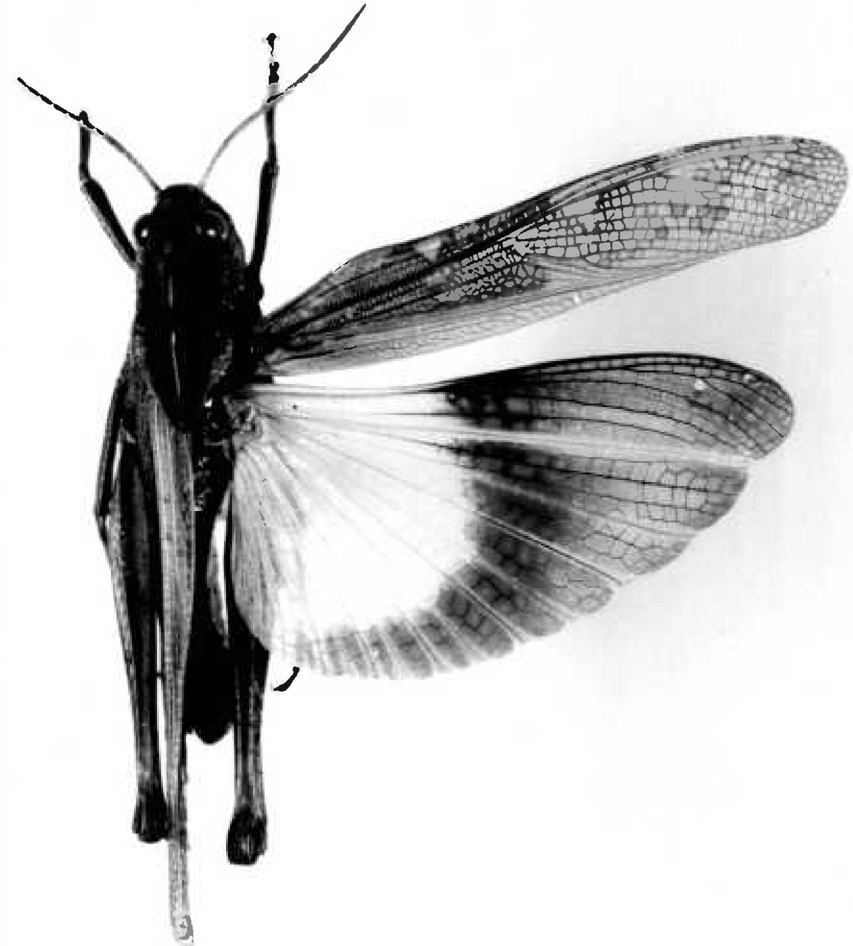
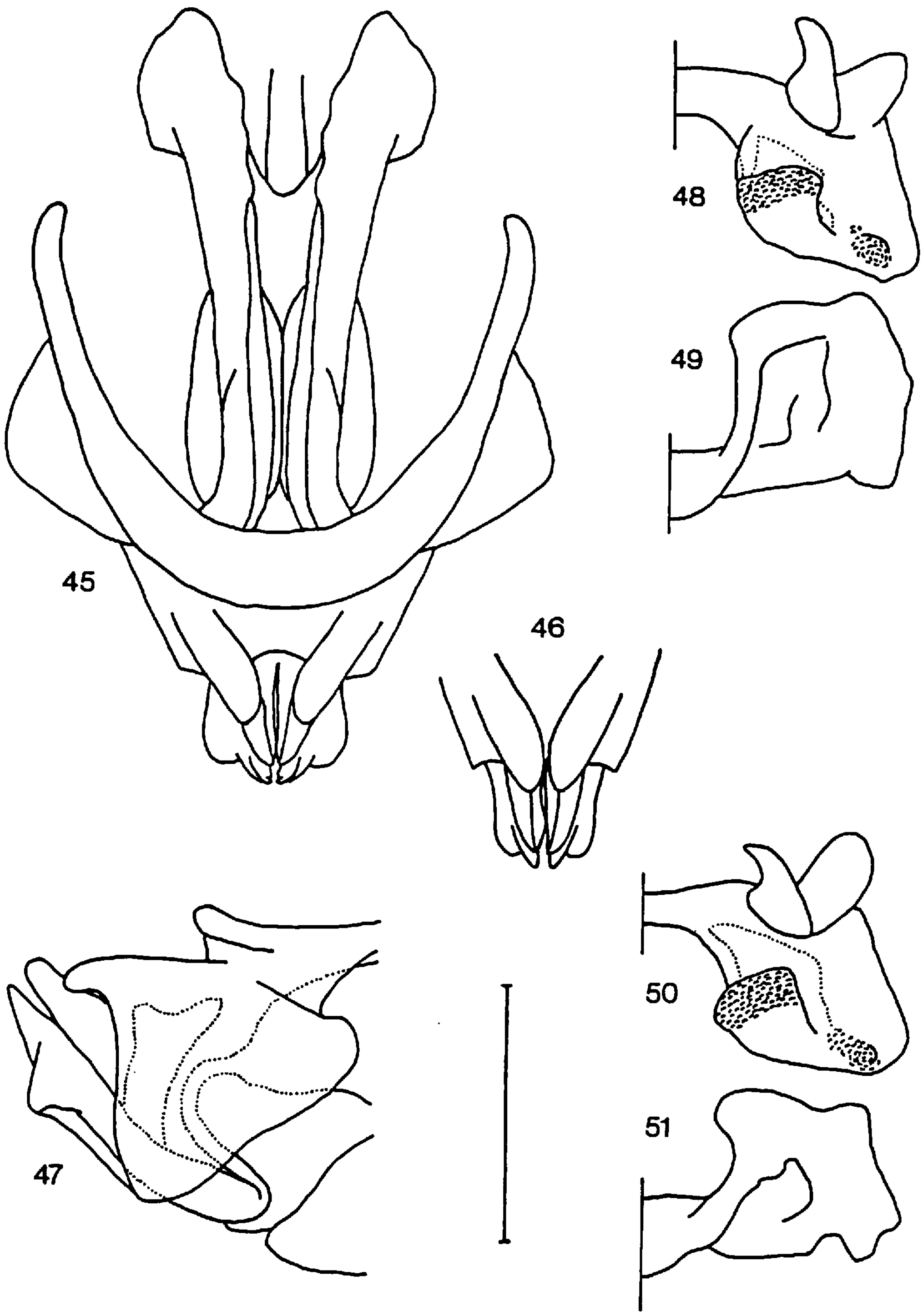


Plate 14. G. verticalis mpwapwae subsp. n. ♂



Figs 45-51. Gastrimargus verticalis (Saussure), genitalia. 45, G. v. verticalis, phallic complex, dorsal view; 46, G. v. mpwapwae, same, posterior portion only; 47, G. v. verticalis, same, lateral view; 48, G. v. verticalis, epiphallus, right half, dorsal; 49, same, posterior view; 50, G. v. mpwapwae, same, dorsal view; 51, same, ventral view.

wing fascia are especially variable characters in the female, and unsuitable for characterising new species. The unique holotype of G. aethiopicus Bolivar from Ethiopia represents the extreme condition of the hind wing with almost complete loss of the fascia.

Measurements: Table 17

Gastrimargus verticalis mpwapwae subsp. n.

Diagnosis. The male of this subspecies differs from the nominate race by the possession of darker tegmina with the pale cross-banding reduced or absent, the hind wing with the apical half infumate (Plate 14), and the hind femur ventral surface tinged with blue grey. The aedeagus (Fig. 46) is somewhat more slender. The female is indistinguishable from the nominate race.

Measurements: Table 18

Material examined (both subspecies): Appendix 2, p. 382.

Distribution (Fig. 113, and Biogeography section, p. 322 et seq.).

Eastern and south-eastern Africa. Two specimens from Nigeria which may belong to this species are discussed below and included on the distribution map (Fig. 113).

Affinities

As already noted above (p. 261), G. verticalis is allied to the montane G. rothschildi. However it also has affinities with G. determinatus and G. miombo with both of which it has sometimes been confused. All three species have the hind femur ventrally straw-coloured (except in G. v. mpwapwae), a strongly protruding aedeagus with large ventral lobe,

Table 17

Measurements

G. verticalis verticalis: Uganda

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	31.46	4.62	7.51	23.02	17.94	3.67	4.99	3.88	3.07	1.29
Range	29.15–33.60	4.20–4.90	6.60–8.20	21.15–24.55	16.00–19.80	3.35–4.05	4.49–5.34	3.56–4.19	2.82–3.32	1.21–1.34
S.D.	1.201	0.162	0.428	0.921	0.826	0.164	0.625	0.122	0.142	0.038
No.	30	30	29	30	30	30	30	30	29	30
♀ Mean	48.20	7.93	12.03	34.52	27.00	5.75	4.70	3.41	2.87	1.28
Range	45.50–52.30	7.35–8.65	11.05–13.35	32.00–39.95	24.50–29.90	5.45–6.25	4.40–5.04	3.20–3.63	2.62–3.60	1.20–1.50
S.D.	1.803	0.309	0.668	1.716	1.249	0.209	0.183	0.102	0.185	0.062
No.	29	29	28	29	29	29	29	29	28	29

Table 18

Measurements

G. verticalis mpwapwae: Tanzania, Mpwapwa

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	34.10	4.94	8.31	25.29	18.23	3.88	4.70	3.69	3.05	1.39
Range	32.35–36.80	4.80–5.15	7.70–8.90	23.70–27.80	17.70–19.15	3.70–4.10	4.63–4.78	3.66–3.72	2.82–3.21	1.34–1.45
S.D.	1.900	0.155	0.557	1.771	0.674	0.185	0.066	0.025	0.188	0.047
No.	4	4	4	4	4	4	4	4	4	4
♀ Mean	48.10	8.19	11.70	33.70	26.36	5.89	4.49	3.22	2.90	1.26
Range	47.05–49.20	8.00–8.35	10.10–13.10	32.00–34.60	25.95–27.30	5.55–6.35	4.13–4.75	3.11–3.33	2.44–3.39	1.17–1.32
S.D.	0.879	0.144	1.510	1.161	0.634	0.340	0.286	0.092	0.476	0.082
No.	4	4	3	4	4	4	4	4	3	3

and a pronotal x-marking with the anterior and posterior arms of similar thickness.

Biology

Unknown. There is one record of damage to pasture in Kenya (Le Pelley, 1952).

Discussion

Two specimens from Nigeria, a male from Bambur, and a female from Jakiri, both collected by F. D. Golding in May 1946, appear to be close to this species. The localities are shown on the distribution map (Fig. 113). The two insects are both very pale brownish green with very indistinct markings (♂, Plate 15). The male aedeagus bears a larger and more rounded subapical ventral process than is normal in G. verticalis. A firm assignment of this material must await the discovery of further specimens. However in the meantime it is certain that these insects do not belong to any of the species presently known from west Africa.

2.1.5.11 Gastrimargus miombo sp. n.

(Figs 52-56, 111 ; Plate 16)

Diagnosis. Fastigium of vertex convex. Pronotum with median carina arcuate, not intersected by posterior sulcus; hind margin acutangular; dorsum of female with scattered globular warts. Tegmen surpassing folded hind knees by one fifth to one tenth of hind femur length in male; tegmen variable in female, sometimes failing to reach hind knees (Ufipa plateau). Genitalia (Figs 52-56) with strongly protruding aedeagus and large bulbous subapical ventral process. Ventral ovipositor valves with external lateral margin deeply excavated (Fig. 56).

Colouration typical for genus. Pronotal x-marking with anterior and posterior arms similar in length and thickness, meeting at an angle of 90-120° (Plate 16). Tegmen with distinct pale cross-banding. Hind wing with complete fascia (Plate 16), widening anteriorly; basal area pale greenish yellow. Hind femur externally with or without indistinct oblique transverse bands. Internal surface straw-coloured; carinulae with dark dots. Hind tibia straw-coloured.

Synonymy

The specimen from Moxico, Angola, collected by Burr was incorrectly identified by Uvarov (1953: 114) as G. brevipes Sjöstedt.

Measurements: Table 19

Material examined: Appendix 2, p. 382.

Distribution (Fig. 111, and Biogeography section, p. 330).

Angola, Zaire, Zambia, Tanzania.

Table 19

Measurements

G. miombo: Central Africa, various localities

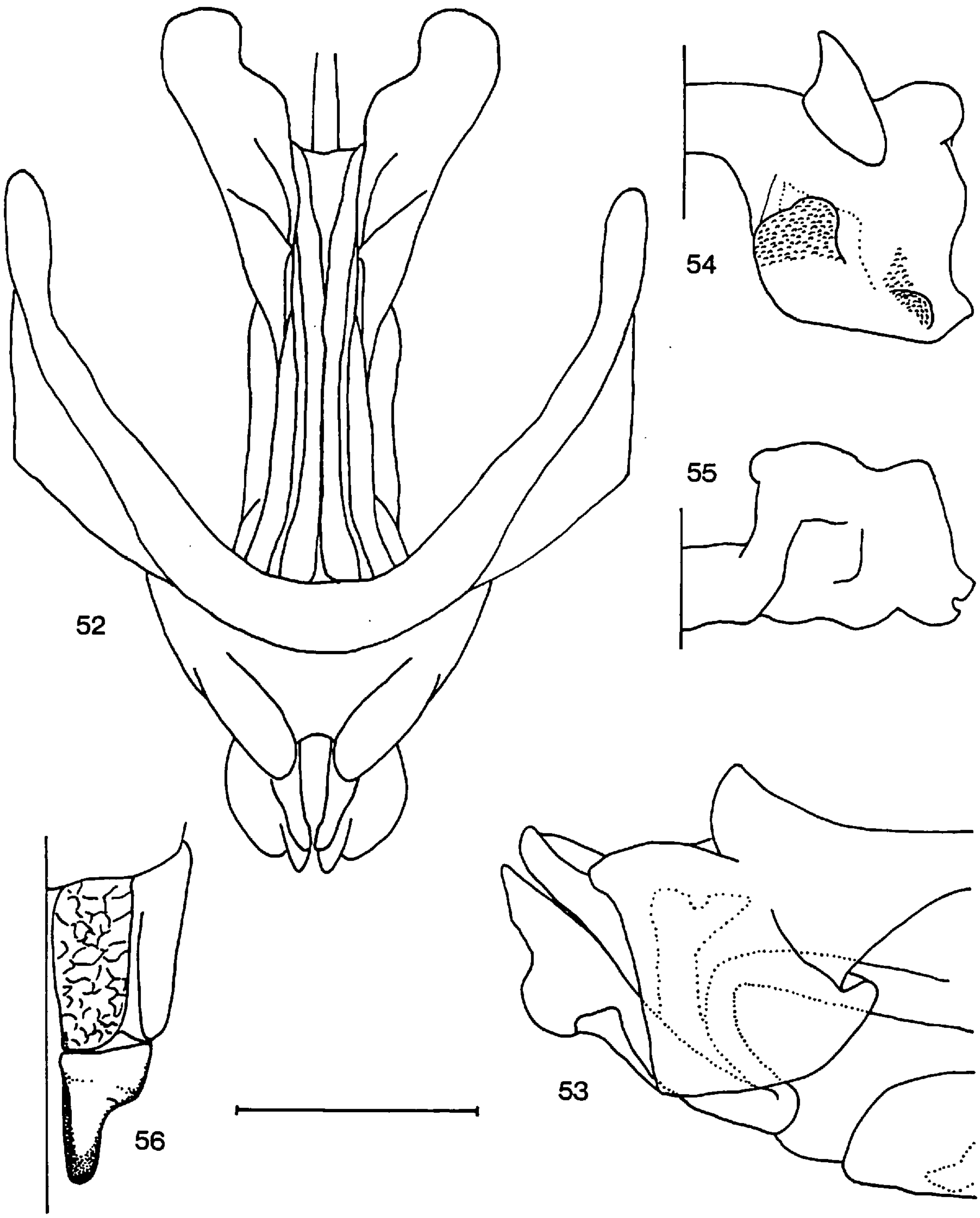
	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	33.28	5.23	8.39	24.55	17.83	3.86	4.62	3.43	2.93	1.37
Range	29.70–39.60	4.70–5.95	7.45–9.40	21.70–29.55	15.95–21.50	3.30–4.25	4.30–5.06	3.23–3.69	2.49–3.33	1.28–1.48
S.D.	2.973	0.379	0.610	2.463	1.621	0.282	0.222	0.146	0.257	0.073
No.	10	10	10	10	9	9	9	9	10	9
♀ Mean	48.91	7.86	12.12	35.06	24.59	5.65	4.36	3.13	2.91	1.43
Range	44.85–53.15	7.10–9.40	10.15–15.30	30.85–38.55	21.65–27.95	5.15–6.35	4.01–4.99	2.91–3.49	2.02–3.38	1.11–1.60
S.D.	3.577	0.734	1.616	2.637	2.171	0.405	0.287	0.159	0.370	0.129
No.	7	11	11	10	11	11	11	11	10	10

Table 20

Measurements:

G. determinatus determinatus: South Africa

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
Holotype ♀	-	-	-	36.50	28.15	6.70	4.20	-	-	1.30
Unique ♂	-	5.70	8.65	28.80	22.40	4.70	4.77	3.93	3.19	1.23



Figs 52-56. Gastrimargus miombo sp. n., genitalia. 52, phallic complex, dorsal view; 53, same, posterior portion, lateral view; 54, epiphallus, right half, dorsal view; 55, same, posterior view; 56, ovipositor, left half, ventral view.

Plate 15. G. ?verticalis ♂: Nigeria

Plate 16. G. miombo sp. n. ♂

Affinities

G. miombo is allied to G. verticalis and G. determinatus on the basis of the general form and colouration, especially the absence of dark pigment on the undersides of the hind femora, and the genital morphology. It may be distinguished by the characters outlined in the key.

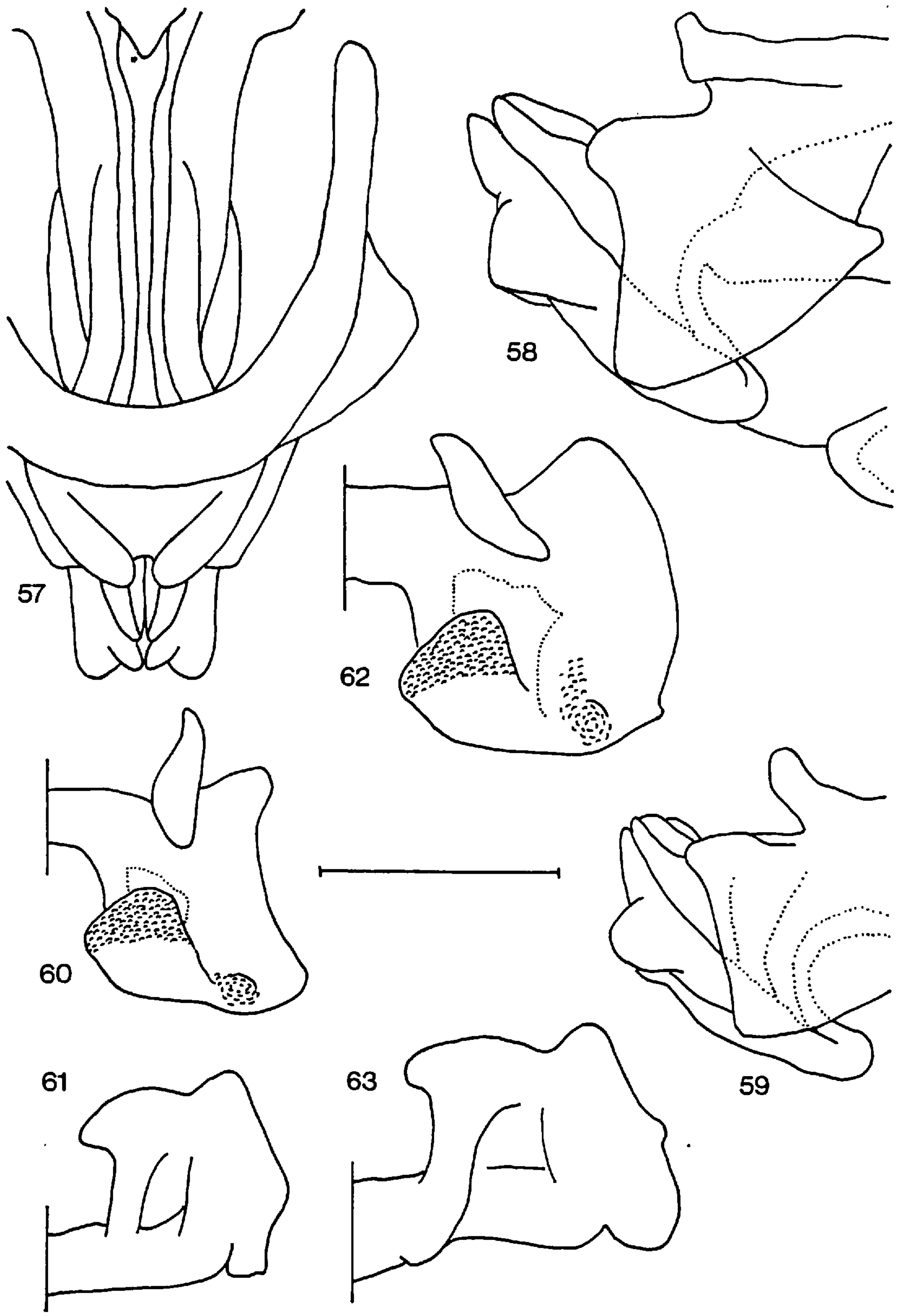
2.1.5.12 Gastrimargus determinatus (Walker, 1871)

(Figs 57-63, 115; Plates 17-20)

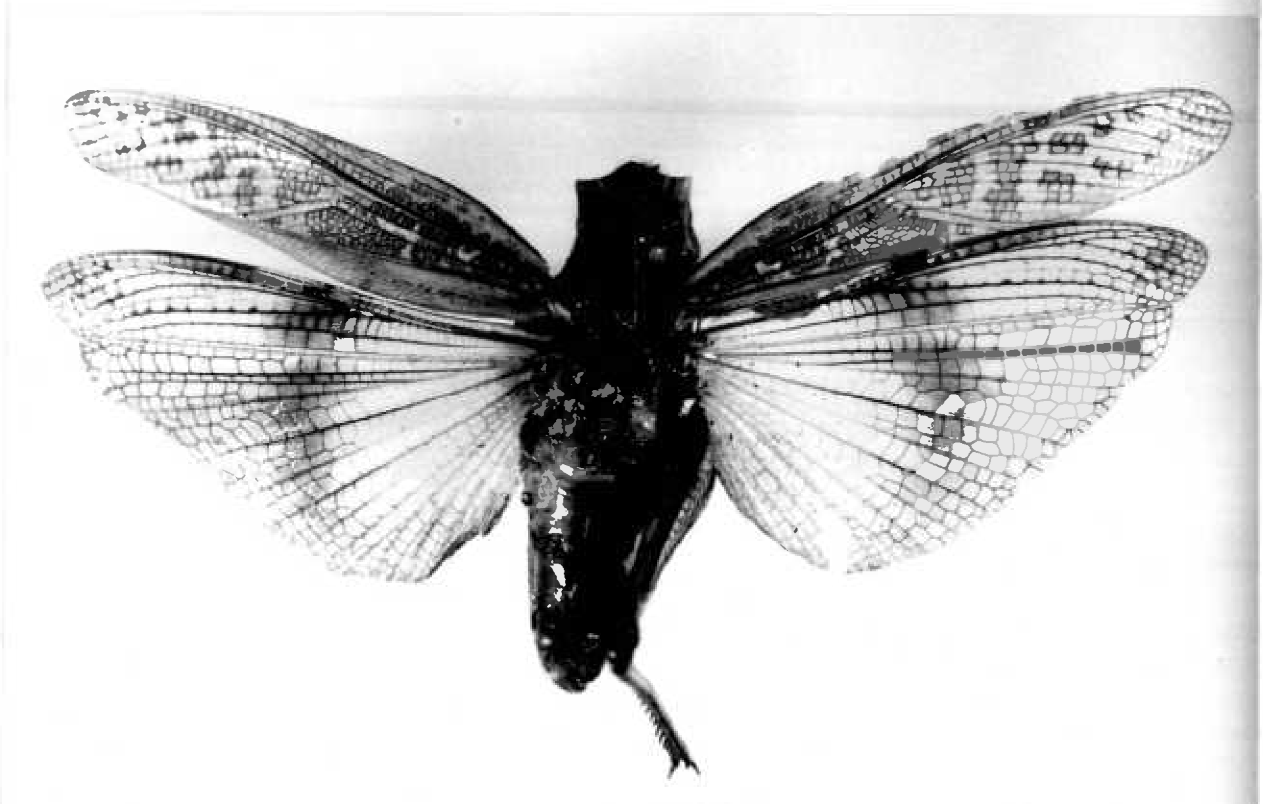
This species is here divided into four subspecies under which the specific synonymy is separately listed.

Diagnosis. Fastigium of vertex convex. Pronotum with median carina arcuate, not intersected by posterior sulcus; dorsum with variable scattering of small shiny warts; hind margin sharply acutangular. Tegmen surpassing folded hind knees by one sixth to one quarter of hind femur length. Genitalia (Figs 57-63) with aedeagus strongly protruding; subapical ventral process large, bulbous; epiphallus with variable lateral plate and outer lobe of lophi slightly divergent.

Colouration variable. Pronotal x-marking variable in emphasis, sometimes obsolete, with posterior arms of variable length and angle to anterior arms (90-160°). Tegmen light brown with pale cross-bands poorly contrasting (Plates 17-20). Hind wing fascia variable, present or absent according to subspecies (Plates 17-20); basal area pale yellow. Hind femur externally with or without oblique banding, but always with internal and external upper and lower carinulae with row of black dots; medial and ventral areas of internal surface straw-coloured. Hind tibiae light greyish brown becoming reddish in apical half with black-tipped spines.



Figs 57-63. Gastrimargus determinatus (Walker), genitalia. 57, phallic complex, dorsal view, G. d. procerus; 58, same, posterior portion, lateral view, G. d. determinatus; 59, same, G. d. procerus; 60, epiphallus, right half, dorsal view, G. d. procerus; 61, same posterior view; 62, same, dorsal view, G. d. determinatus; 63, same, posterior view.



Plates 17-18. G. determinatus determinatus (Walker). 17 (above), unique male; 18 (below), lectotype female.

Key to subspecies of *G. determinatus*

1. Hind wing without fascia, but anal veins sometimes darkened medially (Plate 20) 2

-. Hind wing with partial fascia posterior to 2A, or with complete fascia (Plates 17–19) 3

2. Larger, longer-winged insects (Tegmen length 26–32 mm ♂, 40–45 mm ♀) with pronotal pattern variable; x-marking usually present (eastern and southern Africa) *Gastrimargus determinatus vitripennis* (Sauss.)

-. Smaller, shorter-winged insects (Tegmen length 24–26 mm ♂, 36–40 mm ♀) with pronotal pattern fixed as two separate dark longitudinal bands on a straw-coloured background, flanking median carina; x-marking absent in females (Arabia) *G. determinatus arabicus* Uvarov

3. Hind wing fascia of male complete, narrowly interrupted between Cu 2 and 1A, not following hind margin of wing beyond 6A (Plate 17); fascia of female paler, and fading posteriorly (Plate 18) (Cape Province) ... ... *G. determinatus determinatus* (Walker)

-. Hind wing fascia incomplete, widely interrupted, occupying posterior half of wing beyond 2A at greatest extent, often less advanced (all intermediates occur between this and the unfasciated subspecies *G. d. vitripennis*) (West and central Africa) ... ... *G. determinatus procerus* (Gerstäcker)

Gastrimargus determinatus determinatus (Walker, 1871)

Pachytylus determinatus Walker, 1871: 72. LECTOTYPE ♀, SOUTH AFRICA (BMNH) here designated [examined].

Gastrimargus determinatus (Walker); Kirby, 1902: 71.

Measurements: Table 20

Plate 19. *G. determinatus procerus* (Gerstäcker) ♂

Plate 20. *G. determinatus vitripennis* (Saussure) ♂

Gastrimargus determinatus procerus (Gerstäcker) comb. et stat. n.

Pachytylus determinatus var. Walker, 1871:72.

Oedaleus (Humbella) procerus Gerstäcker, 1889: 48. Type lost. NEOTYPE ♂, GHANA (BMNH) here designated [examined].

Humbe procera (Gerstäcker); Kirby, 1910: 216.

Gastrimargus volkensi var. nigericus Uvarov, 1926: 437. Holotype ♂, NIGERIA (BMNH) [synonymised with G. procerus by Dirsh, 1961: 49] [examined].

Gastrimargus amplus Sjöstedt, 1928:16. Holotype ♀, SIERRA LEONE (NR, Stockholm) [synonymised with G. procerus by Dirsh, 1970: 496] [examined].

Gastrimargus nigericus Uvarov; Sjöstedt, 1928: 17 [synonymised by Dirsh, 1961: 49].

Gastrimargus silvicola Sjöstedt, 1928: 17. Holotype ♂, ZAIRE (NR, Stockholm) [synonymised by Dirsh 1970: 496] [examined].

Gastrimargus vittatus Sjöstedt, 1928: 18. Holotype ♂, ZAIRE (NR, Stockholm) [examined]. Syn. n.

Gastrimargus foveolarum Sjöstedt, 1928: 19. Holotype ♀, CAMEROON (MNHU, Berlin) [synonymised by Dirsh, 1970: 496] [examined].

Gastrimargus foveolarum var. immaculata Sjöstedt. 1928: 20. Holotype ♀, ZAIRE (MRAC, Tervuren) [synonymised by Dirsh, 1970: 496] [examined].

Gastrimargus testaceus Sjöstedt, 1928: 20. Holotype ♂, CAMEROON (MNHU, Berlin) [examined]. Syn. n.

Gastrimargus procerus (Gerstäcker); Dirsh, 1961: 49.

Measurements: Table 21

Gastrimargus determinatus vitripennis (Saussure, 1888) comb. et stat. n.

Oedaleus (Gastrimargus) vitripennis Saussure, 1888: 38. Holotype ♀, SOUTH AFRICA (MHN, Geneva) [examined].

Table 21

Measurements

G. determinatus procerus: W. Africa, various localities

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	39.86	5.51	8.38	29.84	20.29	4.17	4.83	3.67	3.55	1.48
Range	34.15–45.05	5.05–6.00	7.40–9.10	25.00–34.10	17.70 24.00	3.75–4.50	4.51–5.21	3.25 4.06	3.17–3.93	1.33–1.58
S.D.	2.284	0.208	0.452	1.878	1.455	0.199	0.209	0.213	0.196	0.061
No.	29	29	28	29	26	25	25	26	28	26
♀ Mean	59.99	8.48	12.45	45.06	30.60	6.21	5.01	3.62	3.61	1.50
Range	55.90–63.60	7.45–9.55	10.70–13.65	42.35–47.25	26.95–34.95	5.70–6.80	4.61–5.54	3.25–4.11	3.30–3.99	1.39–1.61
S.D.	2.062	0.446	0.679	1.554	1.750	0.556	0.222	0.180	0.150	0.059
No.	26	29	29	26	29	29	29	29	26	26

Table 22

Measurements

G. determinatus vitripennis: Rhodesia

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	40.03	5.86	8.85	29.36	21.13	5.03	4.21	3.59	3.31	1.39
Range	35.45–43.20	5.25–6.30	7.95–10.05	26.00–32.15	18.55–23.40	4.50–5.45	3.91–4.63	3.39–3.80	3.12–3.60	1.35–1.49
S.D.	1.786	0.304	0.477	1.459	1.093	0.270	0.164	0.116	0.137	0.039
No.	15	20	20	17	20	20	20	20	17	17
♀ Mean	57.15	8.78	12.98	41.94	29.87	6.87	4.36	3.40	3.23	1.41
Range	54.45–60.70	8.25–9.70	12.05–14.40	39.75 45.05	27.80–31.95	6.25–7.65	4.09–4.92	3.21–3.76	2.96–3.51	1.26–1.50
S.D.	1.933	0.338	0.695	1.560	1.317	0.325	0.218	0.123	0.142	0.054
No.	19	22	22	19	22	22	22	22	19	19

[Oedaleus (Gastrimargus) acutangulus (Stål); Saussure, 1884: 109, 114; 1888: 39. Misidentifications; Sjöstedt, 1928:43.]

Gastrimargus vitripennis (Saussure); Kirby, 1902: 233.

Gastrimargus volkensi Sjöstedt, 1909: 171. Holotype ♀, TANZANIA (NR, Stockholm) [examined]. Syn. n.

Gastrimargus fallax Sjöstedt, 1928: 24. Holotype ♀, TANZANIA (MNHU, Berlin) [examined]. Syn. n.

Gastrimargus volkensi var. minor Sjöstedt, 1928: 44. Holotype ♀, KENYA: Victoria Nyanza, Sesse Is., Bugala, -.vii.08, (Bayon) (MCSN, Genoa) [synonymised with G. volkensi by Dirsh, 1966: 429].

Gastrimargus volkensi var. minor forma rectinotum Sjöstedt, 1928: 44. Holotype ♀, KENYA: Bugala (MCSN, Genoa) [unavailable infrasubspecific name] [synonymised by Dirsh, 1966: 429].

Gastrimargus pallidus Sjöstedt, 1928: 45. Holotype ♀, KENYA: Victoria Nyanza, Sesse Is., Bugala, -.-.08, (Bayon) (MCSN, Genoa). Syn. n.

Gastrimargus femoralis Sjöstedt, 1928: 45. Holotype ♀, SOUTH AFRICA (BMNH) [synonymised with G. volkensi by Dirsh: 1961a: 395] [examined].

Measurements: Table 22

Gastrimargus determinatus arabicus Uvarov, 1936 comb. n.

Gastrimargus volkensi arabicus Uvarov, 1936: 542. Holotype ♂, YEMEN: Sanaa, -.vii.31, (Rathjens) (ZM, Hamburg).

Measurements: Table 23

Material examined: Appendix 2, pp. 382-383.

Synonymy

The variability of the colouration of G. determinatus led Sjöstedt

Table 23

Measurements

G. determinatus arabicus: Arabia

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	33.84	4.82	6.78	24.92	17.52	3.91	4.48	3.64	3.68	1.42
Range	32.40–34.85	4.45–5.05	6.15–7.20	23.85–25.55	16.70–18.45	3.70–4.15	4.27–4.64	3.55–3.75	3.55–3.88	1.39–1.48
S.D.	0.824	0.227	0.383	0.560	0.614	0.182	0.117	0.065	0.149	0.032
No.	8	8	9	9	7	7	7	6	9	7
♀ Mean	51.98	8.48	11.48	37.68	27.96	6.35	4.40	3.26	3.20	1.36
Range	49.45–55.20	8.10–8.85	10.35–12.35	36.00–40.10	26.20–29.20	6.05–6.65	4.25–4.63	3.14–3.35	2.39–3.82	1.28–1.47
S.D.	1.857	0.238	0.662	1.586	1.109	0.220	0.156	0.371	0.371	0.064
No.	8	8	9	9	7	7	7	6	9	7

Table 24

Measurements

G. crassicollis: various localities, southern Africa

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	31.42	4.95	6.66	22.93	17.28	4.29	4.05	3.50	3.45	1.33
Range	27.95–35.75	4.45–5.65	6.00–7.90	20.00–26.75	15.35–19.70	3.55–4.95	3.49–4.65	3.17–3.88	3.23–3.66	1.23–1.41
S.D.	1.733	0.312	0.467	1.458	1.066	0.332	0.334	0.206	0.127	0.049
No.	30	30	30	30	30	30	30	30	30	30
♀ Mean	44.12	7.51	9.76	31.78	23.90	6.01	4.00	3.19	3.26	1.33
Range	38.65–50.00	6.40–8.35	8.40–11.00	26.75–37.50	21.45–27.25	5.10–6.90	3.60–4.51	2.96–3.50	2.99–3.54	1.22–1.46
S.D.	2.839	0.546	0.715	2.226	1.444	0.499	0.276	0.162	0.163	0.060
No.	25	30	30	30	30	30	30	30	30	30

(1928) to erect no less than twelve taxa based on material of the same species from different parts of Africa. The unique female holotype and the newly-recognised unique male of G. determinatus determinatus are both labelled as from 'Cape', presumably indicating collecting sites in SW Cape Province. However the precise locality is unknown. Apart from the hind wing fascia this subspecies is identical with G. determinatus vitripennis. The intermediate stage in the loss of the fascia is represented by G. determinatus procerus in W Africa. The subspecific status of the partly banded race was first recognised by Uvarov (1926: 427) who described it as G. volkensi nigericus.

Distribution (Fig. 115, and Biogeography section, p. 327).

G. determinatus procerus extends eastward and southward across Africa from Senegal to Ethiopia, Uganda, and Angola. In eastern and southern Africa it is replaced by G. d. vitripennis, with some overlap and intergradation at the boundary. G. d. determinatus is probably restricted to Cape Province, but since the precise area is unknown it is not shown on the distribution map (Fig. 115).

Affinities

G. determinatus has affinities with G. miombo on the basis of the overall morphology, differing from it by the larger size, less contrasted colouration, and shorter cingular rami (see also characters in the key, p. 208).

2.1.5.13 Gastrimargus crassicollis (Saussure, 1888)
(Figs 64-67; 112; Plate 21)

Oedaleus (Gastrimargus) crassicollis Saussure, 1888: 38. Holotype ♀, SOUTH AFRICA (MHN, Geneva) [incorrectly attributed by Saussure to Blanchard] [examined].

Oedaleus crassicollis Saussure; Kirby, 1910: 226 [incorrectly synonymised with G. assimilis].

Gastrimargus transvaalensis Sjöstedt, 1928: 25. Holotype ♀, SOUTH AFRICA (MNHN, Paris) [examined]. Syn. n.

Gastrimargus crassicollis (Saussure); Sjöstedt, 1928: 27.

Gastrimargus clepsydrae Sjöstedt, 1928: 29. Holotype ♀, SOUTH AFRICA ZM, Hamburg) [examined]. Syn. n.

Gastrimargus crassipes Sjöstedt, 1928: 29. Holotype ♀, SOUTH AFRICA (MNHU, Berlin) [♂ allotype, labelled 'Typ. des ♂' is G. verticalis] [examined]. Syn. n.

Gastrimargus grossiceps Sjöstedt, 1931: 25. Holotype ♀, SUMATRA (NR, Stockholm) [locality data incorrect] [examined]. Syn. n.

Diagnosis. Fastigium of vertex convex. Pronotum with median carina arcuate, not intersected by posterior sulcus; dorsum with a few small globular warts; hind margin sharply or bluntly acutangular. Tegmen variable, surpassing folded hind knees by one quarter to one half of hind femur length in male, less in female. Genitalia (Figs 64-67) similar to G. miombo and G. determinatus, with short cingular rami, strongly protruding aedeagus, and large subapical ventral process; epiphallus as in G. d. procerus.

Colouration typical for genus. Pronotal x-marking variable in thickness and emphasis, sometimes almost obsolete. Tegmen with two pale transverse bands. Hind wing fascia (Plate 21) complete, of variable width, curving inwards along anal margin in male; in female sometimes faded or obsolete in posterior part of anal area, appearing less curved than male; basal area of wing bright sulphur yellow. Hind femur externally with 2-3 oblique transverse bands; internal surface with basal half of medial area blackish; external and internal upper and lower carinulae with row of irregular black dots; internal ventral carinula and ventral surface of hind femur tinted with blue-grey of variable depth in male, blue-grey to straw-coloured in female. Hind tibiae red.

Synonymy

The holotype female of G. crassicollis is a small discoloured specimen in poor condition. This may partly explain why Sjöstedt (1928) failed to associate any of his material with this species. G. crassicollis varies greatly in general colouration, and Sjöstedt mistakenly erected new species on the basis of this variability.

Measurements: Table 24

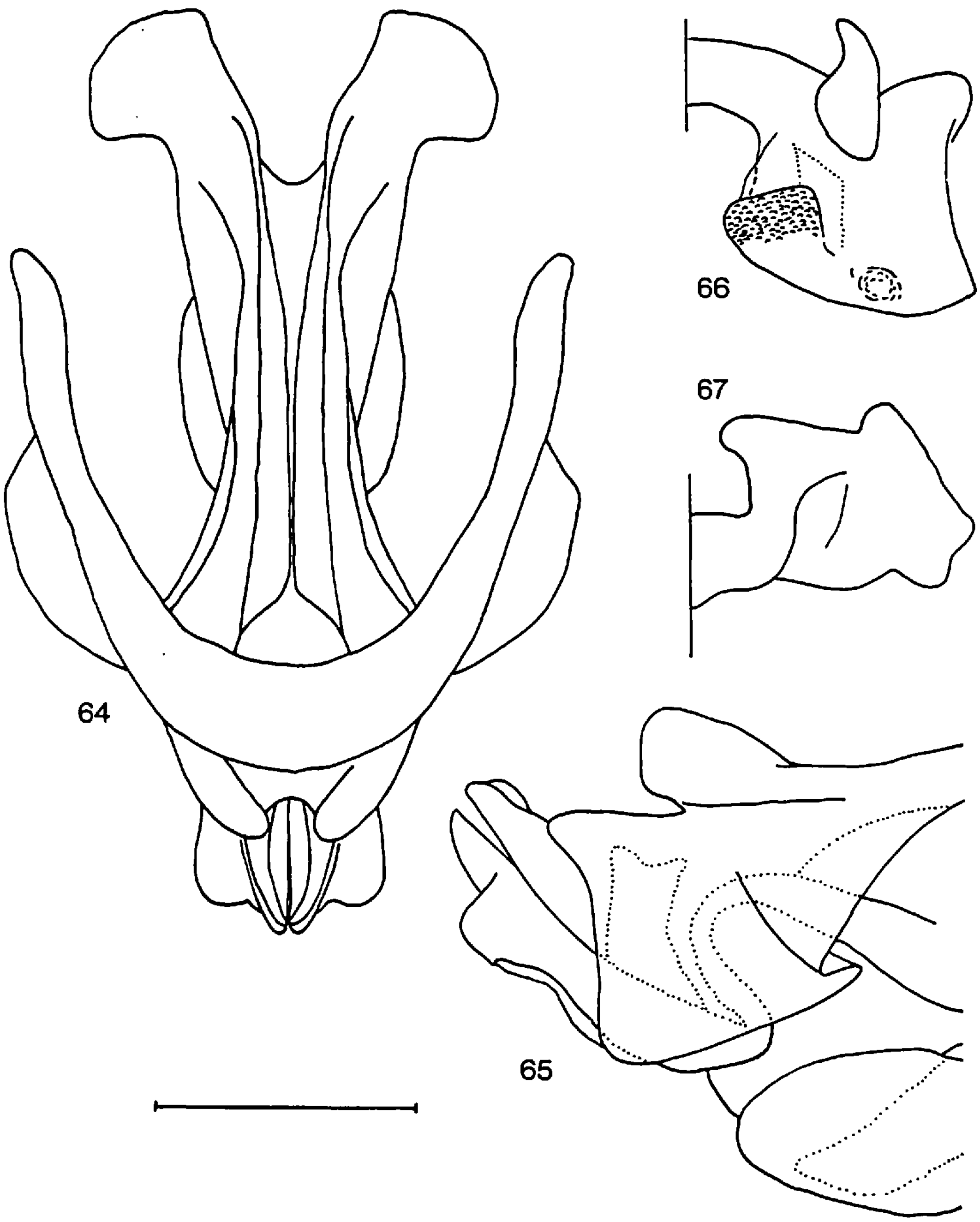
Material examined: Appendix 2, p. 383.

Distribution (Fig. 112, and Biogeography section, p. 322).

Zimbabwe, Lesotho, South Africa. The record from pasture in Kenya (Zacher, 1917) is erroneous.

Affinities

G. crassicollis is allied to G. drakensbergensis in general appearance, though less sombre in colour, and with a longer aedeagus, similar to that of G. determinatus and G. verticalis.



Figs 64-67. Gastrimargus crassicollis (Saussure), genitalia. 64, phallic complex, dorsal view; 65, same, posterior portion, lateral view; 66, epiphallus, right half, dorsal view; 67, same posterior view.

Plate 21. G. crassicollis (Saussure) ♂

Plate 22. G. drakensbergensis sp. n. ♂

2.1.5.14 Gastrimargus drakensbergensis sp. n.

(Figs 68-71, 112; Plate 22)

Diagnosis. Fastigium of vertex convex. Pronotum with median carina arcuate, not intersected by posterior sulcus; dorsum in female with sparse globular warts. Tegmen surpassing folded hind knees by one seventh to one eighth of hind femur length. Genitalia (Figs 68-71) somewhat similar to those of G. africanus with very short weakly projecting aedeagus.

Colouration generally sombre dark brown. Pronotal x-marking variable, sometimes obsolete, especially in males. Hind wing fascia complete, of variable width, widening anteriorly; basal area of wing pale greenish yellow. Hind femur with row of irregular brown dots on external and internal upper and lower carinulae, sometimes absent in males, and with 2-3 variable oblique cross-bands on external medial area; internal surface in male with medial area black, becoming blue-black on ventral surface; female with black area on internal surface reduced or absent, and ventral surface straw-coloured. Hind tibiae reddish.

Measurements: Table 25

Material examined: Appendix 2., p. 384.

Distribution (Fig. 112, and Biogeography section, p. 322).

South Africa.

Affinities

G. drakensbergensis is allied to G. crassicollis, differing by the darker colouration and absence of bright yellow colour in the hind wing. These are characteristic features of adaptation to montane habitats. The aedeagus in this species is distinctly shorter than that of G. crassicollis (Figs 69, 65). Measurements of the two species are similar (Tables 24,25).

Table 25

Measurements

G. drakensbergensis: South Africa

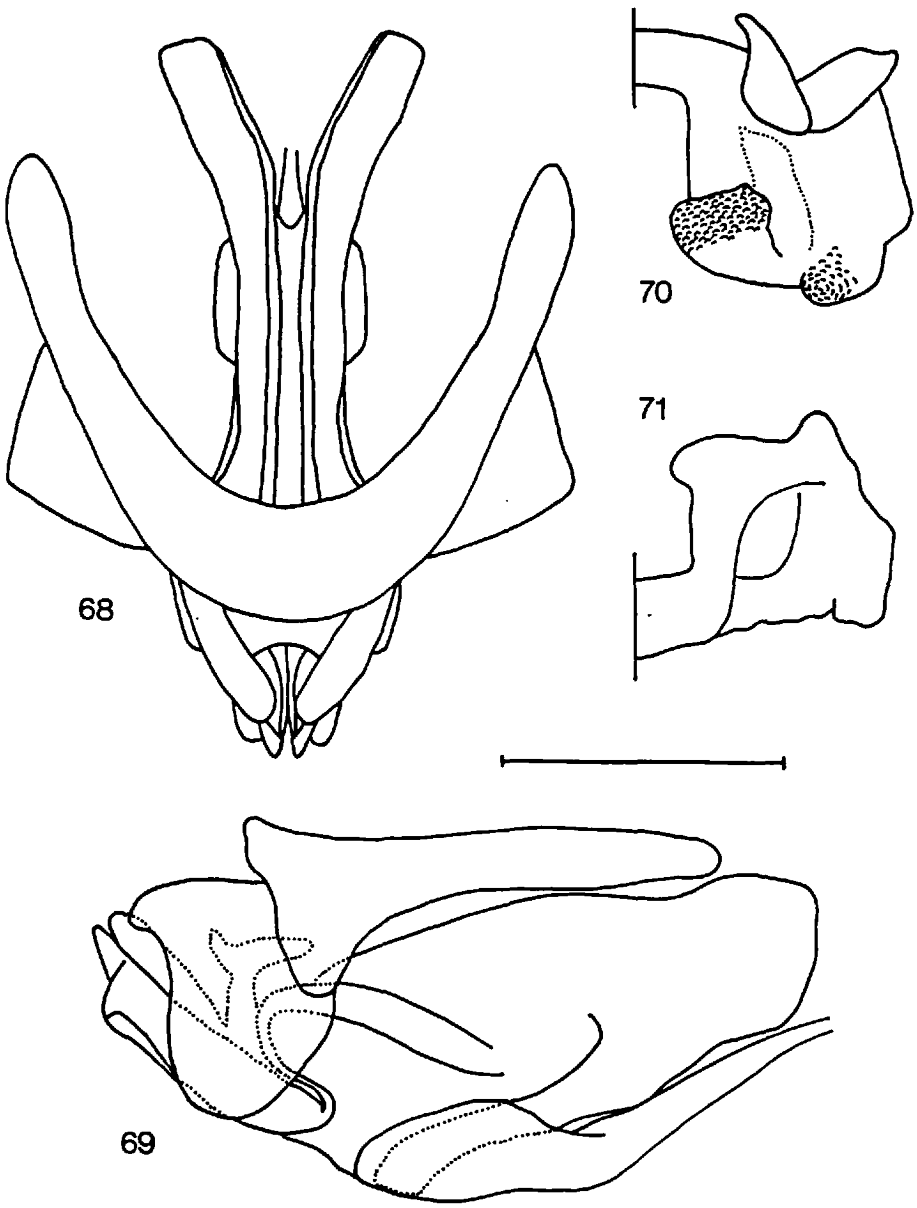
	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	32.84	5.00	7.25	23.91	17.96	4.16	4.33	3.6	3.31	1.33
Range	29.75–36.05	4.65–5.30	6.55–7.70	21.40–27.05	16.35–19.75	3.70–4.50	4.07–4.65	3.34–3.87	3.10–3.6	1.22–1.57
S.D.	1.641	0.185	0.416	1.491	0.790	0.218	0.186	0.149	0.162	0.079
No.	13	14	13	14	14	14	14	14	13	14
♀ Mean	41.59	6.93	9.28	30.03	23.08	5.38	4.29	3.33	3.21	1.30
Range	38.75–46.35	6.55–7.10	8.65–10.10	27.40–30.95	20.95–26.15	5.00–5.75	3.98–4.81	3.15–3.71	2.90–3.52	1.26–1.33
S.D.	1.939	0.204	0.422	1.756	1.309	0.247	0.224	0.166	0.161	0.022
No.	12	12	12	12	12	12	12	12	12	12

Table 26

Measurements

G. obscurus: Zaire and Angola

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
Holotype ♂	33.05	5.20	8.60	23.75	16.40	3.60	4.56	3.15	2.76	1.45
Paratype ♀	38.95	8.00	10.90	25.65	20.40	5.40	3.78	2.55	2.35	1.26
Paratype ♀	40.10	7.70	11.55	27.25	21.35	5.45	3.92	2.77	2.36	1.28



Figs 68-71. Gastrimargus drakensbergensis sp. n., genitalia. 68, phallic complex, dorsal view; 69, same, lateral view; 70, epiphallus, right half, dorsal view; 71, same, posterior view.

2.1.5.15 Gastrimargus obscurus sp. n.

(Figs 72-75, 111; Plates 23,24)

Diagnosis. Antennae of male lacking. Fastigium of vertex slightly concave, with triangular foveolae. Pronotum with median carina high arcuate, sometimes inflated in prozona, irregular in dorsal view, not intersected by posterior sulcus; median carina and vicinity distinctly rugose; hind margin rounded acutangular. Tegmen surpassing folded hind knees by one fifth of hind femur length in male, less in female. Genitalia (Figs 72-75) with aedeagus strongly protruding and with large subapical ventral process; epiphallus with outer lobe of lophi small and rounded.

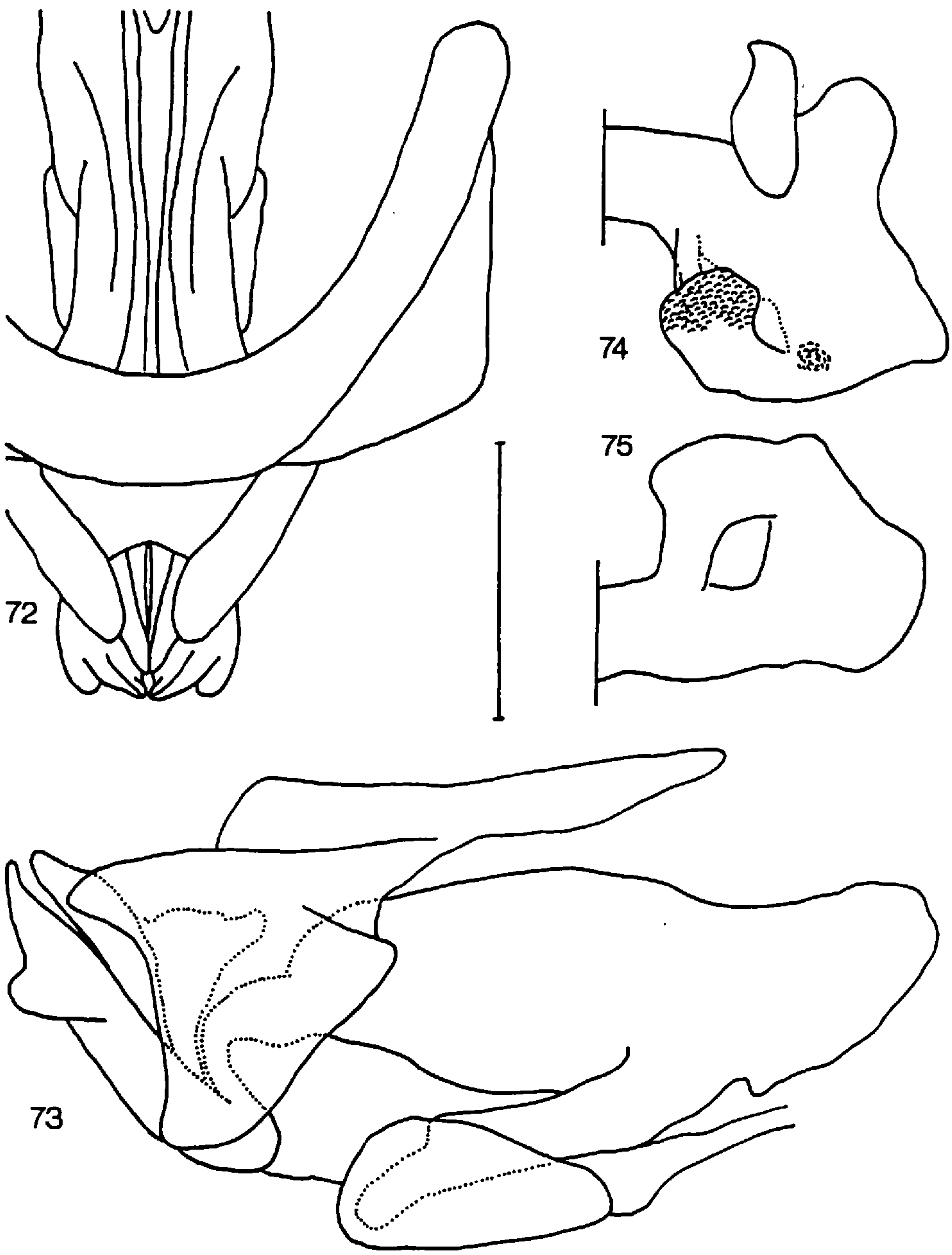
Colouration unusual for genus, blackish brown with lighter markings. Pronotum with blackish ground colour; light x-marking with posterior arms much thicker than anterior arms (Plate 23). Tegmen dark in basal half, with reduced transverse bands three and five eighths along from base (Plates 23,24); apical half dark in male, lighter speckled in female. Hind wing with fascia complete, narrowly interrupted between Cu2 and 1A; basal area pale greenish yellow, apical half of wing with dark shading and darkened veins in male, paler in female. Hind femur externally with two oblique cross-bands in medial and upper marginal areas; chevron pattern of sulci in medial area and external lower marginal area blackish brown; internal surface mostly black continued on ventral surface. Hind tibiae red.

Measurements: Table 26

Material examined: Appendix 2, p. 384.

Distribution (Fig. 111, and Biogeography section, p. 330).

Angola, Zaire.



Figs 72-75. Gastrimargus obscurus sp. n., genitalia. 72, phallic complex, dorsal view; 73, same, lateral view; 74, epiphallus, right half, dorsal view; 75, same, posterior view.

Plate 23. *G. obscurus* sp. n. ♂

Plate 24. *G. obscurus* sp. n. ♀

Affinities

G. obscurus is allied to G. angolensis by the infuscate apical half of the hind wing, the form of the pronotal x-marking, and the heavily pigmented ventral surface of the hind femur. The degree of rugosity of the pronotum, the generally very dark colouration, and the small rounded outer lobe of the lophi are however distinctive characters for this species.

2.1.5.16 Gastrimargus wahlbergii (Stål, 1873)
(Figs 76–80, 111; Plate 25)

Pachytylus (Oedaleus) wahlbergii Stål, 1873: 124. Holotype ♀, SOUTH AFRICA (NR, Stockholm) [examined].
Pachytylus wahlbergii Stål; I. Bolivar, 1881: 117 [probably misidentified].
Oedaleus (Gastrimargus) wahlbergii (Stål); Saussure, 1884: 113.
Oedaleus wahlbergii (Stål); I. Bolivar, 1889: 103.
Oedaleus marmoratus wahlbergi [sic] (Stål); Griffini, 1897: 6.
Gastrimargus wahlbergii (Stål); Kirby, 1910: 227.
Oedaleus wahlbergi [sic] (Stål); Bruner, 1910: 634.
Gastrimargus wahlbergi [sic] (Stål); Zacher, 1917: 164.
Pachytylus (Oedaleus) wahlbergi [sic] Stål; Sjöstedt, 1932: 20.

Diagnosis. Antennae of male lacking. Fastigium of vertex convex. Pronotum with median carina high arcuate, sometimes intersected by posterior sulcus; dorsum with numerous pale globular warts, often forming rows; hind margin elongated, rounded acutangular (Plate 25). Tegmen surpassing folded hind knees by one fifth of hind femur length. Genitalia (Figs 76-79) with strongly protruding aedeagus and large bulbous subapical ventral process; outer lobe of lophi laterally elongated, forming a low, lozenge-shaped bump (Figs 78,79). Ventral ovipositor valves with external lateral surface distinctly excavated (Fig. 80).

Colouration typical for genus. Pronotal x-marking with posterior arms thicker than anterior arms; metazona with several indistinct pale striae extending outwards and backwards on each side of median carina. Tegmen as in G. africanus, with two transverse light bands two and four sevenths along from base. Hind wing with strong complete fascia (Plate 25); basal area pale greenish yellow with some pale bluish tinting at the bases of main veins, more extensive in females. Hind femur externally with two indistinct oblique bands; internal and external upper and lower carinulae with regularly spaced black dots; internal surface in male with some dark shading in basal half, in female straw-coloured; ventral surface from lower carinula blue-grey. Hind tibia orange red, spines black-tipped.

Measurements: Table 27

Material examined: Appendix 2, p. 384.

Distribution (Fig. 111, and Biogeography section, p. 322).

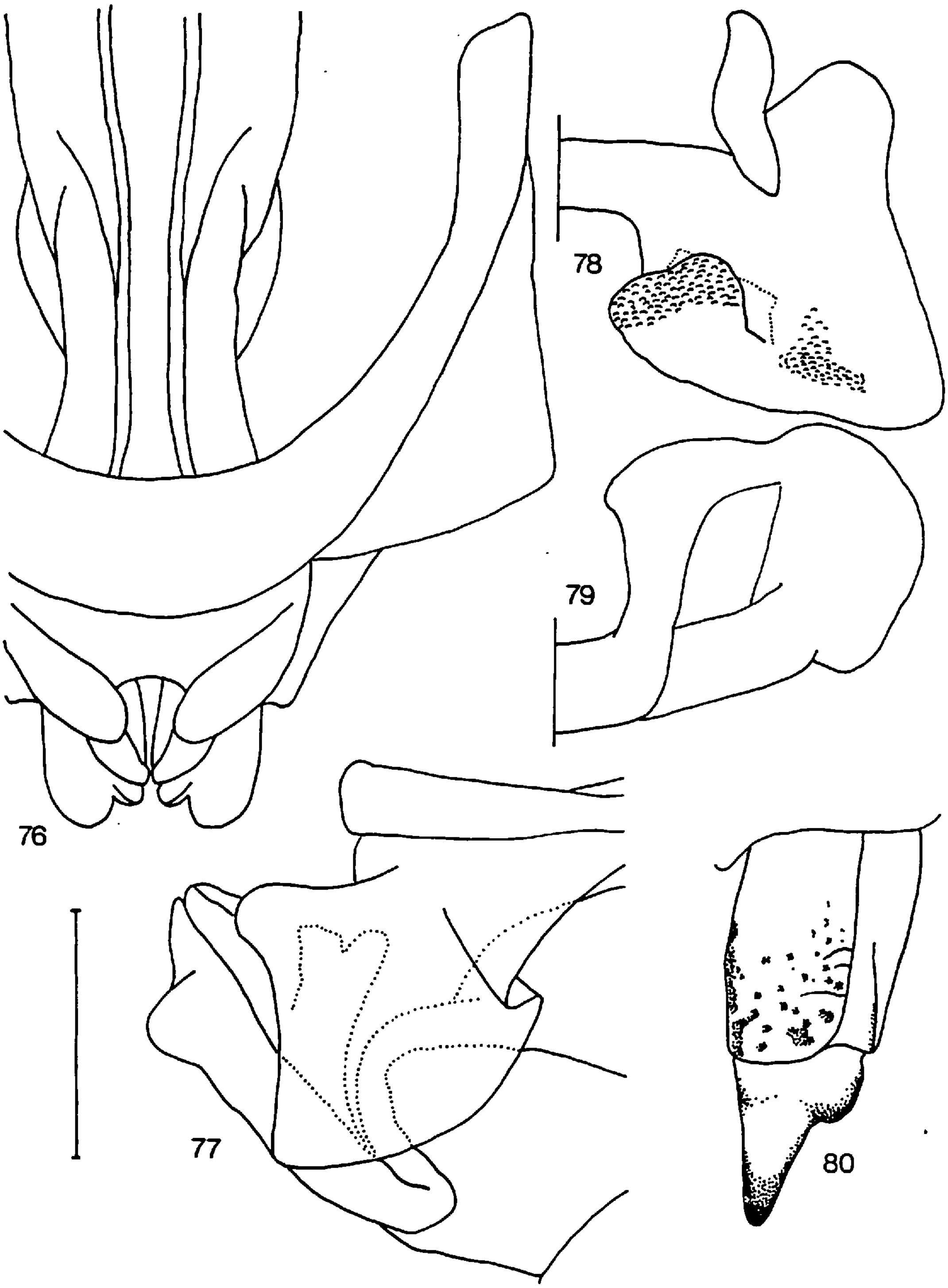
G. wahlbergii is known from the eastern half of South Africa, and Lesotho. The record from Angola (Bolivar, 1881) is probably erroneous.

Affinities

G. wahlbergii is allied to G. angolensis (p. 298) on the basis of the genitalia, the rugosity of the pronotum, and the blue tint of the ventral surface of the hind femur.

Biology

Unknown. The record of this species from Tobacco (Ballard, 1914; Zacher, 1917) is unconfirmed, and in view of the rarity of the species should be regarded with suspicion.



Figs 76-79. Gastrimargus wahlbergii (Stål), genitalia. 76, phallic complex, dorsal view; 77, same, lateral view; 78, epiphallus, right half, dorsal view; 79, same, posterior view; 80, ovipositor, left half, ventral view.

Table 27

Measurements

G. wahlbergii: Southern Africa, various localities

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	42.50	6.32	10.82	31.52	22.00	5.85	3.76	3.47	2.92	1.43
Range	41.70–43.30	6.30–6.35	10.35–11.30	31.00–32.05	21.95–22.05	5.65–6.05	3.63–3.90	3.47–3.48	2.84–3.00	1.41–1.46
S.D.	-	-	-	-	-	-	-	-	-	-
No.	2	2	2	2	2	2	2	2	2	2
♀ Mean	53.13	8.85	14.01	40.25	28.07	7.15	3.93	3.17	2.89	1.45
Range	49.15–57.10	8.25–9.55	11.30–15.55	35.60–44.30	24.55–31.75	5.75–8.05	3.50–4.27	2.97–3.33	2.83–3.02	1.38–1.55
S.D.	5.622	0.566	1.390	3.723	3.107	0.907	0.282	0.181	0.088	0.076
No.	2	5	5	4	5	5	5	5	4	4

Table 28

Measurements

G. angolensis: Central Africa, various localities

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	34.62	5.74	9.20	25.03	17.23	4.67	3.69	3.01	2.72	1.45
Range	32.00–35.85	5.30–6.00	8.30–9.75	23.10–26.30	16.25–18.00	4.30–4.95	3.56–3.87	2.88–3.23	2.56–2.85	1.41–1.53
S.D.	1.140	0.226	0.344	1.000	0.496	0.155	0.200	0.094	0.081	0.039
No.	14	14	14	14	14	14	14	14	14	14
♀ Mean	50.03	8.87	13.01	36.10	24.50	6.55	3.74	2.77	2.80	1.48
Range	47.60–53.30	8.70–9.45	12.20–13.95	34.20–39.50	22.75–25.95	6.30–6.85	3.56–3.96	2.56–3.05	2.56–3.02	1.39–1.55
S.D.	1.287	0.211	0.544	1.220	0.719	0.172	0.102	0.107	0.139	0.039
No.	17	18	20	17	20	20	20	18	17	17

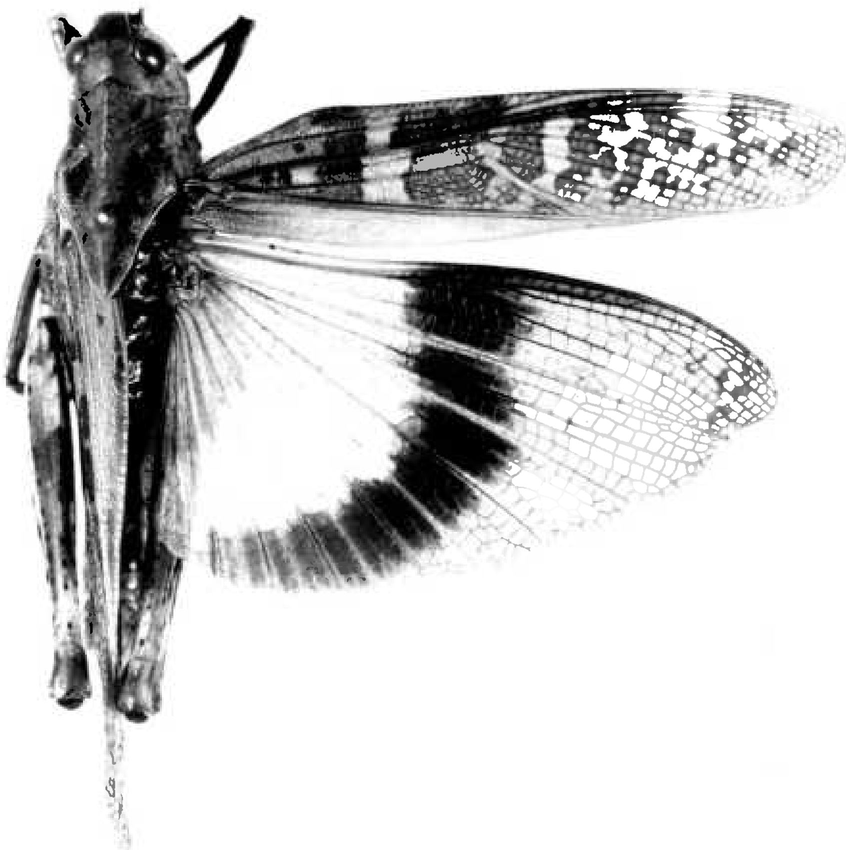


Plate 25. G. wahlbergii (Stål) ♂

Plate 26. G. angolensis Sjöstedt ♂

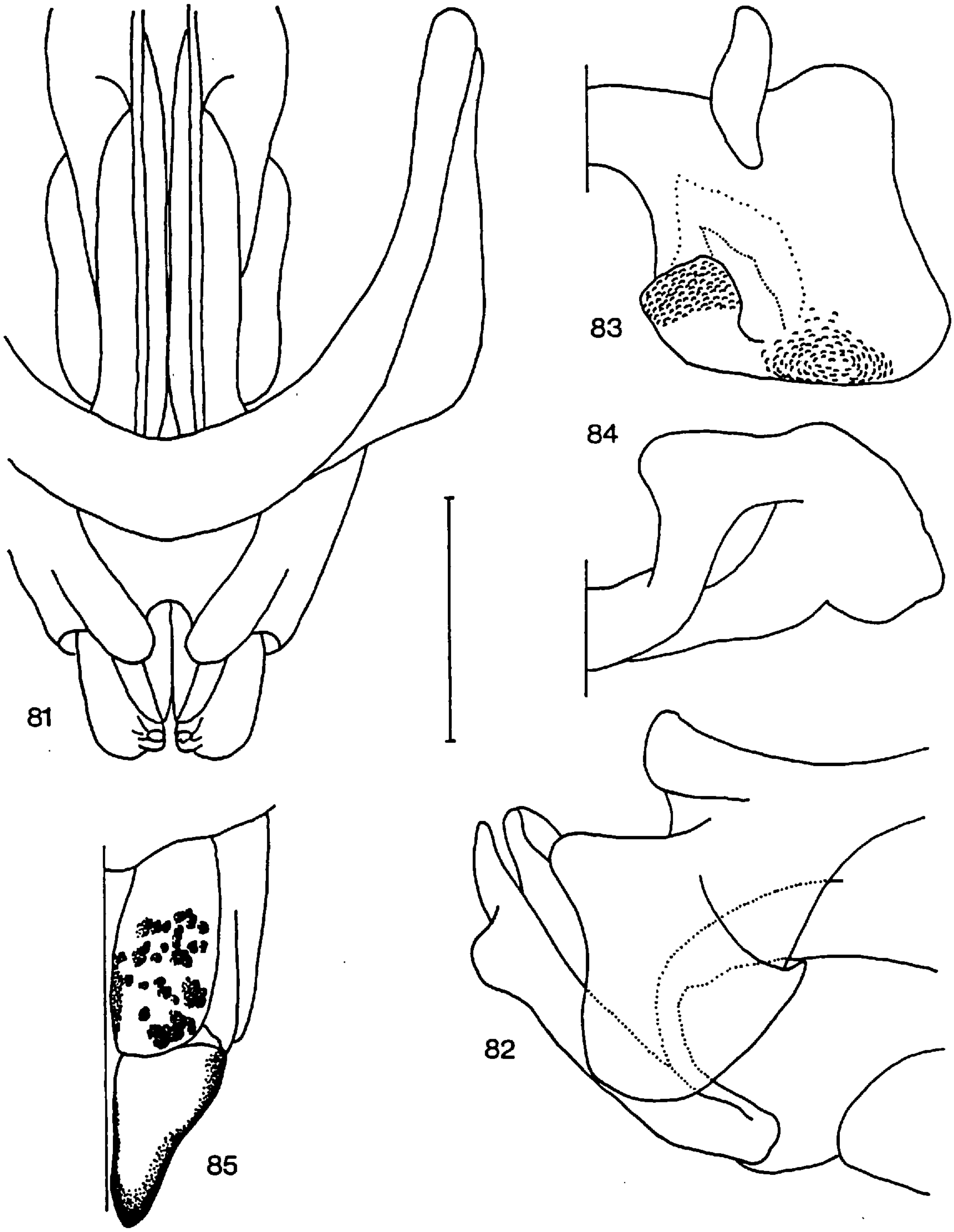
2.1.5.17 Gastrimargus angolensis Sjöstedt, 1928 nom. rev.
(Figs 81-85, 111; Plate 26)

Gastrimargus angolensis Sjöstedt, 1928: 30. Holotype ♀, ANGOLA (MNHU, Berlin) [incorrectly synonymised with G. vitripennis by Dirsh, 1966: 429] [examined].

Gastrimargus corallipes Sjöstedt, 1928: 31. Holotype ♀, ZAIRE (MRAC, Tervuren) [examined]. Syn. n.

Diagnosis. Antennae short, four fifths as long as head and pronotum together in male. Fastigium of vertex convex. Pronotum with median carina arcuate, not intersected by posterior sulcus; dorsum with some scattered globular warts; hind margin acutangular. Tegmen surpassing folded hind knees by one fifth of hind femur length. Genitalia (Figs 81-85) similar to G. wahlbergii; aedeagus strongly protruding, with large bulbous subapical ventral process; outer lobe of lophi laterally elongated, forming a low lozenge-shaped bump (Figs 83-84). Ventral ovipositor valves (Fig. 85) with external lateral surface shallowly and smoothly incurved.

Colouration typical for genus, similar to G. wahlbergii. Pronotal x-marking green or rarely light brown; posterior arms much thicker than anterior arms; metazona with indistinct pale striae as in G. wahlbergii. Tegmen with pale cross-bands about one third and one half along from base. Hind wing with fascia complete but very faint (Plate 26); basal area of wing pale greenish yellow; apical half of wing faintly infumate with darkened veins, paler in female. Hind femur unbanded or occasionally with traces of banding on external surface; external dorsal and ventral carinulae and internal dorsal carinula each with a row of irregular black dots; internal surface blackish brown in medial area of male, female blackish brown in basal half only or not at all; internal ventral surface blue-black. Hind tibia dull light red.



Figs 81–85. Gastrimargus angolensis Sjöstedt, genitalia. 81, phallic complex, dorsal view; 82, same, posterior portion, lateral view; 83, epiphallus, right half, dorsal view; 84, same, posterior view; 85, ovipositor, left half, ventral view.

Synonymy

This species was synonymised with G. vitripennis by Dirsh (1966) without any examination of the holotype. The banded hind wing and the blue-black ventral surface of the hind femur preclude this however. Sjöstedt (1928) described G. angolensis and G. corallipes, both from unique female specimens, on succeeding pages of his monograph. They were artificially separated by trivial colour characters in his key, but the distinctions are no longer tenable in the light of more recently discovered material.

Measurements: Table 28

Material examined: Appendix 2, p. 384.

Distribution (Fig. 111, and Biogeography section, p. 330).

Angola, Zaire, Zambia.

Affinities

As stated above (p. 294), G. angolensis is closely allied to G. wahlbergii.

2.1.5.18 Gastrimargus mirabilis Uvarov, 1923

(Figs 86–89, 111; Plate 27)

Gastrimargus mirabilis Uvarov, 1923: 675. Holotype ♀, UGANDA (BMNH, London) [examined].

Diagnosis. Fastigium of vertex convex. Pronotum with dorsal surface scattered with globular warts; median carina high arcuate, forming a blade-like crest, not intersected by posterior sulcus; hind margin very elongated and sharply acutangular, forming an angle of less than 45°.

Tegmen surpassing folded hind knees by about one third of hind femur length. Hind femur long and thin, length/depth ratio 5.16-5.71 ♂, 4.89-5.72 ♀. Genitalia typical for genus, with aedeagus strongly protruding and with prominent subapical ventral process; epiphallus with small protruding outer lobe of lophi.

Colouration normal for genus. Pronotal x-marking with lateral angles very obtuse, posterior arms sometimes obliterated; sides of raised pronotal crest always brown. Tegmen dark, rarely with faint transverse bands. Hind wing fascia complete (Plate 27), fading anteriorly in female; basal area of wing pale yellow. Hind femur unmarked except for rows of irregularly spaced dots on inner and outer dorsal and ventral carinulae. Hind tibia dull reddish in male, brown or reddish brown in female.

Measurements: Table 29

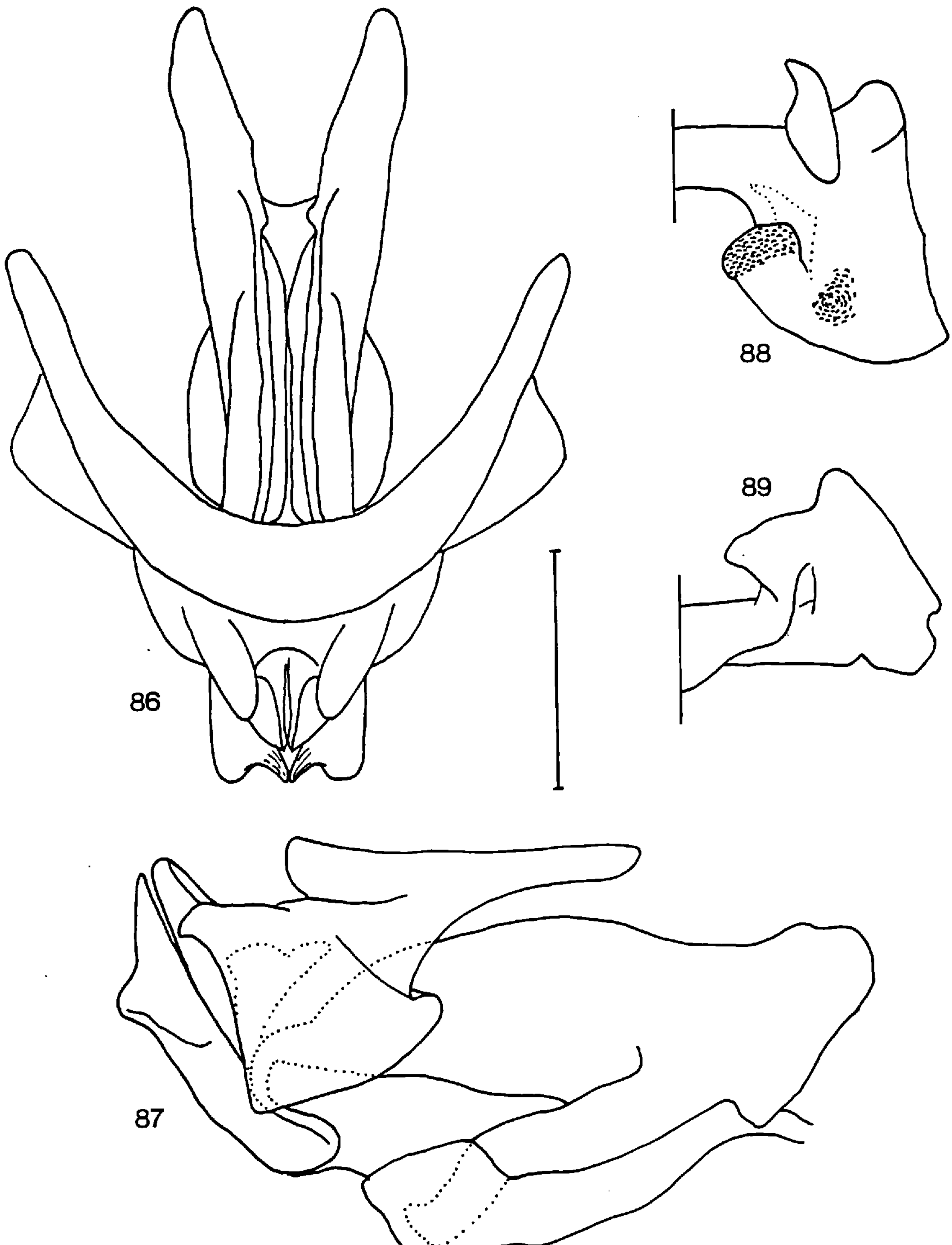
Material examined: Appendix 2, p. 385.

Distribution (Fig. 111, and Biogeography section p. 330).

Uganda, Zaire, Zambia, Angola.

Affinities

G. mirabilis is not closely allied to any other member of the genus. However it has affinities with G. wahlbergii and its allies in the large aedeagus with pronounced subapical ventral process, and the warty integument of the pronotum with its raised carina.



Figs 86–89. Gastrimargus mirabilis Uvarov, genitalia. 86, phallic complex, dorsal view; 87, same, lateral view; 88, epiphallus, right half, dorsal view; 89, same, posterior view.

Table 29

Measurements

G. mirabilis: Central Africa, various localities

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	32.90	4.44	9.93	24.35	15.67	2.85	5.51	3.54	2.46	1.55
Range	31.35–34.40	4.25–4.65	9.30–10.25	23.35–25.80	15.25–16.00	2.70–3.05	5.16–5.71	3.46–3.68	2.32–2.59	1.47–1.64
S.D.	1.154	0.160	0.372	0.991	0.382	0.180	0.302	0.124	0.105	0.086
No.	5	5	5	5	3	3	3	3	5	3
♀ Mean	52.93	7.87	15.08	38.31	25.69	4.87	5.29	3.34	2.51	1.50
Range	47.45–59.60	7.10 8.85	14.05–15.70	34.05–44.00	23.25–30.60	4.35–5.85	4.89–5.72	3.22–3.46	2.42–2.66	1.44–1.57
S.D.	3.947	0.679	0.604	3.187	2.370	0.514	0.259	0.094	0.100	0.048
No.	6	7	6	7	7	7	7	6	5	6

Table 30

Measurements:

G. insolens: unique holotype, Angola

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
Holotype ♀	39.70	6.70	9.80	28.55	21.20	4.90	4.33	3.16	2.91	1.35

Plate 27. G. mirabilis Uvarov ♂

Plate 28. G. insolens sp. n. ♀

2.1.5.19 Gastrimargus insolens sp. n.

(Fig. 111; Plate 28)

Male Unknown. Diagnosis (based on unique female). Antennae about two thirds as long as combined length of head and pronotum. Fastigium of vertex convex. Pronotum with median carina arcuate, not intersected by posterior sulcus; hind margin acutangular. Tegmen surpassing hind knees by one seventh of hind femur length. Ventral ovipositor valves short, less than one and a quarter times as long as perpendicular basal width.

Colouration generally greenish brown. Pronotal x-marking thin. Tegmina green with large irregular brown blotches separated by green cross-banding in basal two thirds, becomingclear with brown speckles in apical third (Plate 28). Hind wing fascia (Plate 28) indistinct, with darkened cells diffused along costal margin from fascia towards wing tip; basal area of wing pale yellow. Hind femur externally green with bluish tinge in medial area, unmarked; internal medial area blue-black, becoming blue-grey apically; ventral surface brownish red; interior ventral carina orange red. Hind knee green. Hind tibia orange.

Measurements: Table 30

Material examined: Appendix 2, p. 385.

Distribution (Fig. 111, and Biogeography section, p. 330).

Sa da Bandeira, SW Angola.

Affinities

G. insolens has similar pronotal markings to G. verticalis, but is otherwise differentiated from that species by its short ovipositor, the colouration of the hind femur, and the form of the reduced wing fascia. Without the male it is impossible accurately to assess the relationships of the species. However in the context of a revision of all the known species of the genus, it is clear that the unique female belongs to a previously undescribed species of Gastrimargus.

2.1.5.20 Gastrimargus acutangulus (Stål, 1873)

(Figs 90-97, 111; Plate 29)

This species is here presented as two subspecies under which the specific synonymy is separately listed.

Diagnosis. Fastigium of vertex convex with distinct medial carinula. Pronotum with median carina high arcuate almost blade-like, not intersected by posterior sulcus; dorsum scattered with small pale globular warts; hind margin elongate acutangular. Tegmen exceeding hind knees by about one quarter to one third of hind femur length. Intercalary vein shiny, not serrated. Genitalia (Figs 90-97) with long cingular rami, aedeagus weakly protruding with small subapical ventral process; epiphallus with lophi varying according to locality (Figs 92-97).

Colouration. Green morphs with a more bluish tinge than in other species. Pronotal x-marking with anterior arms thinner than posterior arms. Tegmen with three to five pale cross-bands of variable extent. Hind wing with fascia (Plate 29) complete and very broad; basal area of wing bright blue. Hind femur externally with three indistinct oblique cross-bands in medial area; internal surface with large dark brown patch in basal half, overlaid in places by opaque pale bluish sheen; internal ventral surface red.

Key to subspecies of Gastrimargus acutangulus

1. Pronotum with posterior arms of x-marking forming an angle between themselves of about 70° and recurving posteriorly to meet pale marking on pronotal shoulders without forming a distinct angle before continuing round hind margin; enclosed dark triangles flanking

median carina in metazona with rounded outer angles (Plate 29). Outer lobes of epiphallic lophi strongly divergent (Figs 92,93). Hind tibiae bright orange, at least on inner surface (South Africa, Malawi, Zambia) ... ... G. acutangulus acutangulus (Stål)

-. Pronotum with posterior arms of x-marking forming an angle between themselves of about 80-90°, and meeting pale markings on pronotal shoulders at a distinct obtuse angle before continuing round hind margin; enclosed dark triangles flanking median carina in metazona with sharply obtuse outer angles. Outer lobes of epiphallic lophi weakly convergent or weakly divergent (Figs 94-97). Hind tibiae straw-coloured to pale orange-yellow (Kenya) ... ... G. acutangulus flavipes Johnston

Gastrimargus acutangulus acutangulus (Stål, 1873)

Pachytylus (Oedaleus) acutangulus Stål, 1873: 125. Holotype ♀, SOUTH AFRICA (NR, Stockholm) [examined].

Oedaleus (Gastrimargus) acutangulus (Stål); Saussure, 1884: 114.

Oedaleus (Gastrimargus) dohrnianus Saussure, 1888: 166. Holotype ♀, SOUTH AFRICA, Transvaal (PAN, Warsaw?) (lost) [synonymised by Sjöstedt, 1928: 33].

Oedalus [sic] acutangulus (Stål); Distant, 1892: 257.

Gastrimargus acutangulus (Stål); Kirby, 1902: 72

Measurements: Table 31

Gastrimargus acutangulus flavipes Johnston, 1937 nom. rev.

Gastrimargus acutangulus flavipes Johnston, 1937: 220. Holotype ♂, KENYA (BMNH) [incorrectly synonymised by Dirsh, 1966: 426] [examined].

Measurements: Table 32

Table 31

Measurements

G. *acutangulus acutangulus*: South Africa

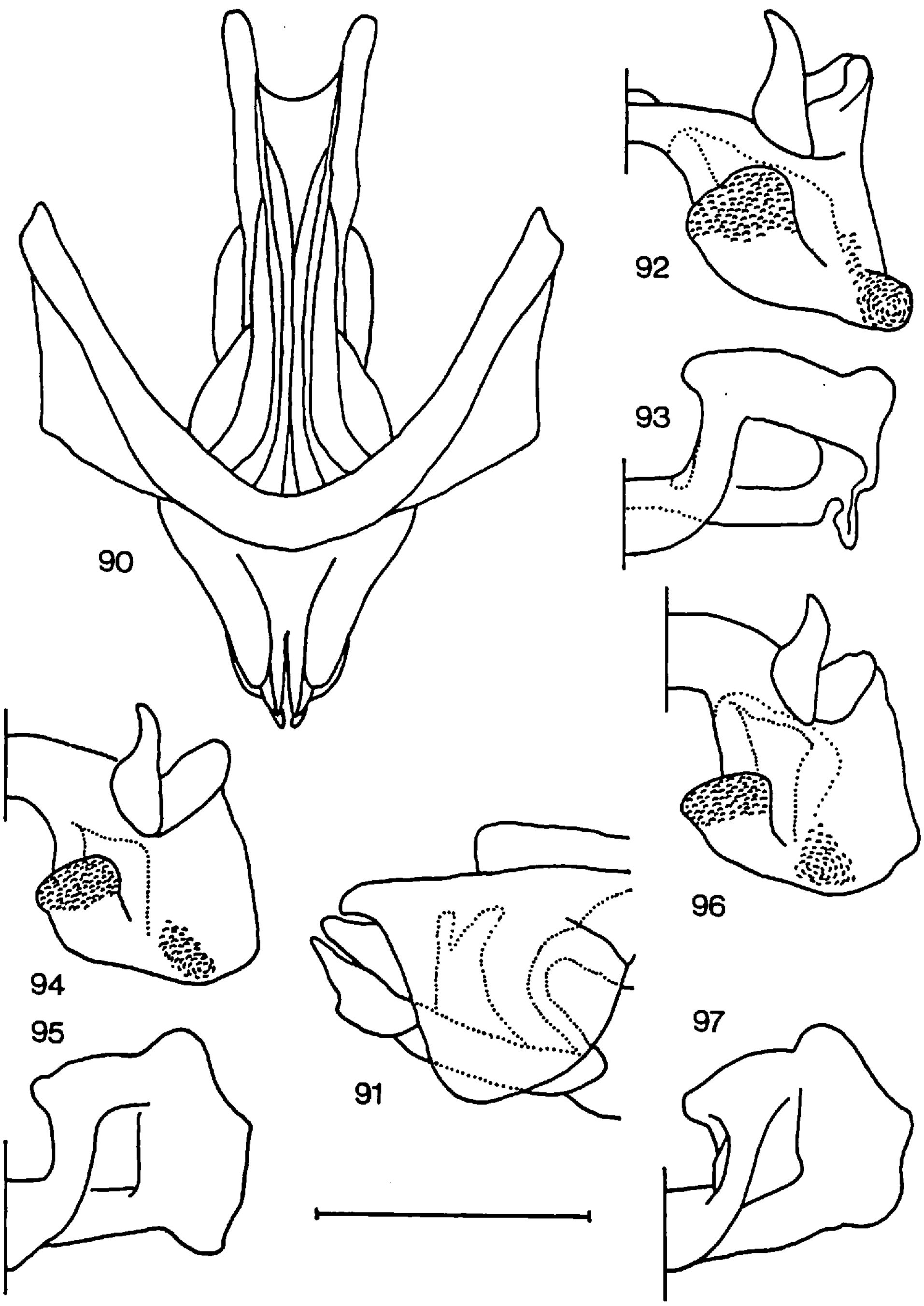
	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	37.68	5.45	9.11	28.72	20.06	4.97	4.04	3.69	3.16	1.43
Range	35.90–39.05	5.20–5.65	8.30–9.60	27.45–29.85	18.50–21.00	4.70–5.10	3.88–4.17	3.46–3.88	3.01 3.31	1.37–1.50
S.D.	1.070	0.136	0.492	0.825	0.780	0.140	0.090	0.118	0.111	0.039
No.	10	12	11	11	12	12	12	12	10	11
♀ Mean	47.53	7.26	12.25	36.10	25.93	6.69	3.90	3.58	2.94	1.38
Range	45.30–50.65	6.25–7.60	11.60–13.10	34.65–39.70	23.30–27.25	5.95–7.65	3.50–4.30	3.45–3.69	2.79–3.35	1.30–1.49
S.D.	1.980	0.253	0.499	1.604	1.176	0.560	0.259	0.075	0.164	0.054
No.	5	11	11	10	10	10	10	10	10	9

Table 32

Measurements

G. *acutangulus flavipes*: Kenya

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	34.66	5.16	8.30	26.15	17.82	4.46	3.99	3.45	3.19	1.45
Range	31.25–35.85	4.65–5.55	7.60–9.35	23.50–27.35	15.90–18.85	4.10–4.75	3.86–4.19	3.16–3.59	2.87–3.40	1.41–1.48
S.D.	1.805	0.334	0.643	1.417	1.236	0.245	0.109	0.140	0.219	0.29
No.	6	7	6	6	7	7	7	7	5	6
♀ Mean	42.88	6.54	10.74	31.99	22.80	5.94	3.85	3.49	3.00	1.41
Range	39.05–45.15	6.00–7.10	10.00 11.55	28.85–33.55	21.30–24.05	5.40–6.80	3.54–3.95	3.36–4.01	2.83–3.20	3.36–4.01
S.D.	2.163	0.347	0.651	1.766	1.111	0.474	0.139	0.215	0.135	0.215
No.	6	8	8	6	8	8	8	8	6	8



Figs 90-97. Gastrimargus acutangulus (Stål), genitalia. 90, phallic complex, dorsal view, G. a. acutangulus (South Africa); 91, same, posterior portion, lateral view; 92, epiphallus, right half, dorsal view, G. a. acutangulus (South Africa); 93, same, posterior view; 94, same, dorsal view (Malawi); 95, same, posterior view; 96, same, dorsal view, G. a. flavipes (Kenya); 97, same, posterior view.

Plate 29. G. acutangulus acutangulus (Stål) ♂

Plate 30. G. ochraceus Sjöstedt ♂

Material examined (both subspecies): Appendix 2, p. 385.

Distribution (Fig. 111, and Biogeography section p. 322).

G. acutangulus occurs in the highlands of Kenya (subspecies *flavipes*) and the eastern part of South Africa (subspecies *acutangulus*). In addition there is a population on the Nyika plateau of Malawi and Zambia which has genitalia intermediate between the two subspecies and colouration typical of *G. a. acutangulus*. The records of *G. acutangulus* from Guinea (Saussure, 1888: 39; Dirsh, 1966: 426), Ivory Coast (Dirsh, 1966: 426), and Zanzibar (Saussure, 1884: 114; Dirsh, 1966: 426; Johnsen & Forchammer, 1975: 51) are erroneous. Sjöstedt (1928: 51) incorrectly refers to Saussure's misidentified specimen from Zanzibar as a type.

Affinities

There does not appear to be any close relationship between this species and other members of the genus.

2.1.5.21 *Gastrimargus ochraceus* Sjöstedt, 1928
(Figs 98-101, 111; Plate 30)

Gastrimargus ochraceus Sjöstedt, 1928: 47. Holotype ♀, GHANA: (BMNH) [examined].

Gastrimargus ochraceus Sjöstedt; Gillon, 1974: 158 [description of male, previously unknown].

Diagnosis. Fastigium of vertex convex. Pronotum with median carina low arcuate, straight in profile, not intersected by posterior sulcus; hind margin rectangular in male, obtusangular in female. Tegmen surpassing folded hind knees by one seventh of hind femur length in male, failing to reach hind knees by one fifth of hind femur length in female. Genitalia (Figs 98-101) with aedeagus strongly projecting, and with very large bulbous subapical ventral process; aedeagal apodemes short, rounded in profile, not elongated anteriorly.

Colouration generally mottled brown. Pronotal x-marking with anterior arms distinct, thin, curved; posterior arms usually obsolete, occasionally faintly visible. Tegmen brown with variable pale cross-banding in basal half; apical half pale, opaque, with large rounded brown patches, clearing towards apex. Hind wing fascia (Plate 30) variable, narrowly interrupted between Cu2 and 2A, or restricted to posterior half of wing beyond 3A. External surface of hind femur with 2-3 oblique cross-bands in medial area; upper and lower marginal areas sometimes with an irregular row of small dark dots; internal surface dark brown; ventral surface light reddish brown in male, red in basal half in female. Hind tibiae brown.

Measurements: Table 33

Material examined: Appendix 2, p. 385.

Distribution (Fig. 111, and Biogeography section, p. 331).

Ghana, Ivory Coast, Zaire. Habitat information for Ivory Coast is given by Gillon (1974).

Affinities

G. ochraceus has no apparent close affinities with other members of the genus. The unusual male genitalia (Figs 98-101), and the distinctive pronotal pattern suggest that the species is not nearly related to other species.

Table 33

Measurements

G. ochraceus: Africa, various localities

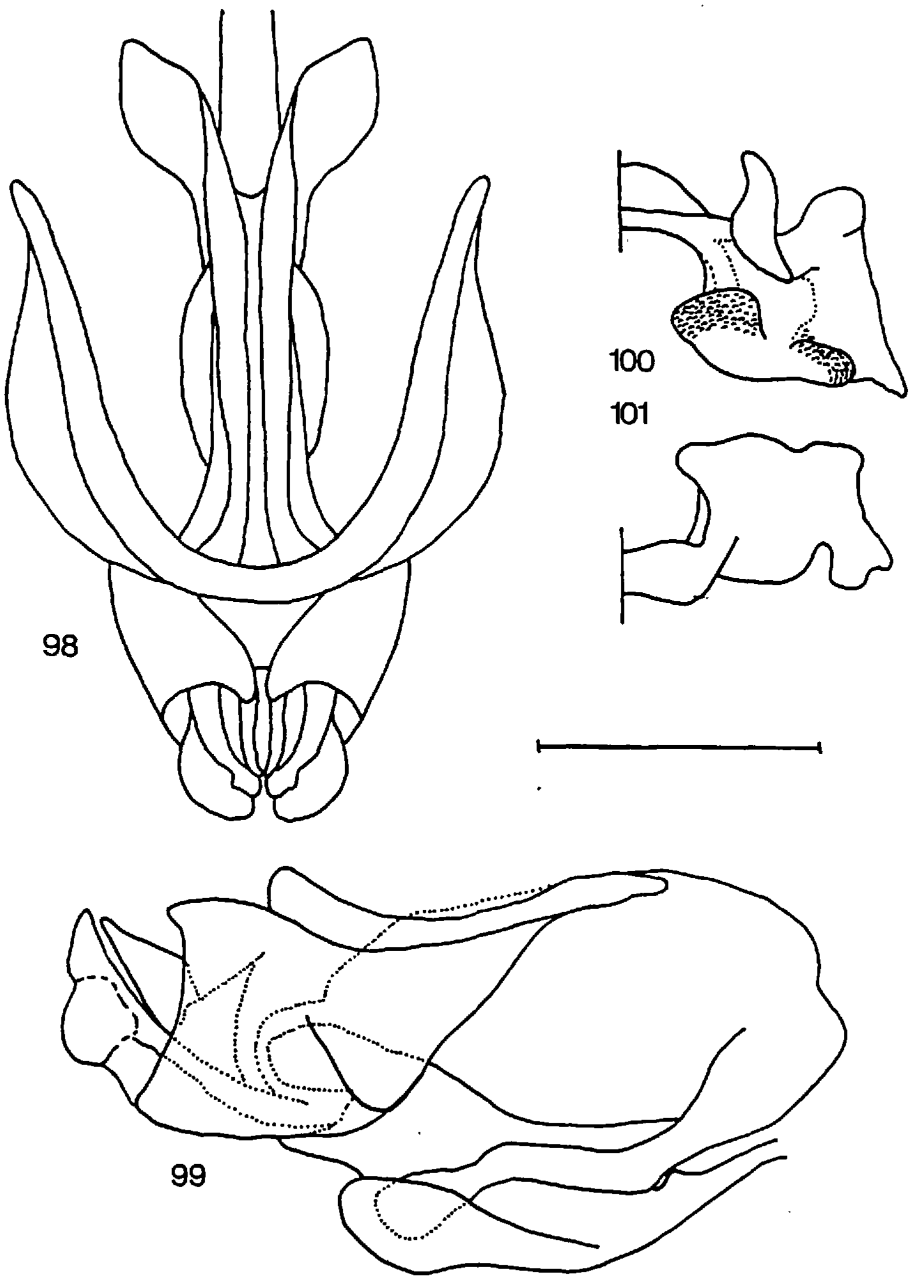
	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	25.33	3.88	5.02	18.02	13.75	2.70	5.10	3.11	3.60	1.31
Range	23.70–27.65	3.45–4.25	4.45–5.50	17.20–19.60	12.20–15.40	2.35–2.90	4.79–5.31	3.46–3.62	3.38–3.87	1.26–1.41
S.D.	2.062	0.404	0.530	1.371	1.602	0.304	0.272	0.128	0.202	0.069
No.	3	3	3	3	3	3	3	3	3	3
♀ Mean	30.97	6.83	8.00	19.62	19.48	4.12	4.73	2.85	2.47	1.01
Range	28.65 33.60	6.30–7.65	7.05–9.35	17.90–21.60	17.75–22.00	3.80–4.65	4.67–4.80	2.82–2.88	2.31–2.55	0.98–1.04
S.D.	2.490	0.718	1.201	1.864	2.231	0.465	0.065	0.031	0.136	0.030
No.	3	3	3	3	3	3	3	3	3	3

Table 34

Measurements

G. willemsei: New Guinea

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	30.18	4.56	6.64	22.17	15.58	3.85	4.05	3.42	3.43	1.42
Range	27.25–32.70	4.25–4.70	6.45–7.05	19.60–24.30	13.75–16.60	3.70–4.20	3.72–4.25	3.15–3.62	2.97–3.97	1.33–1.54
S.D.	2.020	0.148	0.216	1.711	0.968	0.160	0.187	0.160	0.356	0.071
No.	8	8	6	8	8	8	8	8	6	8
♀ Mean	30.46	5.86	8.06	20.71	17.81	4.52	3.95	3.04	2.57	1.16
Range	28.45–33.65	5.45–6.20	7.45–8.60	19.50–22.10	17.00–19.20	3.90–4.90	3.70–4.37	2.91–3.15	2.27–2.97	1.10–1.21
S.D.	1.657	0.290	0.439	1.016	0.867	0.265	0.218	0.095	0.214	0.036
No.	9	9	8	9	9	9	9	9	8	9



Figs 98–101. Gastrimargus ochraceus Sjöstedt, genitalia. 98, phallic complex, dorsal view; 99, same, lateral view; 100, epiphallus, right half, dorsal view; 101, same, posterior view.

2.1.5.22 Gastrimargus willemsei sp. n.

(Figs 102-106, 120; Plate 31)

Diagnosis. Antennae short, four fifths as long as head and pronotum together. Fastigium of vertex concave. Pronotum with median carina low arcuate, flat or concave in profile, not intersected by posterior sulcus in male, sometimes intersected in female; hind margin blunt acutangular. Tegmen surpassing folded hind knees by one third of hind femur length in male, barely surpassing knees in female. Genitalia (Figs 102-106) with thick cingular arch and weakly protruding aedeagus; epiphallic lophi with relatively large bulbous inner lobes and strongly protruding convergent outer lobes. Ventral ovipositor valves elongated and distinctly bifurcated at apex (Fig. 106).

Colouration generally dark brown. Pronotal x-marking sometimes almost obsolete. Tegmen with 2-3 variable cross-bands, often reduced, sometimes obsolete. Hind wing fascia (Plate 31) complete, approaching wing base along costal margin; apical half of wing densely infumate, sometimes less so in female; basal area of wing pale yellow to colourless. Hind femur externally with 3 oblique transverse dark bands; internal surface with large dark brown patch in basal half; internal and external ventral surfaces dark brown to blue-black. Hind tibia dark red.

Measurements: Table 34

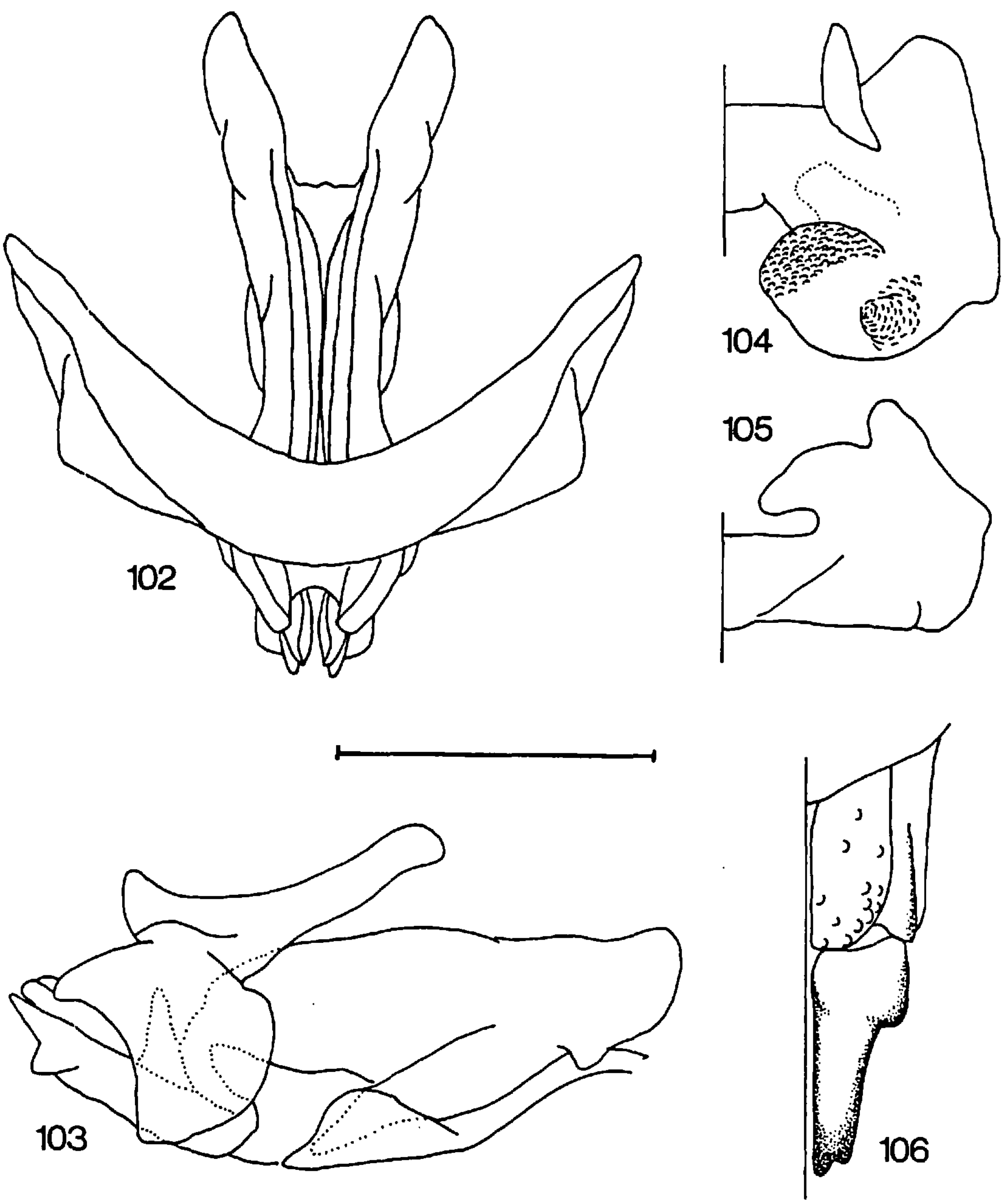
Material examined: Appendix 2, p. 385.

Distribution (Fig. 120, and Biogeography section, p. 342).

Highlands of W New Guinea.

Affinities

G. willemsei appears only distantly related to any other species of the genus. The form of the epiphallus and the bifurcated apex of the ventral ovipositor valves are unlike those of other species, although the



Figs 102-106. Gastrimargus willemsei sp. n., genitalia. 102, phallic complex, dorsal view; 103, same, lateral view; 104, epiphallus, right half, dorsal view; 105, same, posterior view; 106, ovipositor, left half, ventral view.

Plate 31. G. willemsei sp. n. ♂

Plate 32. G. sarasini (Saussure) ♂

clouded apical half of the hind wing is a character which recurs independently in several isolated montane species. It is likely however that G. willemsei has its origins in the africanus-musicus group which has radiated widely in Australasia, despite having evolved a number of unique features, not found in other members of the group.

Discussion

This new species is named in honour of Dr Fer Willemse who kindly loaned the type material.

2.1.5.23 Gastrimargus sarasini (Saussure, 1884)
(Figs 107-110, 120: Plate 32)

Oedaleus (Gastrimargus) Sarasini [sic] Saussure, 1884: 114. LECTOTYPE ♀, NEW CALEDONIA (NR, Stockholm) here designated [examined].
Gastrimargus Sarasini [sic] (Saussure); Kirby, 1910: 228.
Gastrimargus sarasini (Saussure); Willemse, 1923: 102.

Diagnosis. Fastigium of vertex concave, with triangular foveolae. Frons in profile straight, not convex. Pronotum with median carina arcuate, slightly inflated in prozona, sometimes narrowly intersected by posterior sulcus; hind margin sharply acutangular. Tegmen surpassing folded hind knees by one quarter of hind femur length. Genitalia (Figs 107-110) with weakly protruding aedeagus.

Colouration dark brown with lighter markings. Pronotal x-marking not usually visible, obscured by lighter colour on lateral margin of dorsum (Plate 32). Tegmen blackish brown with 2 reduced pale cross-bands. Hind wing fascia (Plate 32) complete; apical half of wing densely infumate in male, lighter in female; basal area of wing bright sulphur yellow. Hind femur externally mottled with indistinct banding; lower marginal area dark brown to black; internal medial area and ventral surface black. Hind tibia coral orange-red.

Synonymy

The newly-designated lectotype of G. sarasini was labelled as type by Saussure, but in his paper (1884: 114) he failed to designate a holotype from his syntype series. Sjöstedt (1928:33) refers to 'cotypes' at Vienna, and there is one male so labelled (not by Saussure) from Brunner's collection at Vienna, now deposited in the NR, Stockholm. All the original series in Vienna, Geneva, and Stockholm, should now be considered as paralectotypes.

Measurements: Table 35

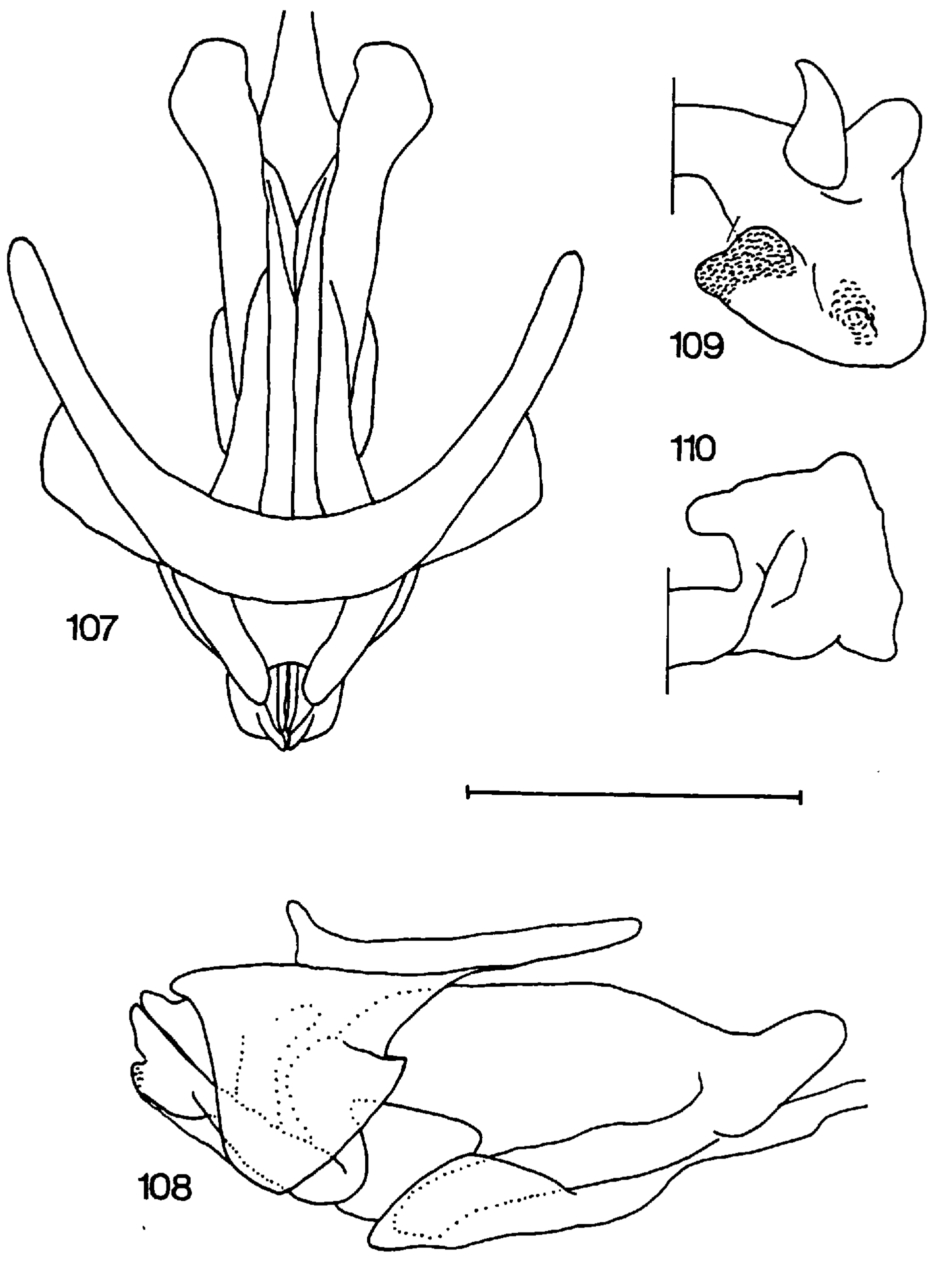
Material examined: Appendix 2, p. 385.

Distribution (Fig. 120, and Biogeography section, p. 342).

New Caledonia.

Affinities

G. sarasini is presumably derived from the africanus - musicus stock which has produced a radiation of species in Asia and Australasia. The general dark colouration is a recurrent response to isolated montane or island habitats.



Figs 107-110. Gastrimargus sarasini (Saussure), genitalia. 107, phallic complex, dorsal view; 108, same, lateral view; 109, epiphallus, right half, dorsal view; 110, same, posterior view.

Table 35

Measurements

G. sarasini: New Caledonia

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♂ Mean	28.31	3.90	5.74	21.41	15.11	3.42	4.42	3.88	3.68	1.39
Range	26.40–31.75	3.65–4.15	5.05–6.60	19.35–23.65	13.85 16.65	3.00–3.80	4.20–4.75	3.62–4.16	3.20–4.08	1.30–1.50
S.D.	1.327	0.149	0.385	1.935	0.665	0.183	0.143	0.122	0.180	0.043
No.	29	30	30	29	30	30	30	30	29	29

	Total length	Caput width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	FL/C	TL/PL	TL/FL
♀ Mean	39.56	5.79	8.49	29.30	21.20	4.80	4.42	3.66	3.45	1.38
Range	37.15–43.65–	5.45–6.20–	7.55–9.80–	26.45–32.55–	19.95–23.05–	4.30–5.10–	4.05–4.69–	3.41–3.91–	3.09–3.74–	1.24–1.46–
S.D.	1.655	0.184	0.589	1.458	0.902	0.200	0.163	0.126	0.165	0.055
No.	24	25	24	24	25	25	25	25	23	24

2.2 BIOGEOGRAPHY OF THE GENUS *GASTRIMARGUS*

2.2.1 The African *Gastrimargus* fauna

Species of *Gastrimargus* exploit a wide range of climatic zones and vegetation types in Africa south of the Sahara. One area of species concentration is the temperate and subtropical montane grassland of south-eastern Africa where *G. wahlbergii* and *G. acutangulus acutangulus* are endemic (Fig. 111). Two other species, *G. crassicollis* and *G. drakensbergensis*, are also centred on this region (Fig. 112) but extend their ranges northwards into the Mopane woodland and westward along the south coast into the Cape macchia. The eastern plateau of southern Africa has provided a buffer zone for grassland species when lowland habitats have been wiped out by adverse climatic conditions. There is some evidence that similar grassland types have been more widespread in the past (Rattray, 1960). At the present day there are widely separated pockets of montane *Themeda*-dominated grassland on the Mocambique / Zimbabwe border and in Malawi between the large montane area of S Africa and the more dissected montane and semi-montane relicts of Kenya and Tanzania. The northern race of *G. acutangulus*, *G. a. flavipes* is associated with this type of vegetation in Kenya, and an intermediate form also occurs on the Nyika plateau of Malawi and Zambia (Fig. 111).

Another species, *G. verticalis*, shows a preference for savannah (Fig. 113). It is found in E Africa mainly east of the rift valley and crosses the *Brachystegia* belt by means of grassland 'stepping-stones' north of L. Malawi and on the Mocambique / Zimbabwe border. At times when the East African 'dry corridor' was open there would have been free interchange between the northern and southern savannahs (Winterbottom, 1967; Van Zinderen Bakker, 1976). The Kibariani mountains at Mpwapwa, Tanzania, are situated on the east side of a narrow tongue of savannah extending south-westwards into the woodland zone at the northern end of the 'dry corridor'.

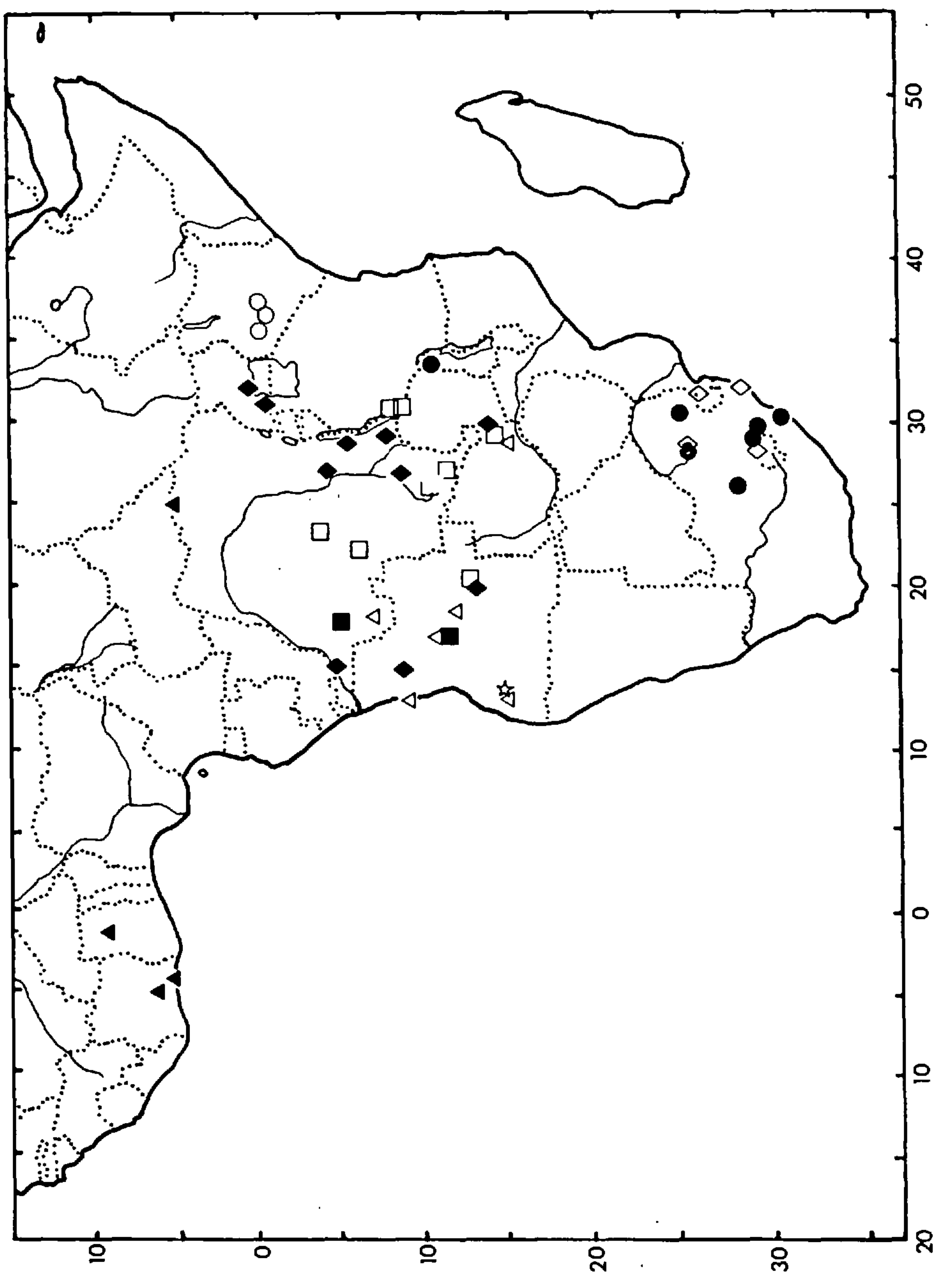


Fig. 111. Distribution of Gastrimargus species in Africa. Closed circles, *G. acutangulus acutangulus*; open circles, *G. a. flavipes*; star, *G. insolens*; open triangles, *G. angolensis*; closed triangles, *G. ochraceus*; open squares, *G. miombo*; closed squares, *G. obscurus*; open diamonds, *G. wahlbergii*; closed diamonds, *G. mirabilis*.

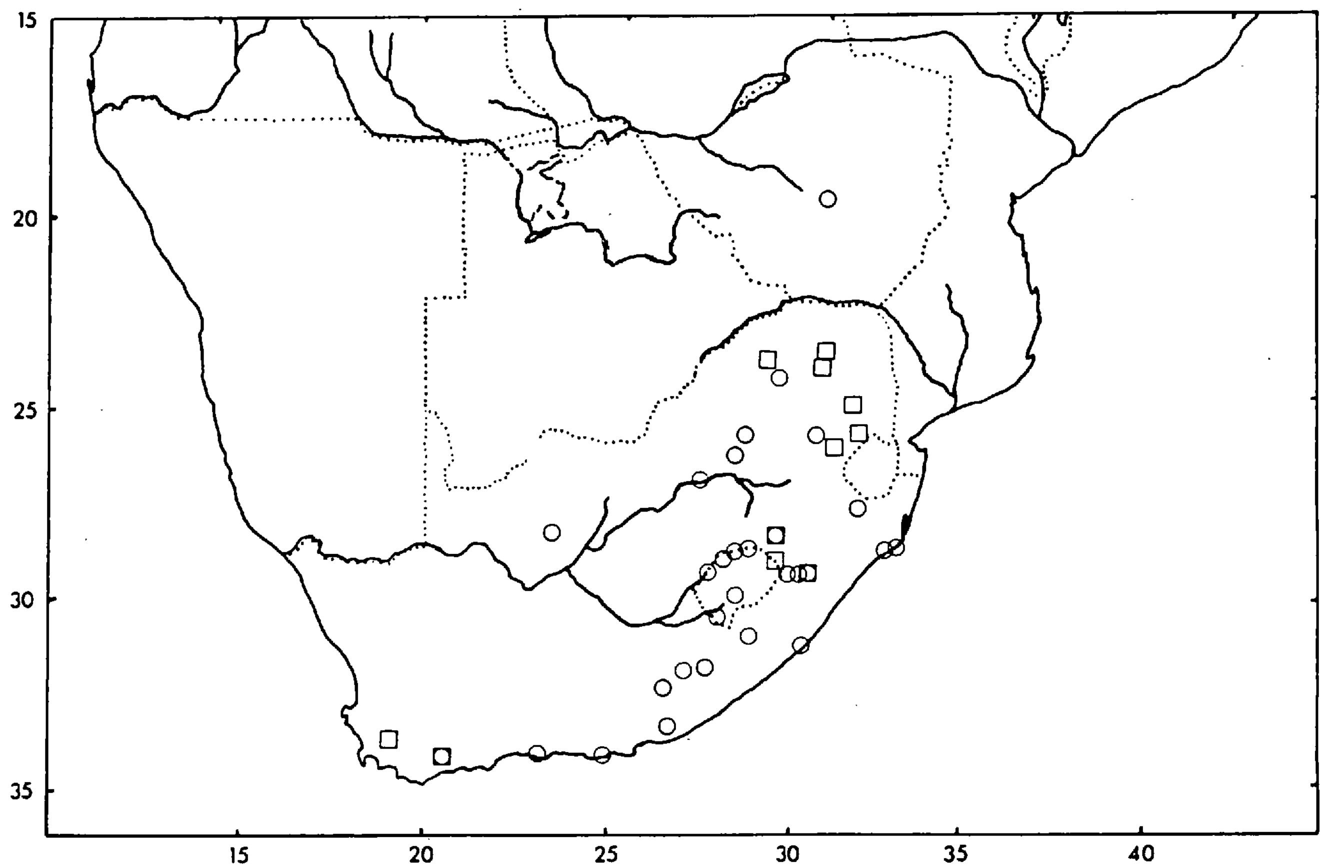


Fig. 112. Distribution of _Gastrimargus crassicollis_ (circles) and _G. drakensbergensis_ (squares) in southern Africa.

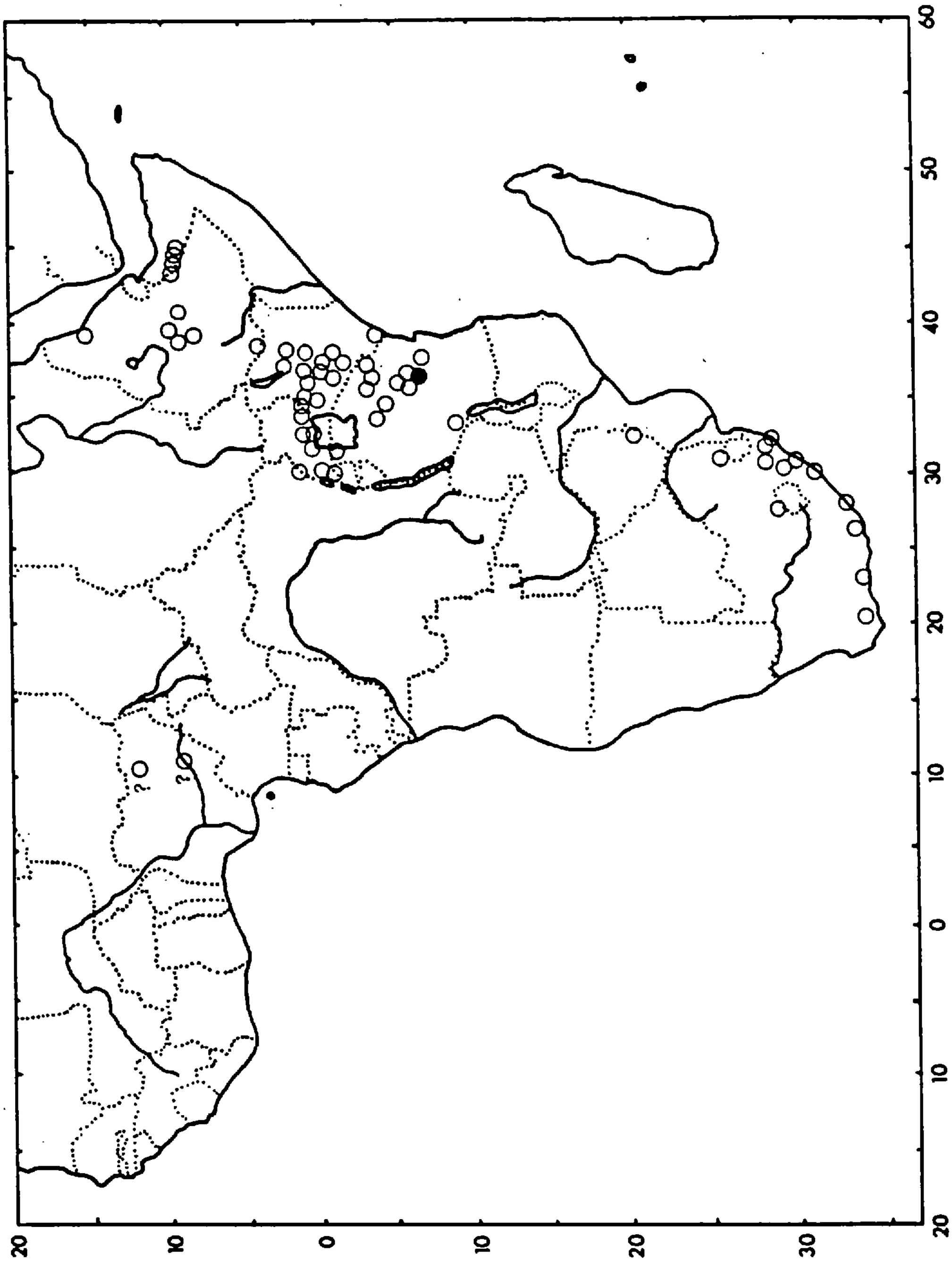


Fig. 113. Distribution of Gastrimargus verticalis verticalis (open circles) and G. verticalis mpwapwae (closed circles) in Africa.

Except for the two relict patches of *G. verticalis* further south mentioned above, Mpwapwa is the furthest point in a south-westerly direction reached by the species in east Africa. It is therefore significant that a distinct race, *G. verticalis mpwapwae*, is found on these mountains. Greenway (1933) has given a brief description of their vegetation. The *Brachystegia* zone contains rare forest trees along stream margins, relicts from a past period of heavier rainfall. The summit carries a patch of evergreen forest (6100') which is encircled by *Protea-Dombeya* highland grassland, overlooked by Greenway. The highland grassland commences at 5500' and is thought to have been derived from the forest, perhaps through the influence of fire (Burtt, B.D., 1942). Unfortunately the collector of the type series of *G. v. mpwapwae*, Eric Burtt, did not specify the type of vegetation in which his specimens were found, but from the altitude (6000') it is probable that it was the *Protea* zone.

The vegetation of Mpwapwa has not apparently been compared in detail with that of the two isolated mountains less than fifty miles to the south and south-east (Gillman, 1949), but it is probable that there are considerable similarities. At times of recession of the *Brachystegia* the Kibariani mountains would have been surrounded not by the thin ring of woodland that exists today, but by savannah from which *G. verticalis* could have colonised directly. During times of expansion of the *Brachystegia*, the area would have been isolated, providing an opportunity for divergence and speciation among the endemic fauna. It is remarkable that nine species of Acridoidea are known only from Mpwapwa despite extensive collecting by E.D. Burtt and others all over Tanzania. The list includes one species each of Pneumoridae, Pamphagidae, Pyrgomorphidae, and Lentulidae, and four Acrididae. A more intensive examination of the montane areas of Tanzania will no doubt reveal a more complex pattern of relict and endemic species since some at least of the Mpwapwa endemics must have had a wider distribution in the past.

At the northern extremity of the range of G. verticalis in Ethiopia there occur two species adapted to high montane habitats. The exact distribution of one of these, G. hyla, is unknown (see p. 255), but the other, G. rothschildi (Fig. 114), is found above the 2000 m contour. The range of this species has been discussed in detail above (p. 261) in relation to geographical races. G. rothschildi and, possibly, G. hyla, have been derived from G. verticalis in the relative isolation of the Abyssinian mountains, and the reduced wing length of the females in these species reflects their montane habitats.

G. determinatus vitripennis (Fig. 115) has a distribution in eastern and southern Africa sympatric with, but more extensive than that of G. verticalis. It is apparently unhindered by the Brachystegia zone and extends westwards to a line running NE - SW through Ethiopia, Uganda, and Angola, where another subspecies, G. d. procerus takes over, occurring on both the northern and southern fringes of the rain forest, and extending westwards to Senegal. This type of distribution is interesting and can be accounted for by reference to past climatic changes in the area during glacial periods (Van Zinderen Bakker, 1976). The northward movement of the cold Benguela current with its associated decline in precipitation and increase in wind desiccation was responsible for the redistribution of Kalahari sand as far as the Zaire river. The miombo woodland was pushed northwards and the western Congo basin forest may have been breached. The present-day intrusion of tall grass savannah/forest mosaic into the forest in the Congo Republic (Keay, 1959) is largely rooted in Kalahari sand with grass associations dominated by Loudetia spp. (Rattray, 1960). From this it may be inferred that a N-S savannah/woodland corridor was created which facilitated the interchange of species between western and southern Africa across the Congo forest. This corridor was not as well-defined or as arid as that in east Africa but would have permitted species like G. determinatus with a wide tolerance of vegetation and climate to

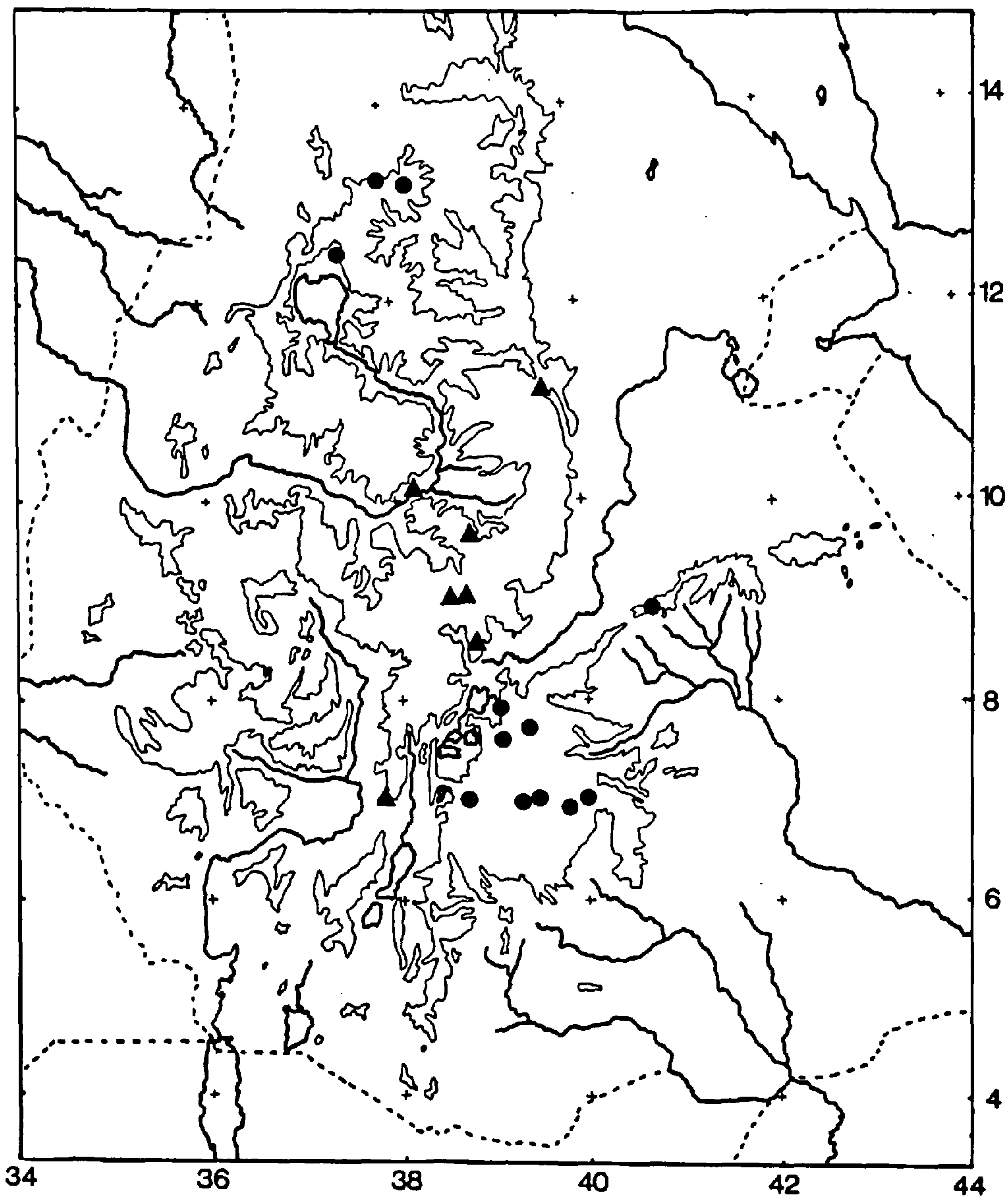


Fig. 114. Distribution of races of G. rothschildi in Ethiopia. Blue-leg race, circles; yellow-leg race, triangles. The 2000 m contour is represented by a thin continuous line.

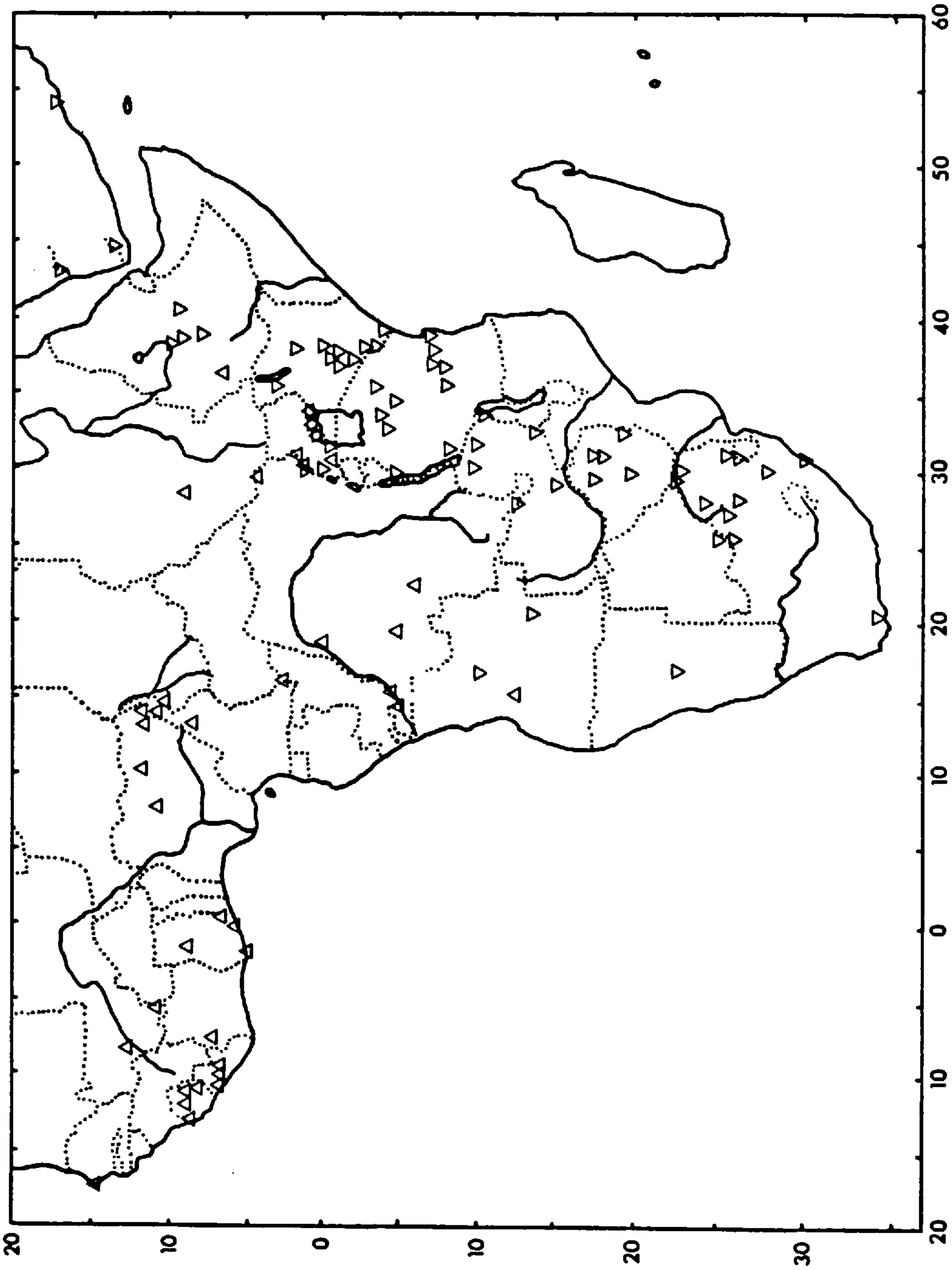


Fig. 115. Distribution of subspecies of Gastrimargus determinatus in Africa and Arabia. G. d. procerus (upright open triangles), G. d. vitripennis (reversed open triangles), and G. d. arabicus (reversed closed triangles).

cross. It is not clear in which direction the movement took place. The nominate subspecies, G. d. determinatus, occurs in Cape Province, though precise localities are unknown, and it has a fully banded hind wing (Plates 17, 18), probably the 'primitive' condition for the species. G. d. procerus has a partial band (Plate 19) which is generally most developed in males from the Congo region ('G. silvicola' Sjöstedt) and G. d. vitripennis (Plate 20) has no band on the hind wing. The most reasonable model for the development of the three subspecies is that procerus arose from determinatus, and vitripennis from procerus, with the progressive loss of the hind wing fascia in the process. In Arabia a fourth subspecies, G. d. arabicus, which also lacks the hind wing band, has been derived from the north east fringe of the distribution of G. d. vitripennis across the Red Sea in Ethiopia.

The largest concentration of Gastrimargus species occurs in central Africa south of the equator, in and around the Brachystegia woodland and the moist woodland and forest/ savannah mosaic zones (Keay, 1959) (Fig. 111). The members of this geographical assemblage are morphologically diverse. The most extensive range is that of G. mirabilis, the only member of the group to cross the rift valley, penetrating as far east as SW Uganda. G. angolensis, G. miombo, and G. obscurus are more restricted in range, but their relative rarity precludes any meaningful discussion of their precise distribution. The unique locality of G. insolens, Sa da Bandeira, is situated on an isolated massif at the south-western extremity of the Angolan plateau. The mountain is capped with forest but otherwise the vegetation is Brachystegia woodland with a Hyparrhenia grass association different from that of the lower altitude, lower rainfall areas around. At present it is not certain that this species is absent from similar vegetation in the montane area further north, west of Nova Lisboa. However the isolated location of Sa da Bandeira at the tip of a peninsula of miombo projecting into the hotter, drier 'mopane' belt suggests that the species may be a relict from one of the periods of Kalahari expansion mentioned above. During such a period the miombo woodland would have receded further north except for an isolated patch on this mountain acting as a refuge for species of more humid habitats. None of the Gastrimargus species endemic to the Brachystegia zone have been recorded east of a line from the east end of L. Rukwa south along the Luangwa valley to the Zambezi. This line follows the course of the 'arid corridor' which divided the woodland during glacial periods. The absence of these species in similar vegetation to the east of the corridor suggests either that they evolved in the west during a period when the woodland was divided and have failed to expand their ranges since, or that they have been wiped out east of the corridor by even more severe glacial conditions.

West Africa is relatively poor in endemic non-forest species of Acrididae, presumably as a result of the climatic instability of the area during the Pleistocene (Moreau, 1966) discussed in Part 1 (pp. 167-172). G. ochraceus, the only species of the genus endemic to this region was known until recently only from Ghana and Ivory Coast wher it extends from the Isoberlinia woodland (northern Guinea savannah) to the forest/savannah mosaic. It is now reported from similar country on the northern border of Zaire in the centre of the continent. This species and many other non-arid faunal elements occurring in West Africa today have probably moved westwards from central Africa where there have been suitable refuges on the northern fringe of the Congo forest when similar habitats in W Africa were reduced or destroyed by desert encroachment.

Gastrimargus africanus, the most ecologically tolerant species in the genus, is found very widely in Africa (Fig. 116), even occurring, presumably in clearings, deep in the Congo forest. However it avoids dry savannah and semi-desert, as for example in Namibia, Botswana, and Somalia. The wide tolerance and high vagility of the species have uniquely equipped it for expansion not only within Africa but across Asia as well. Around

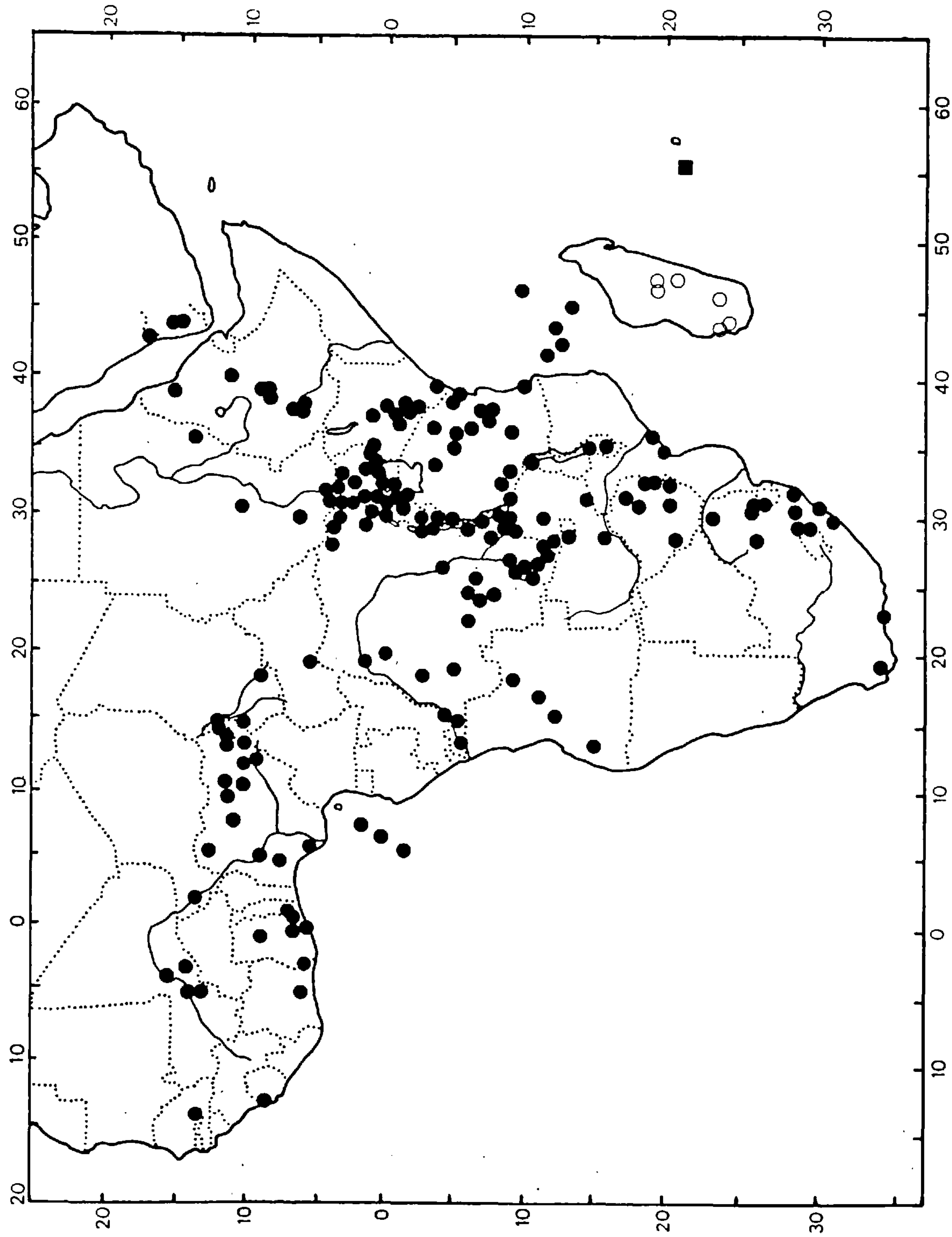


Fig. 116. Distribution of Gastrimargus species in Africa, Arabia, & neighbouring islands. G. africanus africanus (closed circles); G. a. madagascariensis (open circles); G. immaculatus (square).

the continental margin of Africa G. africanus extends, apparently unaltered into the Comoro Is, Aldabra, and the SW corner of Arabia, but in Madagascar has given rise to a separate subspecies G. a. madagascariensis.

2.2.2 The Gastrimargus fauna of Asia

G. africanus reappears in western India (Fig. 117), the nominate subspecies being replaced by G. a. sulphureus in Pakistan, Kashmir, and Nepal, and NE India above 2000 m. In east Asia there is a gradual replacement of the nominate subspecies by G. a. parvulus which tends to lose the bright yellow wing colour and the blue underside of the hind femur. The distribution of this subspecies is disjunct between Indo-China and the south coast of Java, avoiding the intervening rain forest areas of Malaya and Sumatra. The remaining species endemic to mainland Asia, G. nubilus, is closely allied to G. africanus and is adapted to the mountains of southern China north of the Burma border on the NE edge of the range of that species (Fig. 117). As stated above (p. 230) G. nubilus has probably been derived from G. africanus under the influence of montane conditions. G. immaculatus, an island endemic species from Réunion in the Indian Ocean (Fig. 117), is presumably also related to G. africanus, but the relationship is not very close (see p. 252). The subspeciation of G. africanus in Asia and the existence of a closely-related species there, as against the absence of any distinct subspeciation in Africa, suggests that the species may have originated in Asia and moved into Africa rather than the reverse. The question remains open.

2.2.3 The Gastrimargus fauna of Malesia

The name Malesia has been coined to describe the area between the mainland of Asia, bounded by the Kra isthmus of the Malay peninsula and the Bashi channel north of the Philippines, and Australia, bounded by the

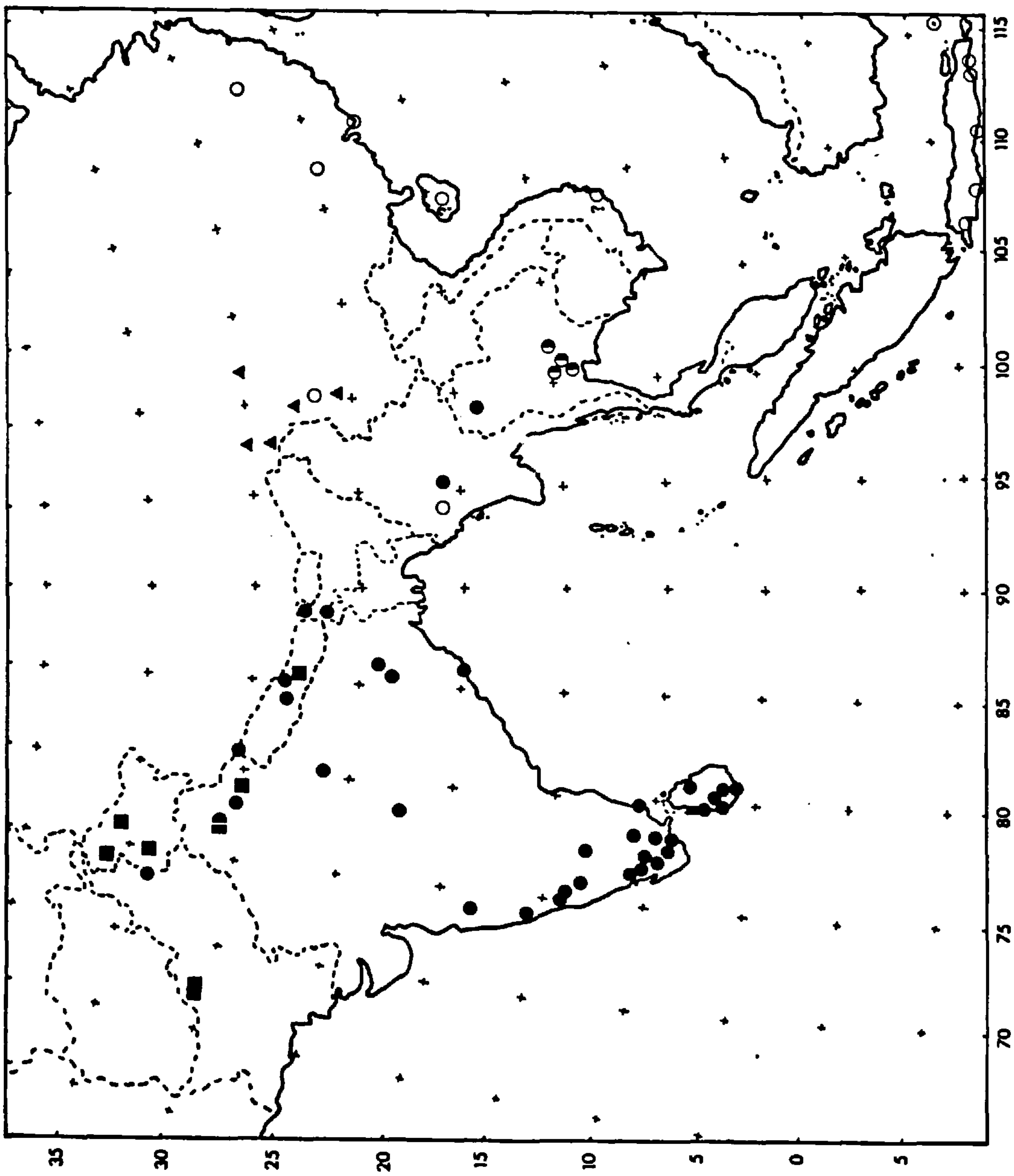


Fig. 117. Distribution of Gastrimargus species and subspecies in Asia. G. a. africanus (closed circles), G. a. parvulus (open circles), intermediates (half-closed circles), G. a. sulphureus (squares), and G. nubilus (triangles).

Torres strait (Whitmore, 1975). The islands of Malesia have been the setting for a radiation of Gastrimargus species best understood against the background of the physical characteristics and vegetation of the region, both past and present. The flora of Malesia is highly distinct, with more than forty percent of the species endemic, and with a total of more than 2000 genera retained or excluded by the barriers described above (Whitmore, 1975).

Within Malesia, the 200 m submarine contour defining the Sunda shelf, the asian continental shelf, includes the islands of Sumatra, Java, and Borneo. Sumatra and Borneo carry a floristically similar type of rain forest, but Java with its seasonally dry climate has a more open monsoon forest. At certain times during the Pleistocene the sea level in this area has dropped about 100 m, uniting these islands (Haile, 1971) and presumably producing drier conditions in Malesia. Botanical evidence for the past extension of seasonally dry habitats is provided by drought-loving species of Papilionaceae which are now not found anywhere between monsoon Asia and Java, but which must have had continuous distributions in the past. They probably crossed the intervening space via the Philippines, the Celebes, and the Moluccas, which even today form a N - S sequence of seasonally drier climates between the ever wet Sunda and Sahul shelves (Whitmore, 1975). However the fact that G. africanus has only become established in Java and not in any of the northern islands suggests that it reached there via the Malay peninsula from the mainland when seasonally drier climates were more widespread. Specimens from Java closely resemble those from the mainland, possibly indicating that the species has become established fairly recently, perhaps during the last glaciation when rain forest in N Queensland is known to have been temporarily replaced by sclerophyll forest, evidence of drier conditions in the region at that time (Walker, 1970).

Java and Bali mark the eastern boundary of the Sunda shelf and the area which was part of continental Asia during glacial maxima. Further east the islands of Lombok, Sumbawa, and Flores were separate from Bali though joined to each other. This separation is largely responsible for the striking impoverishment of the fauna to the east of the dividing line known as Wallace's line. For example, 68 species of birds found on Bali are absent from Lombok (Mayr, 1944). In addition to permanent separation from the continental shelf, the volcanic nature of the islands must have hindered the dispersal of animal species along the chain of islands. Flores and the eastern islands emerged during the late Miocene after Lombok and Sumbawa and many of the volcanoes of eastern Flores and the smaller islands between Flores and Alor are still active today (Norvick, 1979).

Wallace's line is not a distinct limit for plants, as shown above (p. 335), nor for insects at genus level (Gressit, 1961). However at species level and below there are interesting changes. G. africanus does not reach Lombok and has not yet been recorded from Bali. It does however occur on Kangean, the largest and most westerly island of the Kangean archipelago, on the edge of the continental shelf. G. lombokensis, a species closely related to G. africanus and to the australian species, G. musicus, occurs on Lombok, Flores, Sumba, and Sumbawa (Fig. 118). It is now also known from Sepandjang, the most easterly of the Kangean Is, demonstrating the ability to cross 130 km of open water, probably blown by the southern monsoon. The prevailing monsoon winds blowing from Australia, are responsible for the relatively dry conditions in all the Lesser Sunda Is including Timor.

In contrast to the inner arc of islands from Lombok to Alor, the outer arc, including Timor and Roti, is now thought to have been part of the Australian continental margin since the Palaeozoic era (Audley-Charles et al., 1972), originally separated from the islands to the north by more than 1000 km. After starting to move northwards at the end of the mesozoic

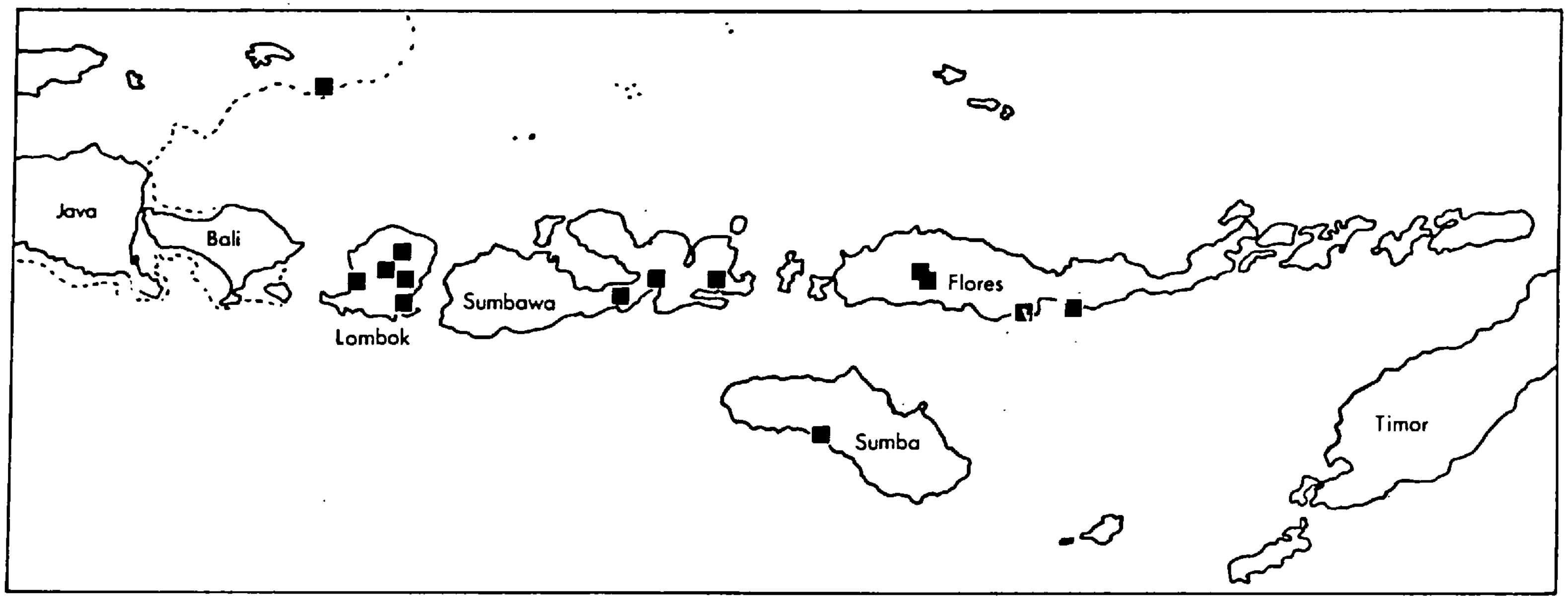


Fig. 118. Distribution of Gastrimargus lombokensis in the Lesser Sunda Is. The 200 m marine contour delimiting the Sunda shelf is represented by a broken line.

on the leading edge of the Australian plate, Timor arrived at its present position in the middle Pliocene, emerging above water in the late Pliocene and continuing to rise until the present (Norvick, 1979). Despite being part of the Australian continental plate, Timor is not part of the Sahul shelf defined by the 2000 m submarine contour surrounding Australia and New Guinea, and is separated from Australia by a deep trench. It has therefore never formed part of the continental land mass during periods of Pleistocene sea level depression. This isolated island has its own distinctive species of Gastrimargus, G. subfasciatus (Fig. 120), which has however strong links with G. lombokensis. The unusual blue pigmentation of the hind wing of G. subfasciatus replaces the pale yellow wing of G. lombokensis but this is probably a simple development in evolutionary terms. Both G. marmoratus and G. wahlbergii possess a very faint blue tint at the wing base on an otherwise pale yellow or greenish yellow wing. Oedaleus decorus bears similar colouration although its near relative O. senegalensis has no trace of blue pigment.

O'Toole (1975), discussing the dispersal of the velvet ant Timulla oculata (F) to the east of Wallace's Line, noted that the most distinctive subspecies were found on Timor and Tanimber Larat which are furthest away from the putative source area. He concluded that the populations on these islands must have undergone the most rapid evolution. The distant origin and consequently different fauna carried by these islands prior to their arrival in proximity to the islands of the inner are will no doubt have influenced the adaptive modification of the colonising species.

In contrast to the pattern of insular speciation in Malesia discussed above, the distribution of G. marmoratus (Fig. 119) is geographically and ecologically wide. The species is able to tolerate both the everwet climates of Borneo and Malaya and the seasonally dry regime of Sumbawa and Flores. This is a large, long-winged species of high vagility, attested by its presence in areas as remote from each other as the Vogelkop

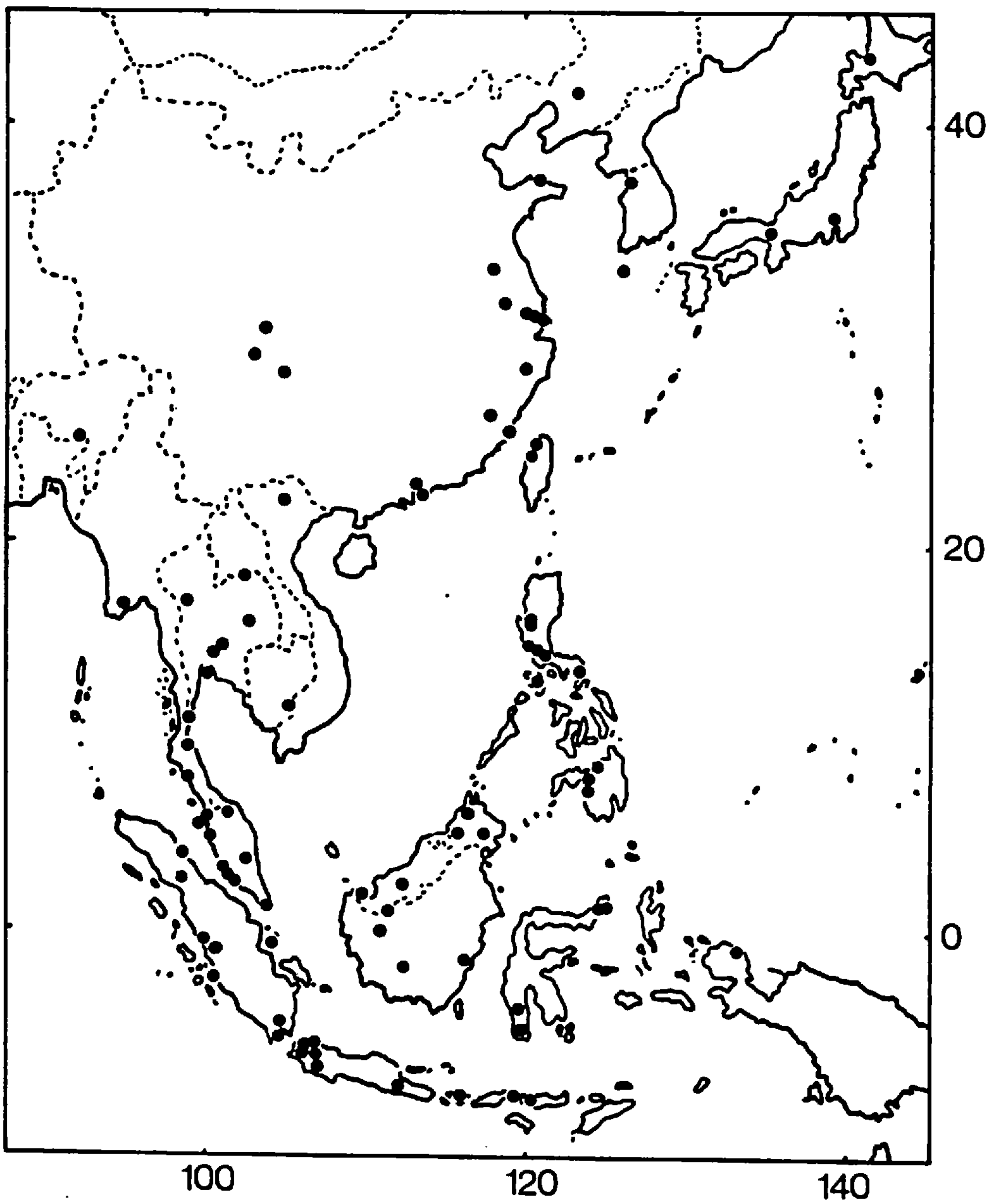


Fig. 119. Distribution of Gastrimargus marmoratus in SE Asia.

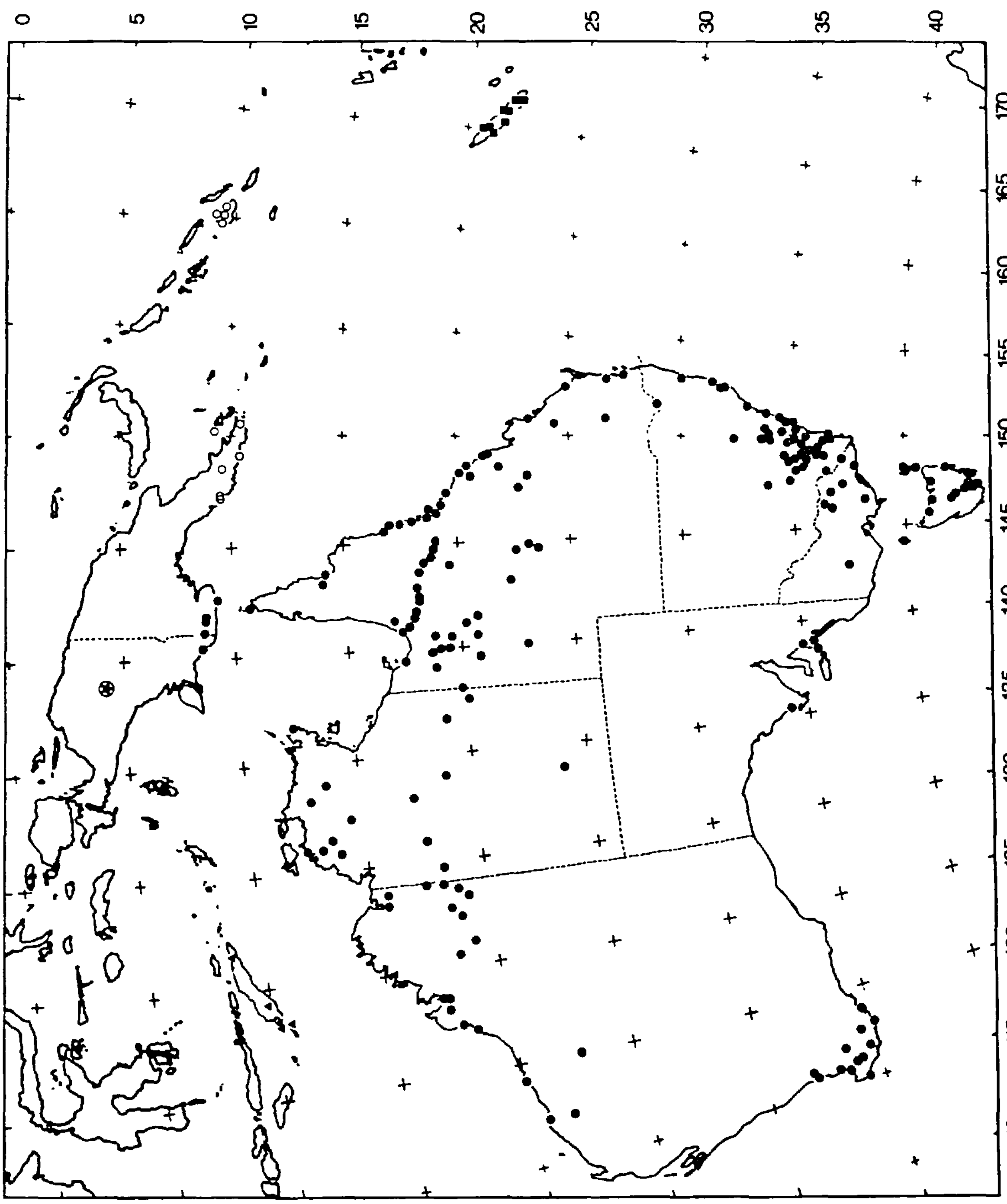


Fig. 120. Distribution of Gastrimargus species in Australasia. Closed circles, G. musicus (nominate race); open circles, G. musicus (pale-winged race); squares, G. sarasini; triangles, G. subfasciatus; circled star, G. willemsei.

peninsula of New Guinea and Hokkaido island, Japan. In mainland Asia the distribution map suggests a preference for coastal areas, but the known range especially in China is probably very incomplete.

2.2.4 The Gastrimargus fauna of Australasia

The only Gastrimargus species endemic to Australia, G. musicus (Fig. 120), is widespread and common in areas with 500 - 1500 mm of annual rainfall, and also occurs less commonly in drier areas. To some extent the collecting localities reflect the distribution of roads and population rather than of the insects themselves, as for example the line of records across the southern end of the Cape York peninsula, following the road from Normanton to Clarke River. In New Guinea the species is only found in the drier areas of the southern coast opposit Cape York and along the eastern peninsula. Specimens from eastern New Guinea and the Solomon Is differ in colour from the main population (see p. 242), indicating that separation by rain forest and by a wide tract of open sea respectively have initiated the process of subspeciation. At present G. musicus is known from Guadalcanal in the Solomons group but it may also occur on neighbouring islands.

G. musicus bears a strong resemblance to G. africanus to the extent that some specimens of the two species from the Solomon Is and Java respectively may be almost indistinguishable (see p. 212). It is likely that G. musicus, G. lombokensis, and G. subfasciatus all evolved from a common ancestor which had the red undersides to the hind femora which these species all share. How this ancestor was related to G. africanus is not clear. It is less likely that G. musicus is derived from G. lombokensis which must also have evolved from an ancestor close to G. africanus by a process which has included the loss of the bright yellow basal area of the hind wing and the modification of the wing band. It is unlikely that G. musicus could have regained these features just as they are found in G.

africanus when once they had been lost.

The remaining species known from New Guinea, G. willemsei (Fig. 120) is apparently restricted to the central mountains of Irian Jaya between 3250 and 4100 m. It appears to be only distantly allied to the other SE Asian species, and exhibits the familiar wing reduction and dark pigmentation associated with a montane existence. New Caledonia is the furthest point reached by Gastrimargus in its eastward radiation from its putative source areas in Africa and Asia. Here, 1200 km east of the coast of Australia, there is one species, G. sarasini (Fig. 120). This species also is not closely allied morphologically to its neighbours but presumably represents an early off-shoot from the africanus - musicus stock. It is not at present certain that this or some other species does not occur on the islands of the New Hebrides to the north east of New Caledonia, since collections from this part of the world tend to be aggregated around the more populous administrative centres.

2.2.5 General discussion

The distribution of the genus Gastrimargus offers some interesting points of comparison with that of Oedaleus (Part 1, pp. 152-195). In both genera there are several species centred on the high grasslands of eastern South Africa, Lesotho, and Swaziland. However in Oedaleus the most intense speciation has occurred in the East African savannah and semi-desert, whereas Gastrimargus in Africa is centred on the Brachystegia woodland south of the Congo forest, a habitat which supports only one species of Oedaleus, O. nigeriensis. This area has been little studied by acridologists and may be expected to yield further new species of grasshoppers.

Outside Africa the contrast between the two genera is even more marked. In Oedaleus there is a clear discontinuity between the eastern seaboard of Indo-China and the south-east coast of New Guinea where the unique

Australasian endemic, O. australis, is first encountered. For Gastrimargus with its greater tolerance of humid habitats, the intervening islands of Malesia have been the setting for a secondary radiation of species.

Overall there is a clear tendency for Gastrimargus to occupy more humid habitats than those favoured by Oedaleus. This is strikingly illustrated by a comparison of the number of montane species with restricted ranges in the two genera, excluding the species of the high veldt of eastern Africa. In Oedaleus there is only one species, O. formosanus, in this category, whereas there are five species and one subspecies of Gastrimargus. This figure reflects the effect of past periods of low rainfall when montane refuges have trapped populations of non-savannah species. Oedaleus, with its more xerophilous habitat preferences is not susceptible to this effect since dry glacial periods would have increased its range rather than the reverse. In both genera adaptation to montane conditions is associated with shortening of the tegmina and wings and darkening of the body colouration, notably the hind wings. This latter effect is independent of the morphometric changes and only occurs in some cases. It may also be observed in long winged populations on islands, as for example in G. sarasini on New Caledonia.

SUMMARY

This thesis is a revisionary study of two closely-related genera of old world oedipodine grasshoppers. Part 1 deals with the genus _Oedaleus_ Fieber, and Part 2 with _Gastrimargus_ Saussure. The study was undertaken because of the economic importance of the insects and the difficulties experienced, even by taxonomists, in making accurate specific determinations based on currently accepted nomenclature.

The work was based on critical examination of cuticular morphology and colouration since other information is lacking for more than a handful of species. Useful characters were derived from the shape and patterning of the pronotum, the dark banding or lack of banding on the hind wing, the colour of the hind wing basal area and the ventral surface of the hind femur, and the morphology of the male genitalia, particularly the epiphallus. For this purpose over 11, 600 specimens from 30 different private and institutional collections were examined, including 98 primary type specimens.

Keys are provided for the 20 species and 3 subspecies of _Oedaleus_ and the 23 species and 7 subspecies of _Gastrimargus_ now recognised. The keys and species descriptions are illustrated by 260 line drawings and 32 black and white photographs. Tables of measurements are given for each species with statistical analyses where appropriate.

Under each species a complete list of synonyms, combinations, and the more important published misidentifications is provided. The following taxa are newly synonymised: _Oedaleus manjius_ Chang, _O. cephalotes_ Uvarov, _O. dilutus_ Miller, _O. villiersi_ Chopard, _O. infernalis montanus_ Bei-Bienko, _O. infernalis amurensis_ Ikonnikov, _O. senegalensis_ var. _dimidiatus_ Bolivar, _O. australis_ var. _plana_ Sjöstedt, _O. infernalis pendulus_ Steinmann, _Gastrimargus pusillus_ Sjöstedt, _G. floresensis_ Sjöstedt, _G. corallipes_ Sjöstedt, _G. transvaalensis_ Sjöstedt, _G. clepsydrae_ Sjöstedt, _G. crassipes_ Sjöstedt, _G. grossiceps_

Sjöstedt, _G. testaceus_ Sjöstedt, _G. fallax_ Sjöstedt, _G. pallidus_ Sjöstedt, _G. abessinicus_ Sjöstedt, _G. cristagalli_ Sjöstedt, _G. longipes_ Sjöstedt, _G. vittatus_ Sjöstedt, _G. volkensi_ Sjöstedt, _G. aethiopicus_ Bolivar, _G. longipes_ var. _recta_ and var. _decliva_ Sjöstedt, _G. africanus orientalis_ Sjöstedt, _G. musicus_ var. _kimberleyensis_ Sjöstedt, _G. rothschildi montanus_ Uvarov.

The following species are here reduced to subspecific status: _Oedaleus asiaticus_ Bei-Bienko, _Gastrimargus somaliensis_ Sjöstedt (transferred to _Oedaleus_), _G. parvulus_ Sjöstedt, _G. sulphureus_ Bei-Bienko, _G. procerus_ Gerstäcker, _G. vitripennis_ (Saussure). The following taxa have been reinstated from synonymy: _G. africanus madagascariensis_ Sjöstedt, _G. acutangulus flavipes_ Johnston, _G. angolensis_ Sjöstedt, _G. verticalis_ (Saussure).

The following taxa are new to science: _Oedaleus nadiae_, _O. plenus browni_, _Gastrimargus miombo_, _G. insolens_, _G. obscurus_, _G. willemsei_, and _G. verticalis mpwapwae_. In addition the males of _Oedaleus miniatus_ Uvarov and _Gastrimargus hyla_ Sjostedt are described for the first time.

Available information on the biology and economic importance of the species is reviewed and distribution maps are provided covering all the recognised taxa of the two genera. These are based on label data of the specimens examined, supplemented by reliable records from the literature and information from correspondents. In many cases species ranges were previously very incompletely known, being based in some cases on a single record.

The biogeography of the genera is analysed in relation to past and present geology, vegetation, and climate. It is shown that _Oedaleus_ has radiated in the drier savannah and semi-arid regions, principally in east Africa, while _Gastrimargus_ has colonised moister woodland and tall grass areas, especially in central Africa and eastern Asia. For

Oedaleus in Africa the Brachystegia woodland is at present a major barrier between northern and southern populations. The occurrence of closel-related species, subspecies, and disjunct populations of the same species is attributed to the fluctuations of the woodland barrier during the Pleistocene and the intermittent appearance of a dry corridor across the woodland zone at some periods. This temporary 'arid corridor' is advanced as a possible cause of much of the observed trans-equatorial speciation in grasshoppers and other dry savannah organisms in Africa.

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APPENDICES

APPENDIX 1. TAXONOMY OF THE GENUS OEDALEUS FIEBER

Material Examined (primary types).

Oedaleus senegalensis (Krauss)

Material examined. Pachytylus senegalensis Krauss, neotype ♂, SENEGAL: Dakar airport, at light, 6.x.74, (Ritchie). Ctypohippus arenivolans Butler, holotype ♀, CAPE VERDE IS: St Vincent I, from sandy patches, 24.x.1878, (Butler). Pachytylus mlokoziewiztcki Bolivar, lectotype ♂, U.S.S.R.: 'Tiflis' [Tibilisi], no further data, (MHN, Geneva). Oedaleus senegalensis var. dimidiatus Bolivar, holotype ♀, CAPE VERDE IS: (Ferreira Borges) (MLZA, Lisbon). Other material: 1642 ♂, 1981 ♀, 117 nymphs.

Oedaleus nigrofasciatus (Degeer)

Material examined. Acrydium nigrofasciatum Degeer, holotype ♀, SOUTH AFRICA: Cape of Good Hope, no further data, (NR, Stockholm). Gryllus arcuatus Thunberg, lectotype ♂, no data, (ZIUU, Uppsala). Oedaleus nigrofasciatus var. gracilis Saussure, lectotype ♀, SOUTH AFRICA: Cape of Good Hope, (MHN, Geneva). Other material: 105 ♂, 109 ♀.

Oedaleus australis Saussure

Material examined. Oedaleus nigrofasciatus var. australis Saussure, lectotype ♀, AUSTRALIA (MHN, Geneva). Oedaleus australis var. plana Sjöstedt, holotype ♀, AUSTRALIA: A.C.T., Canberra, 20.ii.29, (Fuller) (ANIC, Canberra). Other material: 13 ♂, 24 ♀, 1 nymph.

Oedaleus abruptus (Thunberg)

Material examined. Gryllus abruptus Thunberg, lectotype ♂, CHINA: 'abruptus α', (ZIUU, Uppsala). Other material: 74 ♂, 117 ♀, 5 nymphs.

Oedaleus virgula (Snellan van Vollenhoven)

Material examined. Oedipoda virgula Snellan van Vollenhoven, holotype ♂, MADAGASCAR, no further data (RNH, Leiden). Oedaleus (Gastrimargus) madecassus Saussure, lectotype ♀, MADAGASCAR, no further data (MHN, Geneva). Epacromia inclyta Walker, holotype ♀, MADAGASCAR, no further data. Other material: 29 ♂, 47 ♀.

Oedaleus johnstoni Uvarov

Material examined. Oedaleus johnstoni Uvarov, holotype ♂, SUDAN: Khartoum, 25.ix.24, (Johnston). Other material: 51 ♂, 60 ♀.

Oedaleus nigeriensis Uvarov

Material examined. Oedaleus nigeriensis Uvarov, holotype ♂, NIGERIA: Azare, -.vii.25, (Lloyd). Oedaleus cephalotes Uvarov, holotype ♀, ETHIOPIA: Muger Valley, c 5500', 28-29.xii.26, (Scott). Other material: 383 ♂, 404 ♀, 2 nymphs.

Oedaleus carvalhoi Bolivar

Material examined. Oedaleus carvalhoi Bolivar, neotype ♂, Lourenco Marques, 12.vii.10. Other material: 130 ♂, 133 ♀, 2 nymphs.

Oedaleus plenus plenus (Walker)

Material examined. Epacromia plena Walker, lectotype ♂, SOUTH AFRICA: no further data, (Smith?). Oedaleus nigrofasciatus var. caffer Saussure, lectotype ♀, SOUTH AFRICA: no further data, (Delalande) (MHN, Geneva). Oedaleus dilutus Miller, holotype ♂, TANZANIA: Dodoma, Kitope, 6.iv.27, (Miller). Other material: 139 ♂, 137 ♀.

Oedaleus plenus browni subsp. n.

Material examined. Holotype ♂, SOUTH AFRICA: Cape Pr., De Aar, 13.ii. 59, (*Brown*) (DATS Pretoria). Other material: 9 ♂, 6 ♀, paratypes.

Oedaleus decorus decorus (Germar)

Material examined. *Acrydium decorum* Germar, neotype ♂, U.S.S.R.: Daghestan, Chodz-Tau, 5.vii.24, (*Riabov*). Other material: 321 ♂, 428 ♀, 10 nymphs.

Oedaleus decorus asiaticus Bei-Bienko

The holotype of this subspecies was not available for study. Other material: 6 ♂, 9♀.

Oedaleus infernalis Saussure

Material examined. *Oedaleus infernalis* Saussure, lectotype ♂, JAPAN: no further data, (NM, Vienna). *Oedaleus infernalis* var. *amurensis* Ikonnikov, lectotype ♂, U.S.S.R.: Amur (NM, Vienna). Other material: 135 ♂, 312 ♀, 5 nymphs.

Oedaleus formosanus (Shiraki)

Material examined. *Oedipoda formosana* Shiraki, neotype ♂, TAIWAN: Taikeizan, 25.viii.23, (*Shiraki*). Other material: 6 ♂, 4 ♀.

Oedaleus interruptus (Kirby)

Material examined. *Chortoicetes interruptus* Kirby, lectotype ♂, SOUTH AFRICA: Transvaal, Pretoria, (*Distant*). Other material: 11 ♂, 21 ♀.

Oedaleus instillatus Burr

Material examined. *Oedaleus instillatus* Burr, lectotype ♂, SOMALI

REPUBLIC: W Somaliland, 16.iv-7.viii.1895, (Peel) (UM, Oxford). Other material: 247 ♂, 221 ♀, 1 nymph.

Oedaleus obtusangulus Uvarov

Material examined. Oedaleus obtusangulus Uvarov, holotype ♀, SAUDI ARABIA: Buraiman, 17.ii.29, (Philby). Oedaleus villiersi Chopard, holotype ♀, NIGER: Aïr, Tésuar, -.viii.47, (Chopard) (MNHN, Paris). Other material: 23 ♂, 14 ♀, 2 nymphs.

Oedaleus rosescens Uvarov

Material examined. Oedaleus rosescens Uvarov, holotype ♂, INDIA: Rajasthan, Nokh, 1.viii.37. Other material: 7 ♂, 8 ♀.

Oedaleus miniatus Uvarov

Material examined. Oedaleus miniatus Uvarov, holotype ♀, SOMALI REPUBLIC: Shimba Beris, Surud Range, 10° 54' N, 47° 12' E, 6750', 17.xii.29. Other material: 11 ♂, 6 ♀.

Oedaleus nadiae sp. n.

Material examined. Holotype ♂, SOMALI REPUBLIC: between Hargeisa and Mandera, 7.vi.55, (Uvarov). Other material: 7 ♂, 14 ♀, paratypes.

Oedaleus inornatus Schulthess-Schindler

The holotype of this species was not available for study. Other material: 28 ♂, 41 ♀.

Oedaleus flavus flavus (Linnaeus)

Material examined. Gryllus Locusta flavus Linnaeus, lectotype ♀, 'AFRICA': no further data, (ZIUU, Uppsala). Oedaleus nigrofasciatus var. citrinus Saussure, lectotype ♂, Cape of Good Hope, no further data, (MHN, Geneva). Other material: 41 ♂, 53 ♀.

Oedaleus flavus somaliensis (Sjöstedt)

Material examined. _Gastrimargus somaliensis_ Sjöstedt, holotype ♀, SOMALI REPUBLIC: Alessandro, Chismaio, -.-.28, (_Kinell_) (NR, Stockholm). Other material: 51 ♂, 37 ♀.

APPENDIX 2. TAXONOMY OF THE GENUS _GASTRIMARGUS_ SAUSSURE

Material Examined (primary types).

Gastrimargus africanus africanus (Saussure)

Material examined. _Gastrimargus marmoratus_ var. _africana_, lectotype ♂, SOUTH AFRICA: Cape of Good Hope, (MHN, Geneva). _Gastrimargus africanus_ var. _zebrata_, holotype ♀, TANZANIA: Mt Kilimanjaro (NR, Stockholm). _Gastrimargus africanus_ var. _orientalis_, holotype ♀, SRI LANKA: no further data, (MHN, Geneva). Other material: 32 ex., 500 ♂, 594 ♀, 4 nymphs.

Gastrimargus africanus madagascariensis Sjöstedt

Material examined. _Gastrimargus africanus_ var. _madagascariensis_, holotype ♀, MADAGASCAR: Tananarive, (NR, Stockholm). Other material: 30 ♂, 50 ♂.

Gastrimargus africanus sulphureus Bei-Bienko

Material examined. _Gastrimargus sulphureus_, holotype ♂, PAKISTAN: Baluchistan, Ziarat, 8000', 6.viii.29, (_Evans_) (ZI, Leningrad). Other material: 18 ♂, 15 ♀.

Gastrimargus africanus parvulus Sjöstedt

Material examined. _Gastrimargus parvulus_ Sjöstedt, holotype ♀, JAVA:

Mt Merbaboe, 1500 m, -.ix.16, (Roepke) (NHM, Maastricht). Gastrimargus pusillus Sjöstedt, holotype ♀, 'Ned. Oost Indie' [JAVA ?]: no data, (NHM, Maastricht). Other material: 52 ♂, 39 ♀, 1 nymph.

Gastrimargus nubilus Uvarov

Material examined. Gastrimargus nubilus Uvarov, holotype ♂, CHINA: Yunnan, Tacheng, 7300', 1.viii.22, (Gregory). Gastrimargus africanus chinensis Willemse, lectotype ♂, CHINA: Szechwan, Dsachi Bezirk, Tatsienlu, 7.viii.30, (Friedrich) (DEI, Eberswalde). Other material: 22 ♂, 38 ♀.

Gastrimargus lombokensis Sjöstedt

Material examined. Gastrimargus lombokensis Sjöstedt, holotype ♀, LOMBOK I: Sambalun, 4000', -.iv.1896, (Fruhstorfer) (MNHU, Berlin). Other material: 33 ♂, 39 ♀.

Gastrimargus subfasciatus (de Haan)

Material examined. Acridium (Oedipoda) subfasciatum de Haan, lectotype ♂, TIMOR: 'Poeloe Samoe' [Semau I], (Muller) (RNH, Leiden). Other material: 10 ♂, 33 ♀.

Gastrimargus musicus (Fabricius)

Material examined. Gryllus musicus Fabricius, holotype ♀, AUSTRALIA: no further data, (BMNH, London). Gastrimargus musicus var. kimberleyensis Sjöstedt, holotype ♂, AUSTRALIA: Kimberley distr., (Mjöberg) (NR, Stockholm). Other material: 80 ♂, 80 ♀, 8 nymphs.

Gastrimargus marmoratus (Thunberg)

Material examined. Gryllus marmoratus Thunberg, lectotype ♀, Locality unknown [incorrectly labelled 'Cap.'] (ZIUU, Uppsala).

Gryllus transversus Thunberg, lectotype ♀, CHINA: no locality data, (ZIUU, Uppsala). _Gryllus virescens_ Thunberg, holotype ♂, locality unknown (ZIUU, Uppsala). _Gryllus assimilis_ Thunberg, holotype ♂, locality unknown, (ZIUU, Uppsala). _Oedaleus_ (_Gastrimargus_) _marmoratus_ stirps _sundaicus_ Saussure, lectotype ♀, SUMATRA: no locality data, (MHN, Geneva). _Oedaleus_ (_Gastrimargus_) _marmoratus_ var. _grandis_ Saussure, holotype ♀, CHINA: Kiang-si (NR, Stockholm). Other material: 288 ♂, 269 ♀, 12 nymphs.

Gastrimargus immaculatus (Chopard)

Material examined. Oedaleus immaculatus, holotype ♂, LA REUNION: Plaine des Cafres, 29.i.55, (MNHN, Paris). Other material: 23 ♂, 20 ♀.

Gastrimargus hyla Sjöstedt

Material examined. _Gastrimargus hyla_ Sjöstedt, holotype ♀, ETHIOPIA: no locality data, 1897-98, (_Michel_) (MNHN, Paris). _Gastrimargus abessinicus_ Sjöstedt, holotype ♀, ETHIOPIA: no locality data, 1897-98, (_Michel & Potter_) (MNHN, Paris). Other material: 1 ♂, 1 ♀.

Gastrimargus rothschildi Bolivar

Material examined. _Gastrimargus rothschildi_ Bolivar, holotype ♀, ETHIOPIA: Kounhi, -.iv.05, (_Rothschild_) (MNHN, Paris). _Gastrimargus cristagalli_ Sjöstedt, holotype ♀, ETHIOPIA: no data, (_Bowring_), 'one of Walker's series of _Pachytylus determinatus_', (BMNH, London). _Gastrimargus rothschildi montanus_ Uvarov, holotype ♂, ETHIOPIA: Mt Chillálo, c 10000', 22.xi.26, (_Scott_) (BMNH, London). Other material: 95 ♂, 37 ♀, 22 nymphs.

Gastrimargus verticalis verticalis (Saussure)

Material examined: Oedaleus (Gastrimargus) verticalis Saussure, lectotype ♀, SOUTH AFRICA: Natal, no further data, (MHN, Geneva). Gastrimargus longipes Sjöstedt, holotype ♀, SOUTH AFRICA: Natal, Appelbosch, -.iv.-, (Ljungqvist) (NR, Stockholm). Gastrimargus longipes var. recta Sjöstedt, holotype ♀, TANZANIA: Zanzibar, (Hildebrandt) (NR, Stockholm). Gastrimargus longipes var. decliva, holotype ♀, TANZANIA: Kitope, Dodoma, 6.iv.27, (Miller) (BMNH, London). Gastrimargus aethiopicus Bolivar, holotype ♀, ETHIOPIA: Kaussa, -.-.05, (de Rothschild) (MNHN, Paris). Gastrimargus brevipes Sjöstedt, holotype ♀, TANZANIA: Kilimanjaro, 1.i.05-06, (Sjöstedt) (NR, Stockholm). Gastrimargus brevipes var. elgonensis Sjöstedt, holotype ♀, KENYA / UGANDA: Mt Elgon, 1700 m, -.vii.-, (Lovén) (NR, Stockholm). Other material: 354 ♂, 285 ♀, 3 nymphs.

Gastrimargus verticalis mpwapwae subsp. n.

Material examined. Holotype ♂, TANZANIA: Mpwapwa, Mt Wilkins, 6000', 1.xii.48, (Burtt) (BMNH, London). Other material: 3 ♂, 4♀, paratypes.

Gastrimargus miombo sp. n.

Material examined. Holotype ♂, ANGOLA: Palavange, 2.xi.30, (Green) (ANS, Philadelphia). Other material: 8 ♂, 8 ♀, paratypes.

Gastrimargus determinatus determinatus (Walker)

Material examined. Pachytylus determinatus Walker, lectotype ♀, SOUTH AFRICA: 'Cape of Good Hope' (BMNH, London). Other material: 1 ♂.

Gastrimargus determinatus procerus (Gerstäcker)

Material examined. Oedaleus (Humbella) procera Gerstäcker, neotype ♂, GHANA, Accra plain, Nungua, 2.xii.59, (Jago) (BMNH, London).

Gastrimargus volkensi var. nigericus Uvarov, holotype ♂, NIGERIA: Azare, -.vii.24, (Lloyd) (BMNH, London). Gastrimargus amplus, Sjöstedt, holotype ♀, SIERRA LEONE: no data, (NR, Stockholm). Gastrimargus silvicola Sjöstedt, holotype ♂, ZAIRE: Luluabourg (NR, Stockholm). Gastrimargus vittatus Sjöstedt, holotype ♂, ZAIRE: Boko district, (Laman) (NR, Stockholm). Gastrimargus foveolarum Sjöstedt, holotype ♀, CAMEROON: Satsche, 12-21.v.09, (Riggenbach) (MNHU, Berlin). Gastrimargus foveolarum var. immaculata Sjöstedt, holotype ♀, ZAIRE: Eala, 2.i.21, (Schouteden) (MRAC, Tervuren). Gastrimargus testaceus Sjöstedt, holotype ♂, CAMEROON: Mittel-Adamaoua, 300-500 m, m. ü. d. M, v. Garoua u. Rei Buba, n. Monti, -.x.12, (Houy) (MNHU, Berlin). Other material: 1 ex., 86 ♂, 86 ♀.

Gastrimargus determinatus vitripennis (Saussure)

Material examined. Oedaleus (Gastrimargus) vitripennis Saussure, holotype ♀, SOUTH AFRICA: Cape of Good Hope, (Delalande) (MHN, Geneva). Gastrimargus volkensi Sjöstedt, holotype ♀, TANZANIA: Meru (lowland), Ngare na Nyuki, -.i.-, (Sjöstedt) (NR, Stockholm). Gastrimargus fallax Sjöstedt, holotype ♀, TANZANIA, no data, (MNHU, Berlin). Gastrimargus femoralis Sjöstedt, holotype ♀, SOUTH AFRICA: [Transvaal, Pretoria], Masil nek, (Distant) (BMNH, London). Other material: 119 ♂, 132 ♀, 3 nymphs.

Gastrimargus determinatus arabicus Uvarov

The holotype of this subspecies was not studied. Other material: 12 ♂, 13 ♀, 9 nymphs.

Gastrimargus crassicollis (Saussure)

Material examined. Oedaleus (Gastrimargus) crassicollis Saussure, holotype ♀, SOUTH AFRICA: Cape of Good Hope, no further data, (MHN, Geneva). Gastrimargus transvaalensis Sjöstedt, holotype ♀, SOUTH AFRICA: Transvaal, -.-.02, (Bel) (MNHN, Paris). Gastrimargus clepsydrae Sjöstedt, holotype ♀, SOUTH AFRICA: Transvaal, Johannesburg, 4.x.02, (Willvend) (ZM, Hamburg). Gastrimargus crassipes Sjöstedt, holotype ♀, SOUTH AFRICA: Grahamstown, -.i.1891, (Schömand) (MNHU, Berlin). Gastrimargus grossiceps Sjöstedt, holotype ♀, 'SUMATRA: Solok, (Stole)' [incorrect locality data], (NR, Stockholm). Other material: 63 ♂, 52 ♀.

Gastrimargus drakensbergensis sp. n.

Material examined. Holotype ♂, SOUTH AFRICA: Drakensberg Mts, Giant's Castle, -.-.57, (Jago) (BMNH, London). Other material: 14 ♂, 12 ♀, paratypes.

Gastrimargus obscurus sp. n.

Material examined. Holotype ♂, Angola: Bihé Distr., Chitau, 4900', 13.1.31, (R & L Boulton) (ANS, Philadelphia). Other material: 2 ♀, paratypes.

Gastrimargus wahlbergii (Stål)

Material examined: Gastrimargus wahlbergii Stål, holotype ♀, SOUTH AFRICA: Caffraria, (NR, Stockholm). Other material: 2 ♂, 4 ♀.

Gastrimargus angolensis Sjöstedt

Material examined: Gastrimargus angolensis Sjöstedt, holotype ♀, ANGOLA: Huila - Humpata, (Nonfried) (MNHU, Berlin). Gastrimargus corallipes Sjöstedt, holotype ♀, ZAIRE: Kwango, Atene, (Charlier) (MRAC, Tervuren). Other material: 14 ♂, 20 ♀.

Gastrimargus mirabilis Uvarov

Material examined. Gastrimargus mirabilis, holotype ♀, UGANDA: Entebbe, 26–29.vi.12, (Gowdey) (BMNH, London). Other material: 71♂, 47♀, 7 nymphs.

Gastrimargus insolens sp. n.

Material examined. Holotype ♀, ANGOLA: Sá da Bandeira, Huila distr., 12–14.iv.71, (Brown) (DATS, Pretoria). Other material: none.

Gastrimargus acutangulus acutangulus (Stål)

Material examined. Pachytylus acutangulus Stål, holotype ♀, SOUTH AFRICA: 'Caffraria', (Wahlberg) (NR, Stockholm). Other material: 13 ♂, 11 ♀.

Gastrimargus acutangulus flavipes Johnston

Material examined. Gastrimargus acutangulus flavipes Johnston, holotype ♀, KENYA: Mt Kenya, grassy places in forest, 8700–9800', –.v.35, (Hancock) (BMNH, London). Other material: 7 ♂, 8 ♀, 1 nymph.

Gastrimargus ochraceus Sjöstedt

Material examined. Gastrimargus ochraceus Sjöstedt, holotype ♀, GHANA: N Territories, Sankwalla, 4–7.xi.15, (Simpson) (BMNH, London). Other material: 3 ♂, 2 ♀, 1 nymph.

Gastrimargus willemsei sp. n.

Material examined. Holotype ♂, NEW GUINEA: L. Habbema, 3250–3300 m, 3.viii.38, (Toxopeus) (NM, Maastricht). Other material: 8 ♂, 9♀, paratypes.

Gastrimargus sarasini (Saussure)

Material examined. Oedaleus (Gastrimargus) sarasini Saussure, lectotype ♀, NEW CALEDONIA: no locality data, (Deyrolle) (NR, Stockholm). Other material: 63 ♂, 28 ♀, 3 nymphs.