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Editor

Dr F.W. GESS: 1978 –

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GENERA

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SPECIES

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ventermaculus (*Enneapterygius*) Holleman, 1982 123

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Systematic papers should follow the rules of the *International code of zoological nomenclature* or the *International code of botanical nomenclature*, as applicable.

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JUBB, R. A. 1967. *Freshwater fishes of southern Africa*. Cape Town: Balkema.

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VOLUME 14 • PART 1

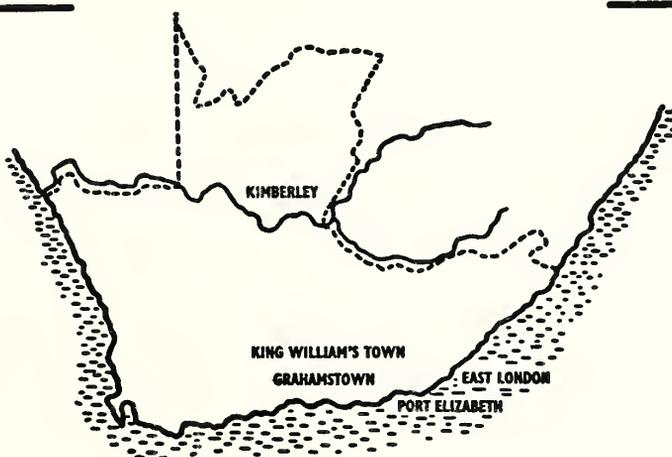
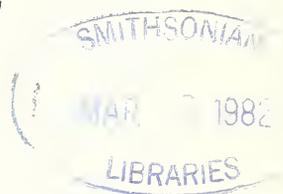
20th OCTOBER 1981

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Some aspects of an ethological study of the aculeate wasps and the bees of a karroid area in the vicinity of Grahamstown, South Africa

by

F. W. GESS

(Albany Museum, Grahamstown)

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ABSTRACT

The present paper is based upon a survey of the aculeate wasps and the bees of a karroid area in the Eastern Cape Province of South Africa. The location, topography, geology, climate and vegetation of the study area are outlined. An annotated list of 241 species arranged on the basis of their ethology is given.

There follows a discussion of the nesting behaviour of the community as a whole showing how the diversity of the ethology of such a large number of sympatric species results in their ecological displacement and giving some indication of the phylogenetic pattern leading to this diversity.

From a dissertation approved for the degree of Doctor of Philosophy, Rhodes University.

INTRODUCTION

During the eleven year period 1970–1980, the aculeate Hymenoptera occurring at Hilton, a farm situated near Grahamstown, South Africa, were the subjects of extensive study by the author and his wife and frequent co-author, S. K. Gess.

The choice of Hilton for the study followed the sampling of insect populations in areas of various differing vegetation types in the vicinity of Grahamstown. From this survey it was concluded that a karroid area showed the greatest promise with respect to potentially interesting species.

Fieldwork at Hilton embraced the formation of extensive collections in the form of frequent samples taken of the populations associated with various ecological situations. Methods of sampling, besides the use of hand nets, included the use of Malaise traps and trap-nests. Concomitant with the sampling of the populations, field studies of the nesting of many individual species belonging to a range of families of both wasps and bees were pursued. An outcome of this work was the publication between 1974 and 1980 of a number of papers dealing with the ethology of certain species of solitary wasps (Gess, 1978, 1980a and 1980b; Gess and Gess, 1974, 1975, 1976a, 1976b, 1980a, 1980b, 1980c and 1980d). Further publications of a similar nature are in preparation.

Among the species already reported upon in the above listed publications are two species of *Dichragenia*, *D. pulchricoma* (Arnold) and *D. neavei* (Kohl) which are of particular interest as, in the Pompilidae, they bridge the gap between fossorial nesters and mud-using aerial nesters. Similarly, in two species of *Bembecinus*, *B. cinguliger* (Smith) and *B. oxydorcus* (Handlirsch), the use of water in the excavation of the nest and the construction of a mud entrance turret appears to represent a nest type previously unknown in the Sphecidae. *Parachilus insignis* (Saussure) is shown to sub-divide the cell into an egg compartment and a pantry compartment in which way it differs in behaviour from other species of Eumenidae. The ethological account of the three species of *Ceramius* (Masaridae) clarifies some uncertainties and serious misconceptions, most notably showing that *C. lichtensteinii* (Klug) is a mass provisioner and not as was previously believed a progressive provisioner. The accounts of the nesting of *Parachilus insignis* (Saussure) (Eumenidae), *Jugurtia confusa* Richards (Masaridae) and *Kohliella alaris* Brauns (Sphecidae) are the first for the three genera to which these species belong. That of *Holotachysphex turneri* (Arnold) (Sphecidae) greatly augments what little was previously known of the ethology of its genus. Of particular interest with respect to *Dasyproctus westermanni* (Dahlbom) (Sphecidae) is the orientation of the pupae which appears to be governed by gravity rather than by the position of the nest entrance which is usually the rule. For the genus *Cerceris* (Sphecidae) twelve new prey associations give weight to the author's hypothesis that *Cerceris* is an Old World genus, that its original prey was hymenopterous and that the taking of Coleoptera is derived.

The present paper represents the hitherto unpublished portion of a dissertation submitted to Rhodes University and approved for the degree of Doctor of Philosophy. Other than in the omission of the above listed previously published papers as well as three further papers of a supporting nature (all bound into the dissertation) the present paper deviates from the dissertation only in the following respects: in the substitution of an abstract for the original summary; in the present expanded introduction; in the modified list of references (omitting references listed in and pertaining to the published papers); in the omission of an appendix listing plant species characterizing the vegetation communities of Hilton.

The study is the first attempt in southern Africa to consider an entire community of aculeate wasps and bees and their interactions with their environment as manifested by their ethology. As far as the author has been able to ascertain it is in fact the most comprehensive of its kind to have been undertaken anywhere. The only comparable account, that of Evans (1970),

is more restricted in its scope as it is mainly concerned with fossorial species and their associates. It moreover deals with a fauna already fairly well known whereas the present study deals with a fauna which is largely unstudied ethologically. By its nature, the present paper serves also to place in correct context within the community of which they are members those species concerning which ethological studies have already been published and provides a matrix within which the subjects of further, yet to be published, ethological studies may be fitted.

All the material, including voucher specimens, amassed during the course of the study is housed in the collection of the Albany Museum, Grahamstown, in which institution are deposited also all relevant fieldnotes.

ASPECTS OF THE ECOLOGY OF THE STUDY AREA

Location and topography

The farm Hilton, the site of the present study, is situated 18 kilometres WNW of Grahams-town (33° 19'S., 26° 32'E.) in the Albany Division of the Eastern Cape Province of South Africa very close to the midpoint of a straight line connecting the village of Riebeeck East and Grahamstown (Figs 1 and 2).

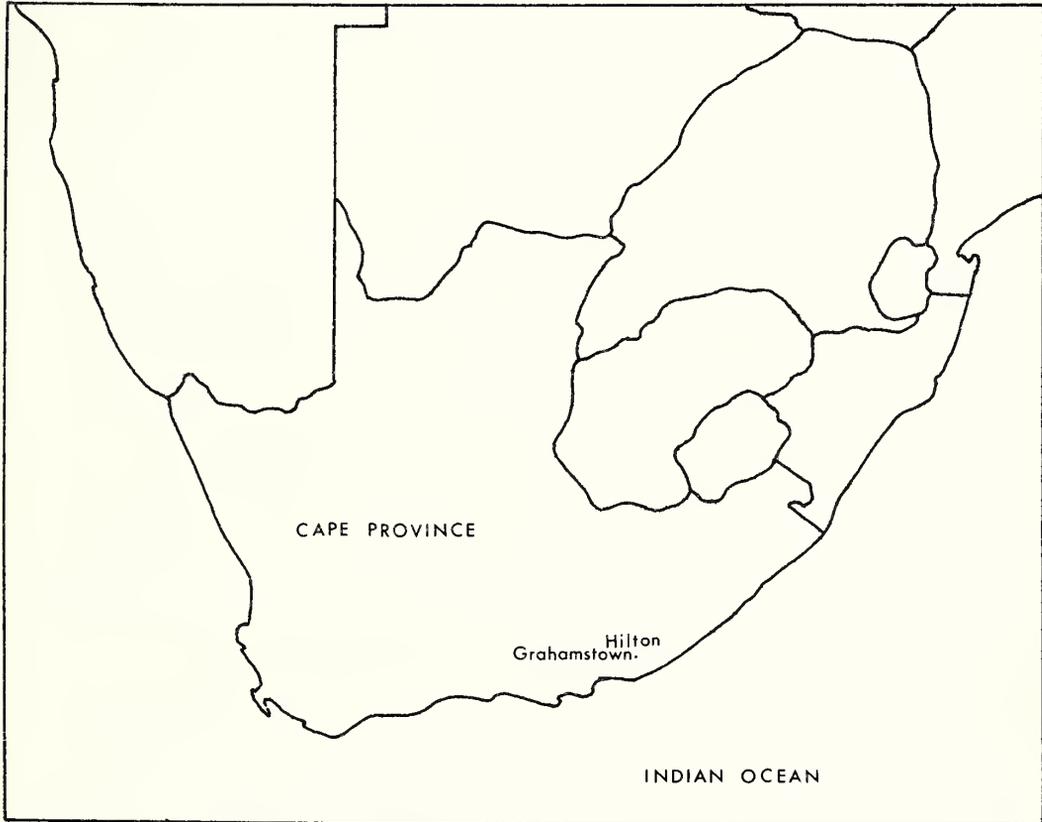


Fig. 1. Map of southern Africa showing position of study area.

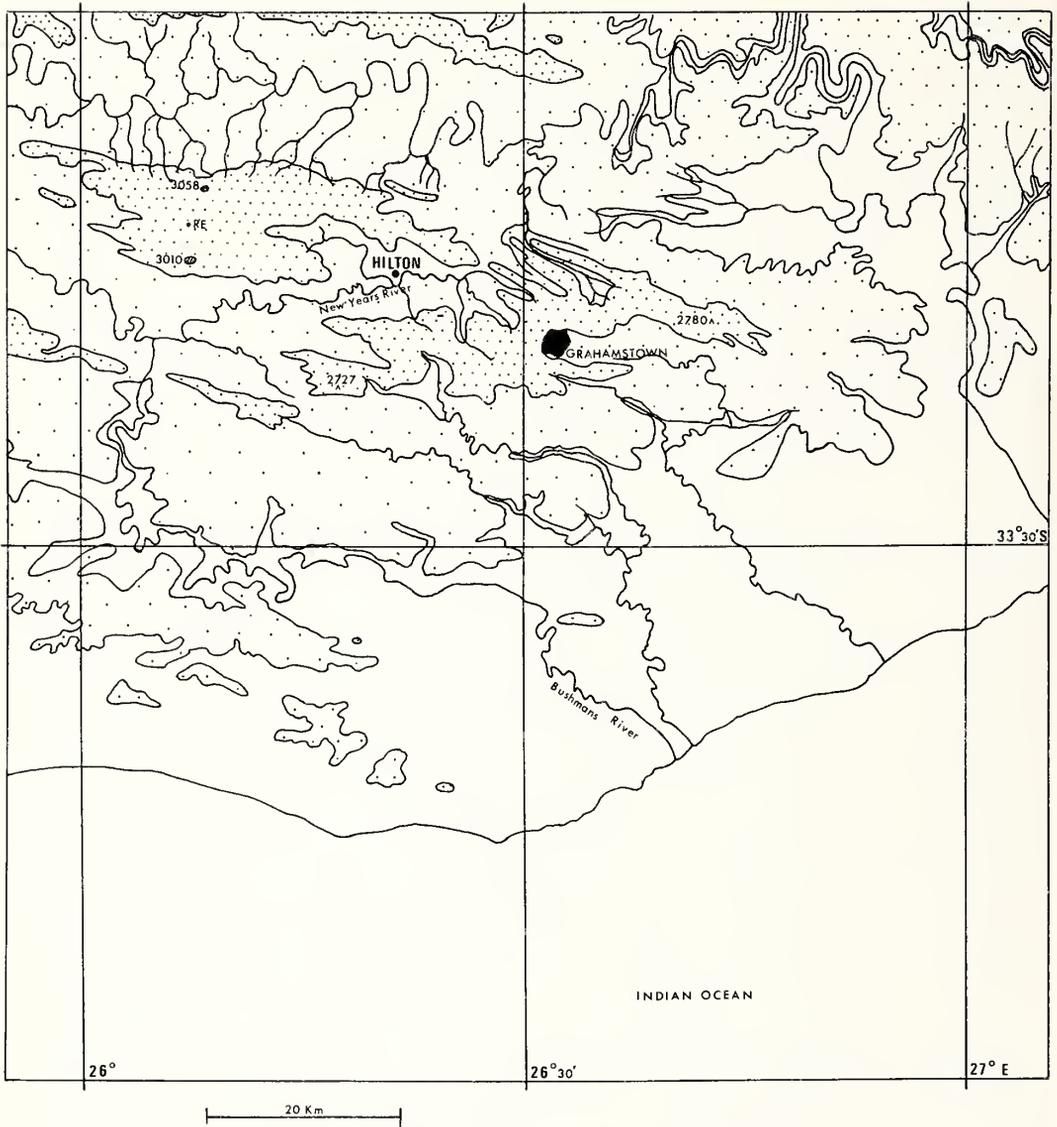


Fig. 2. Topographical map showing position of study area.

Situated on the course of the New Year's River, Hilton at a minimum altitude of 1 550–1 650 feet (472–503 m) above sea level occupies low-lying land more or less surrounded by rising ground forming the lower slopes of a series of sub-parallel mountain ranges running roughly ESE. Within a radius of 25 kilometres of Hilton these ranges consist of an unnamed range passing through the trigonometrical point Grootfontein at 3 058 feet (932 m) just to the

north of Riebeeck East; another range, the Swartwatersberg, just south of Riebeeck East which rises to a height of 3 010 feet (917 m) at the beacon Riebeeck; a third which passes just south of Grahamstown and which, near Highlands at a point roughly 13 kilometres SSW of Hilton, attains 2 727 feet (831 m) and finally Botha's Hill ridge to the north of Grahamstown which rises to 2 780 feet (847 m) at Driver's Hill. South of the range through Highlands the topography consists of a series of dissected peneplains gradually dropping in elevation southwards towards the coast, 58 kilometres due S of Hilton. As will be shown below, the climate of Hilton and especially the rainfall is influenced to a marked extent by the surrounding topography, the ranges immediately to the south being of particular importance.

At Hilton itself the altitude of the study area varies from a minimum of just less than 1 550 feet (472 m) in the river bed at the foot of the cliff to the west to a maximum of about 1 850 feet (564 m) on the slopes of the E-W ridge to the south. Most of the study area, however, is situated at an altitude of between 1 550 and 1 650 feet (472 and 503 m) (Fig. 3.)

The New Year's River which rises just north of Grahamstown enters the study area from the north-east and after a markedly meandering course across the low-lying flat area of Hilton leaves the study area in the south-west shortly before winding through precipitous gorges on its way to Alicedale where it joins the Bushman's River. Along its course through Hilton the river is impounded at two points by stone weirs with the result that upstream from these weirs water is present at all seasons in two reaches of considerable length (1 300–1 500 m). Below the weirs the river breaks up into isolated pools during the dry seasons. Several small seasonal tributaries in wide shallow valleys join the New Year's River along its course through Hilton. Of particular importance with respect to the present study is a tributary, marked as the Iron Put River on the Geological Survey Cape Sheet No. 9, which enters the study area from the south-east, flows more or less parallel to the rising ground in the south and joins the river about 450 m upstream of the lower weir. Arising in the mountains (the third range listed above) and draining an area S to SE of Hilton in the vicinity of Atherstone, this tributary (the Iron Put R.) falls in altitude by 700 feet (213 m) over the distance of about 8 kilometres from its sources to its confluence with the New Year's River at the point indicated above. After an initial rapid rate of descent the rate decreases progressively and over the last 2½ kilometres before the confluence the fall is of the order of 90 feet (27 m). In the study area its course is over only very slightly sloping ground and is in the form of shallowly incised meanders cut into its flood plain. Frequently it is completely dry or at most holds a few pools but following heavy rain in its catchment area comes down in flood, overflowing its banks and spreading over its flood-plain. About 2 kilometres above its confluence with the New Year's River a dam across the course of this tributary provides water for a furrow running below the 1 600 foot contour across the central part of the study area.

Also in this part of the study area is a shallow earth dam fed after rain by run-off from slightly sloping ground to the east and partly by water overflowing from a break in the above furrow, the lower course of which passes immediately to the north of the dam. In both the dam and the furrow water is seasonal and temporary. Water generally flows in the furrow for some time after good rains have fallen in the catchment area but as the dry season advances the water shrinks to stagnant pools and then dries up completely.

Geology and soil types

Geologically Hilton is situated upon three conformable strata: from south to north these are the Lower Witteberg Quartzites, the Upper Witteberg Shales (both belonging to the Cape Supergroup) and Dwyka Tillite (the oldest stratum of the overlying Karroo Supergroup).

The contact between the strata of the Cape and the Karroo Supergroups is situated immediately outside the study area to the north more or less in line with the road to Riebeeck

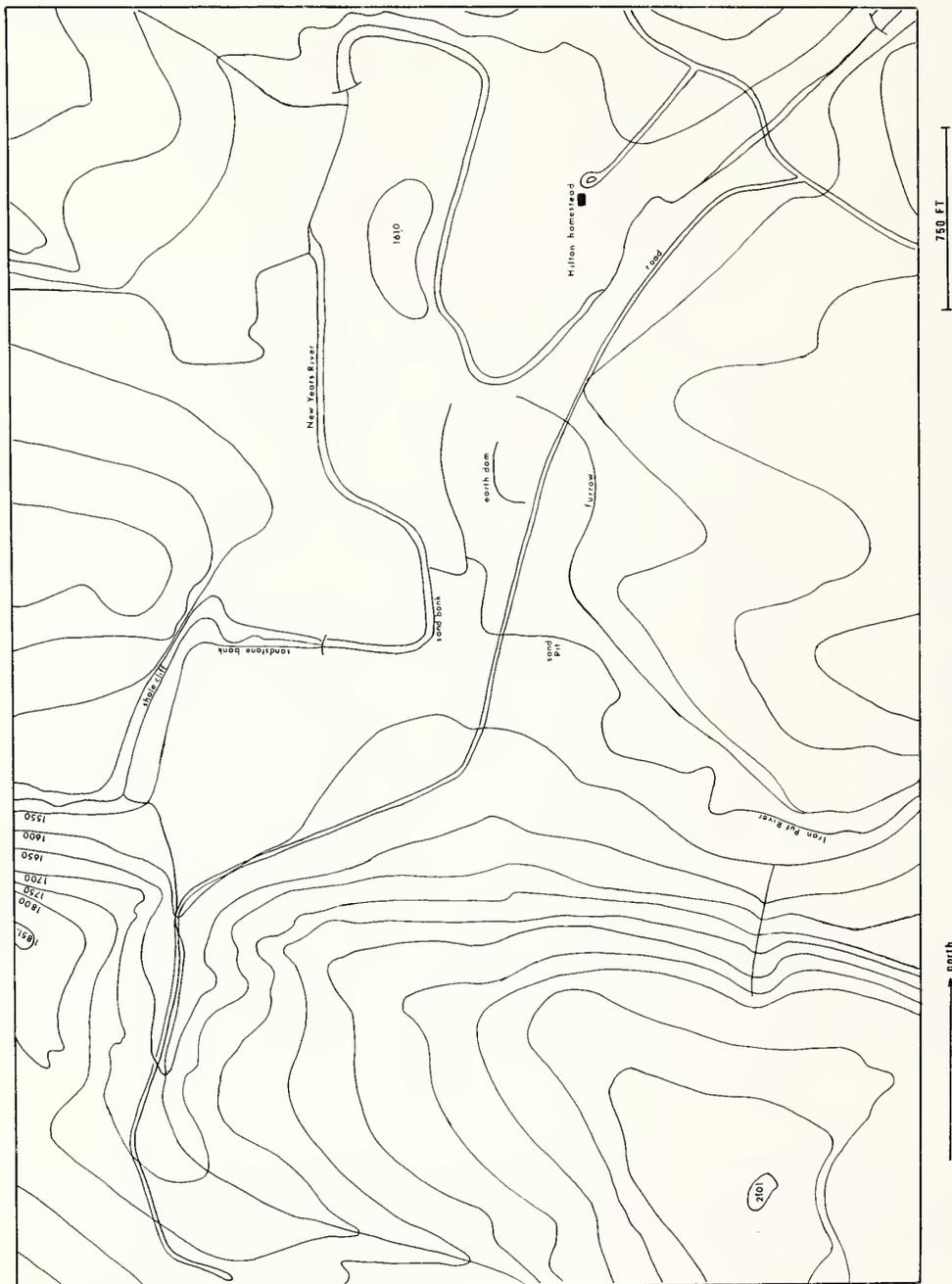


Fig. 3. Map of study area.

East where this passes the turn-off to the Hilton homestead. Strata within the study area are thus limited to the two Witteberg formations.

The pale grey Witteberg Quartzites form the ridge at the south of the study area and indeed are the materials of the entire series of previously listed sub-parallel mountain ranges of which the ridge is a part.

The rather dark coloured Witteberg Shales on the other hand form the lower-lying land between the ridge in the south and the Dwyka Tillite in the north. The cliff at the west of the study area is cut across this shale formation (Fig. 9) which is exposed also in the river bed below the lower weir and at a point where the farm road crosses the 1 600 foot contour on the rise north of the earth dam. On this rise are also found blocks of a dark sandstone derived from a band of this material in the shale.

Upon weathering the Witteberg Quartzites give rise to a light grey sandy soil whereas the Witteberg Shales (as also the Dwyka Tillite) give rise to brownish and reddish clayey soils.

As the entire study area, excepting the ridge in the south, is situated upon Witteberg Shales it follows that the reddish clayey soil derived from this formation is basically the dominant soil of the area. Whereas the clayey soil is somewhat thin in places on slopes such as those of the rising ground north-east and east of the earth dam where the bedrock may be barely covered, considerable thicknesses of this soil are present in lower-lying areas such as that below the 1 600 foot contour east of the earth dam (Fig. 6) At this juncture it may be noted that in describing the clayey soil of this particular locality within the study areas Gess and Gess (1974: 192 and 1975: 24) stated that it was derived from the Dwyka Series. This identification was consequent upon the use of the older geological classification which regarded the shales in question as belonging to the Lower Dwyka rather than to the Upper Witteberg.

In the southern half of the study area light coloured sandy soil occurs overlying the clayey soil and is in places intermixed with it. This sandy soil derived from the weathering of the Witteberg Quartzite has two separate origins. On the higher ground in the south of the study area the overlying sand is derived from the ridge and has been transported downhill by sheet erosion. In thickness this sand tails off downslope (i.e. northwards). On the lower ground below the 1 600 foot contour a wide band of similar sand but of alluvial origin has been deposited upon its flood plain by the tributary of the New Year's River previously referred to as the Iron Put River. Near the middle of the flood plain near the present incised course of the tributary the depth of alluvial sand is of the order of several feet, sufficiently deep for the establishment of a pit (Fig. 5) for the removal of building sand and for the excavation by aardvarks (*Orycteropus afer*) of their deep burrows.

Climate

The Albany Division, situated between the winter and summer rainfall regions, receives rain in moderate amounts throughout the year, the wettest periods being spring and autumn, the driest mid-winter.

The overall rainfall pattern for the region has been indicated by Dyer (1937: 33-34) who showed the marked effect of topography upon precipitation. That author showed that rain clouds from the coast on coming into contact with higher altitudes precipitate moisture either in the form of rain or mist but that they pass uninterruptedly over lower valley levels which are therefore drier. Specifically, regions of greater rainfall were shown to be the previously described series of sub-parallel ESE running mountain ranges and further north the Fish River Rand whereas the low, broad Fish River Valley, situated between these two belts of higher ground, was shown to be a region of low rainfall.

The distribution of rainfall at Hilton and its more immediate surroundings fits well into the overall pattern. This may be illustrated by means of average annual rainfall figures for several localities in the area concerned. At Clifton at 1 276 feet (389 m) above sea level on the

penepain near Seven Fountains, 22 km S of Hilton on the coastal side of the ESE ranges the average annual rainfall is 575 mm (22,6") (Weather Bureau, 1965). Proceeding northwards the rainfall figures rise with increasing altitude till the crest of the ESE range is reached where it is assumed the rainfall is highest. Unfortunately records for the crest are mostly unobtainable for, as Dyer (1937) has pointed out, homesteads, the site of most rainfall stations, are generally placed in more protected positions. Thus of four recording stations on the relevant part of the range only one, Faraway near Coldsprings, is on the crest whereas the other three are below the crest on the inland (drier) side.

Proceeding along the range from west to east, Atherstone at 2 263 feet (690 m) has an average annual rainfall of 573 mm (22,55") (Dyer, 1937); Slaaikraal at 1 949 feet (594 m) has 652 mm (25,7") (Weather Bureau, 1965); Faraway at slightly above 2 400 feet (732 m) has circa 864 mm (34") (pers. comm. C. F. Jacot Guillarmod, Oct., 1978), and Grahamstown at 1 768 feet (539 m) has 688 mm (27,1") (Weather Bureau, 1965).

The average annual rainfall figure for Hilton: circa 356 mm (14") (pers. comm. T. C. White, Febr., 1973) is in marked contrast to the above rainfall figures for localities on the ranges. The low rainfall at Hilton is clearly attributable to the nature of the topography for at 1 600 feet (488 m) the study area lies 700–1 100 feet (213–335 m) below the crests of the ESE ranges only 7–12 kilometres distant to the SW, S and SE and is therefore situated in a rain shadow area similar to that of the Fish River Valley to the north.

The low rainfall in the rain shadow at Hilton raises to considerable ecological importance the fact that the catchment areas of the water courses passing through the study area are in regions of greater rainfall on higher ground. The introduction of water from outside the rain shadow area results in the presence of semi-permanent to permanent water (apart from in-pounded water such as in the earth dam) even when the study area itself is very dry.

Vegetation

From a consideration of "Veld Types of South Africa" (Acocks, 1953) and the accompanying map the study area is seen to lie on the tongue of False Karroid Broken Veld which extends eastwards towards Grahamstown, principally along the valley of the New Year's River. As the land rises to the north and south there is a transition to Valley Bushveld merging into Eastern Province Thornveld in the south-east. False Macchia is present in the highest areas.

The study area is characterized by dwarf karroo scrub with, where sufficient water and bare earth are available, an addition of thorn scrub and along the river banks an admixture of small trees. The sandy foot of the E-W ridge in the south is characterized by grassveld which gives way to scattered succulents, notably *Aloe ferox*, and xerophytic bushes on the dry, rocky north-facing slope (Fig. 13). To the west of the study area the valleys become narrower and steeper and are characterized by Valley Bushveld which gives way as the land rises in the south-west to False Macchia. Further to the south-east and rising from the low-lying study area there is a transition to Eastern Province Thornveld.

The dwarf karroo scrub may be divided into three main communities. These are:

- (1) *Pentzia incana* Scrub which characterizes clayey soil which has not been disturbed by cultivation (Gess, 1980b: Fig. 1).
- (2) *Pentzia incana*—*Chrysocoma tenuifolia* Scrub which characterizes previously cultivated clayey soils in the area extending from above the furrow to the New Year's River below the earth dam (Fig. 6).
- (3) *Chrysocoma tenuifolia* Scrub which characterizes the previously cultivated sand flats of the flood plain of the Iron Put River and extends across to its confluence with the New Year's River (Fig. 5).

All three of these communities are subject to trampling and grazing by sheep and cattle.

The thorn scrub which is characterized by *Acacia karroo* occurs within the dwarf karroo scrub area in places where the soil has been exposed and where in addition the available amount of water in the soil is greater than elsewhere in the area (Fig. 12). Such sites are those where there is seepage from the furrow and earth dam and where the water run-off over eroded land causes the formation of temporary standing water in erosion gullies and low-lying areas.

The rivers represent older and more permanent water erosion gullies and their banks therefore support the same species as are present in the thorn scrub community except that the conditions being more favourable the vegetation no longer falls into the classification of scrub but rather of small trees (Fig. 8 and Gess and Gess, 1975: Plate 3).

Along the New Year's River where permanent and semi-permanent water bodies occur in natural pools and for considerable reaches above the two weirs the water is fringed by beds of *Phragmites australis*, "Common Reed" (Fig. 14). These reeds are also present in the earth dam immediately within the retaining wall (Fig. 15). Sedges which characterize marshy ground are present in clumps along the river banks, along the course of the furrow and fringe and earth dam (Gess and Gess, 1974: Plate 2).

Forage plants

A large number of flowering plants in the study area are visited by aculeate wasps and by bees of both sexes for the purpose of obtaining their own nutriment. Little specificity is shown, the requirement generally appearing to be the availability of nectar, short tubed or open flowers being favoured. Nearness to nesting sites is also of importance, suitable flowering plants growing at any considerable distance from nesting sites not being visited.

Particularly attractive to a large number of species are the flowers of *Maytenus linearis* (Celastraceae) and flowers and sticky young growth of *Acacia karroo* (Leguminosae). However, many species visiting these plants will also forage on low-growing plants, for example *Selago corymbosa* (Selaginaceae), *Melolobium candicans* (Leguminosae), *Senecio* spp. and *Lasiospermum bipinnatum* (both Compositae). Composites are often favoured at the beginning of the summer when *Acacia karroo* and *Maytenus linearis* are not yet in flower.

When plants are used as a source of provision for the young, or as a source of nesting materials, or their tissue is used as a substrate in which to excavate a nesting gallery more specificity is shown. These associations are given in the annotated list.

Seasonal cycles of wasps and bees

The majority of the aculeate wasps and the bees of the study area show marked seasons of activity and quiescence. In these species the period of quiescence extends from the end of the nesting season in the summer until the following spring or summer when activity recommences with the emergence of the adults from the nests in which they have remained in the pre-pupal or pupal stage throughout the cold, usually dry winter months. In most of these species there appears to be one generation per year but in some species such as *Ampulex* sp. near *cyanura* there may be two generations—a non-diapausing first generation and a diapausing second generation.

The minority of species such as the carpenter bees and the social wasps (Vespidae) which emerge as adults before the end of the summer overwinter as adults (both males and females in the bees, fertilized females in the vespids) and may show a certain limited activity on warm days during the winter months.

A CLASSIFICATION OF THE ACULEATE WASPS AND OF THE BEES OF THE STUDY AREA ON THE BASIS OF THEIR ETHOLOGY

The aculeate wasps and the bees collected in the study area are grouped on the basis of three ethological characters, situation of the nest (I, II, III, IV) subdivided into IN and ON

(A, B), nature of substrate (a, b, c) and degree of participation in construction of nest (i, ii, iii) (Fig. 4). This grouping results in the formation of twenty-seven categories numbered 1, 2, 3 . . . 27.

- | | |
|---|----|
| I. NESTING IN THE GROUND (Figs 5 and 6) | |
| (a) <i>In non-friable soils.</i> (Typically compacted clayey soils.) | |
| (i) In nest constructed entirely by the nester. | 1 |
| (ii) In pre-existing cavity modified by the nester. | 2 |
| (iii) In pre-existing cavity <i>not</i> modified by the nester. | 3 |
| (b) <i>In friable soils.</i> (Typically sandy soils, exceptionally disturbed and therefore non-compacted clayey soils.) | |
| (i) In nest constructed entirely by the nester. | 4 |
| (ii) In pre-existing cavity modified by the nester. | 5 |
| (iii) In pre-existing cavity <i>not</i> modified by the nester. | 6 |
| II. NESTING IN OR ON VERTICAL BANKS (Figs 7, 8 and 9) | |
| A. IN VERTICAL BANKS | |
| (i) In nest constructed entirely by the nester. | 7 |
| (ii) In pre-existing cavity modified by the nester. | 8 |
| (iii) In pre-existing cavity <i>not</i> modified by the nester. | 9 |
| B. ON VERTICAL BANKS | |
| (i) In nest constructed entirely by the nester. | 10 |
| (ii) In pre-existing cavity modified by the nester. | 11 |
| (iii) In pre-existing cavity <i>not</i> modified by the nester. | 12 |
| III. NESTING ON STONES (Figs 10 and 11) | |
| (i) In nest constructed entirely by the nester. | 13 |
| (ii) In pre-existing cavity modified by the nester. | 14 |
| (iii) In pre-existing cavity <i>not</i> modified by the nester. | 15 |
| IV. NESTING IN OR ON PLANTS (Figs 12, 13, 14 and 15) | |
| A. IN PLANTS | |
| (a) <i>Within woody stems.</i> | |
| (i) In nest constructed entirely by the nester. | 16 |
| (ii) In pre-existing cavity modified by the nester. | 17 |
| (iii) In pre-existing cavity <i>not</i> modified by the nester. | 18 |
| (b) <i>Within pithy stems.</i> | |
| (i) In nest constructed entirely by the nester. | 19 |
| (ii) In pre-existing cavity modified by the nester. | 20 |
| (iii) In pre-existing cavity <i>not</i> modified by the nester. | 21 |
| (c) <i>Within hollow stems.</i> | |
| (i) In nest constructed entirely by the nester. | 22 |
| (ii) In pre-existing cavity modified by the nester. | 23 |
| (iii) In pre-existing cavity <i>not</i> modified by the nester. | 24 |
| B. ON PLANTS (Irrespective of whether plants are woody, pithy or hollow-stemmed.) | |
| (i) In nest constructed entirely by the nester. | 25 |
| (ii) In pre-existing cavity modified by the nester. | 26 |
| (iii) In pre-existing cavity <i>not</i> modified by the nester. | 27 |

GESS: ASPECTS OF STUDY OF ACULEATE WASPS AND THE BEES

In the annotated list which follows those species for which nesting was definitely confirmed are listed with the symbol***.

Those species which were observed searching for nesting sites or transporting nesting materials or nest provision but for which no nests were discovered are listed with the symbol**.

The remaining species listed with the symbol* have been allocated on the basis of where they were collected in conjunction with morphological features and known biology of related species.

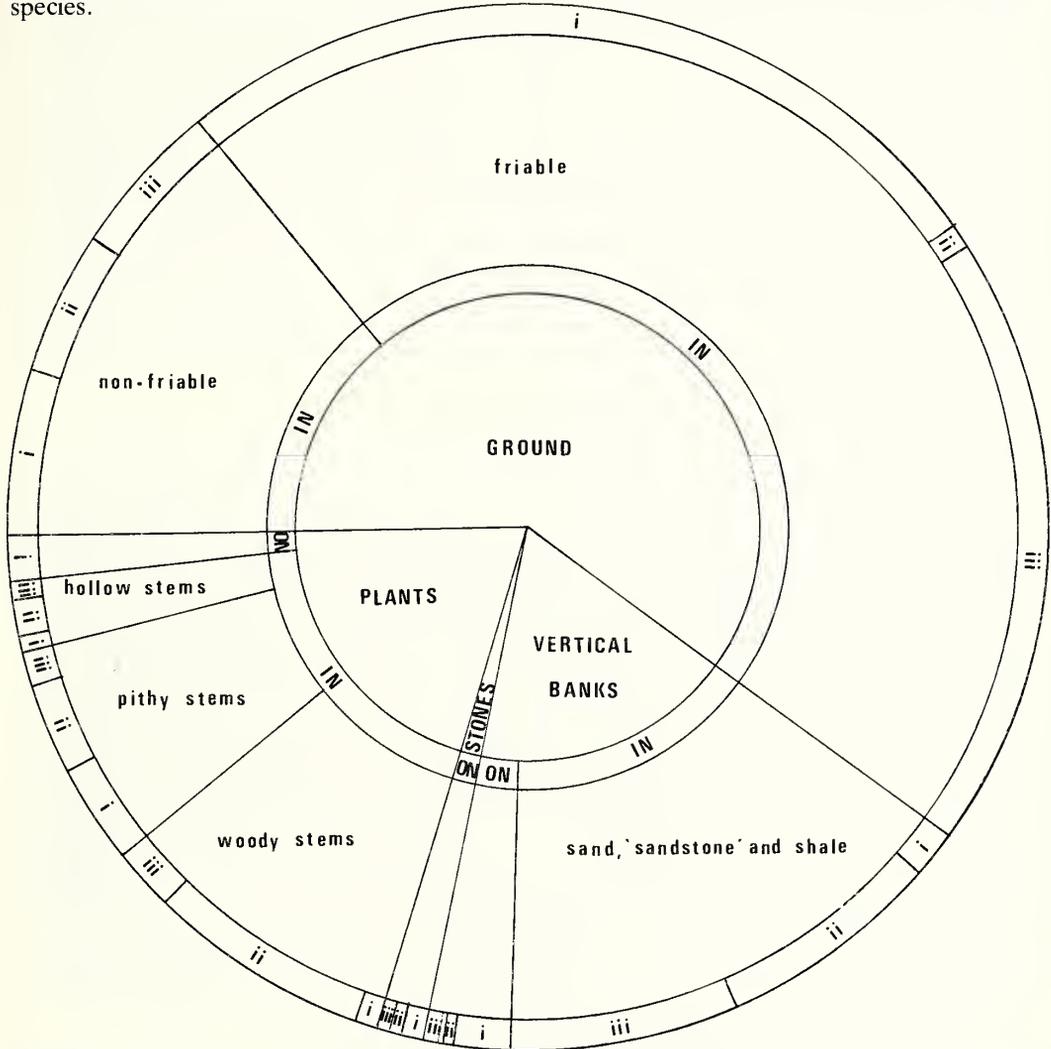


Fig. 4. Diagrammatic representation of the classification of the aculeate wasps and the bees of the study area on the basis of their ethology. The numbers (i, ii, iii) in the outermost ring correspond to the same numbers in the classification. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester. The magnitude of the segments is in proportion to the number of species involved.



Fig. 5. Area of friable soil: the sandpit

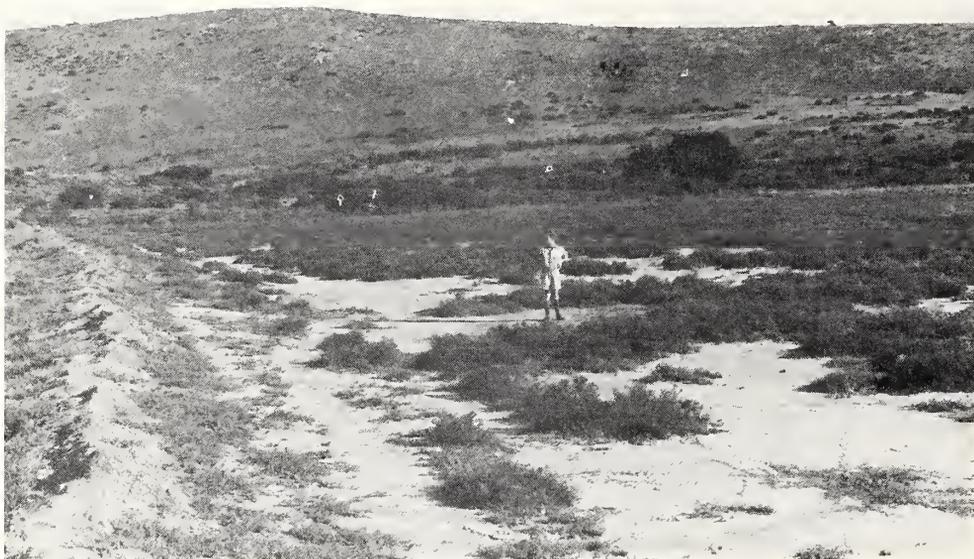


Fig. 6. Area of non-friable soil: below furrow.



Fig. 7

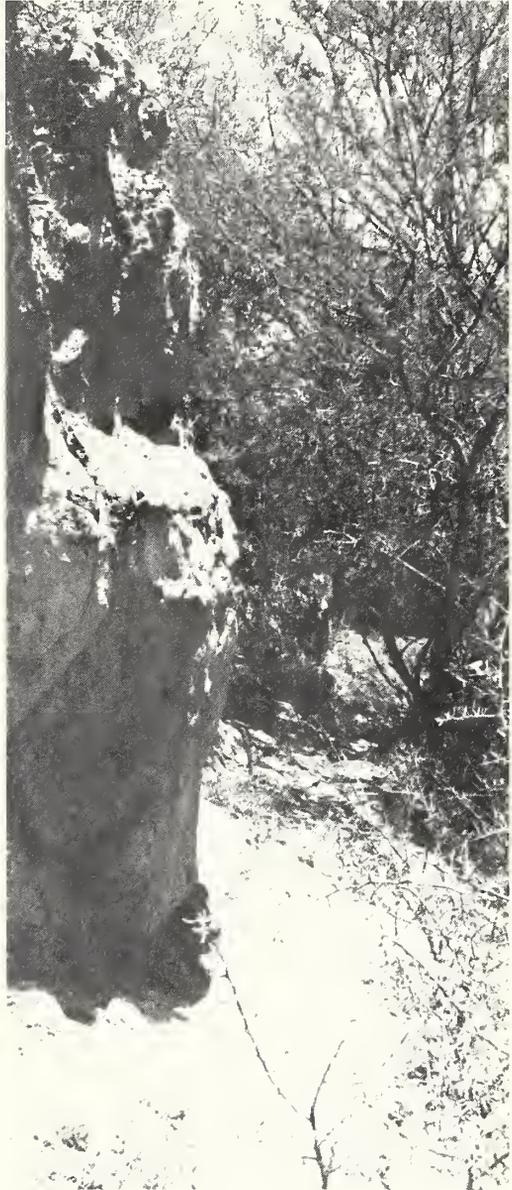


Fig. 8



Fig. 9

Figs 7, 8 and 9. Vertical banks along course of New Year's River: sand (Fig. 7), "sandstone" (Fig. 8) and shale (Fig. 9).



Fig. 10. Stone lying loose on ground and bearing nest of *Auplopus rossi*.



Fig. 11. Stone embedded in ground and bearing nest of *Hoplitus janset*.



Fig. 12. Woody stemmed plant: *Acacia karroo* on bank of watercourse.

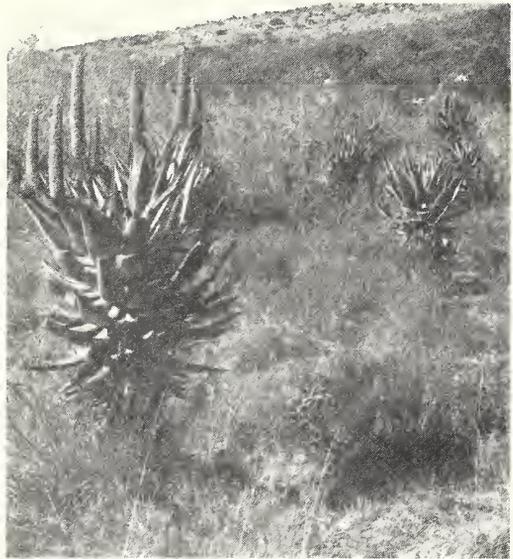


Fig. 13. Pithy stemmed plant: *Aloe ferox* on north-facing slope.



Fig. 14



Fig. 15

Figs 14 and 15. Hollow stemmed plant: *Phragmites australis* fringing New Year's River (Fig. 14), in earth dam (Fig. 15).

ANNOTATED LIST OF THE ACULEATE WASPS AND OF THE BEES OF THE STUDY AREA, ARRANGED ACCORDING TO THE CLASSIFICATION BASED ON THEIR ETHOLOGY.

Category 1.

I. NESTING IN THE GROUND

(a) *In non-friable soils.*

(i) In nest constructed entirely by the nester.

POMPILIDAE

- *** *Dichragena neavei* (Kohl). Uncommon. Nov.–Apr. Constructs turreted multicellular nest; each cell provisioned with a single lycosid or sparassid spider. Nesting described by Gess and Gess (1976b).
 *** *Dichragena pulchricoma* (Arnold). Common. Oct.–Apr. Constructs turreted multicellular nest; each cell provisioned with a single lycosid, pisaurid, sparassid or salticid spider. Nesting described by Gess and Gess (1974).

EUMENIDAE

- *** *Antepipona scutellaris* G. Soika. Common. Oct.–March. Constructs turreted one- or two-celled nest; each cell provisioned with about 12 small pyralidid caterpillars.
 *** *Parachilus insignis* (Saussure). Common. Oct.–Febr. Constructs one- or two-celled nest; each cell provisioned with 8–17 psychid caterpillars. Nesting described by Gess and Gess (1976a).
 *** *Parachilus capensis* (Saussure). Rare. Oct.–Jan. Constructs turreted one- or two-celled nest; each cell provisioned with about 11 psychid caterpillars.
 *** *Pseudepipona erythrospila* (Cameron). Rare. Oct.–March. Constructs collared one-celled nest; cell provisioned with pyralidid caterpillars.
 *** Eumenid sp. G. Rare. Jan. Constructs turreted one-(? or two-) celled nest; cell provisioned with chrysolidid larvae.
 *** Eumenid sp. (minute, black). Rare.

MASARIDAE

- *** *Ceramius capicola* Brauns. Common. Nov.–March. Constructs turreted multicellular nest; each cell provisioned with a mixture of pollen and nectar derived from Mesembryanthemaceae.
 *** *Ceramius lichtensteinii* (Klug). Common. Oct.–April. Constructs turreted multicellular nest; each cell provisioned with a mixture of pollen and nectar derived from Mesembryanthemaceae. Nests perennial.
 *** *Ceramius linearis* (Klug). Rare. Oct.–Jan. Constructs turreted multicellular nest; each cell provisioned with a mixture of pollen and nectar derived from Mesembryanthemaceae.
 * *Jugurtia braunsiella* (von Schulthess). Rare. Sept.–Dec.
 *** *Jugurtia confusa* (Richards). Common. Sept.–Febr. Constructs turreted multicellular nest; each cell provisioned with a mixture of pollen and nectar derived from Mesembryanthemaceae.

Nesting of above Masaridae described by Gess & Gess (1980c).

SPHECIDAE

- *** *Bembecinus cinguliger* (Smith). Very common. Nov.–March. Constructs turreted one- or two-celled nest; each cell provisioned with numerous Cicadellidae (and also Fulgoroidea). Nesting described by Gess & Gess (1975).
 *** *Bembecinus oxydorus* (Handlirsch). Common. Jan.–Apr. Constructs turreted one- or two-celled nest; each cell provisioned with numerous Cicadellidae. Nesting described by Gess & Gess (1975).

Category 2.

I. NESTING IN THE GROUND

(a) *In non-friable soils.*

(ii) In pre-existing cavity modified by the nester.

EUMENIDAE

- *** Eumenid sp. Very rare. March. One record. Curved, lacy turret constructed surmounting turret of empty burrow of *Bembecinus oxydorcus*. (Gess & Gess, 1975: 40).

SPHECIDAE

- * *Ampulex mutilloides* Kohl. Very rare. Jan. One record. Circumstantial evidence suggests that nesting may be in ground burrow of cockroach, *Pilema* sp.
- *** *Prionyx kirbii* (Van der Linden). Common. Nov.–May. Nesting in old or abandoned burrows of *Parachilus insignis* (Fig. 24). Single cell provisioned with 1–2 grasshoppers (Acrididae: *Acrotylus*, *Aiolopus*, *Anaeolopus*, *Calliptamulus* and other genera).
- * *Tachysphex modestus* Arnold. Rare. Dec.
- *** *Tachysphex* sp. near *modestus* Arnold. Rare. Dec.–Jan. Nesting in old or abandoned burrows of *Parachilus insignis* (Fig. 25). Single cell provisioned with 2 grasshoppers (Lentulidae).
- ** *Pison allonymum* Schultz. Rare. Oct.–May. Strong circumstantial evidence suggesting that nesting is in old or abandoned burrows of *Bembecinus cinguliger* and *B. oxydorcus*. Prey consists of small spiders (e.g. Salticidae). In Gess & Gess (1975: 40) incorrectly referred to as *Pison ?montanum* Cam.

MEGACHILIDAE

- ** *Megachile (Eutricharaea) alicae* Cockerell. Rare. Oct.–Dec. Nesting in old burrows of *Parachilus insignis*. Cells constructed of ?leaves. (Gess & Gess, 1976a: 98).
- *** *Megachile (Eutricharaea) meadewaldoi* Brauns. Uncommon. Sept.–March. Nesting in old or abandoned burrows of *Bembecinus oxydorcus*, *Parachilus insignis* and *Antepipona scutellaris*. Cells constructed of petals from low-growing flowers (*Oxalis* sp., *Wahlenbergia* sp.). (Gess & Gess, 1975: 40 and 1976a: 98).
- ** *Megachile (Eutricharaea) semiflava* Cockerell. Common. Sept.–March. Nesting in old or abandoned burrows of *Parachilus insignis*. Cells constructed of leaves. (Gess & Gess, 1976a: 98).
- *** *Megachile (Eutricharaea) stellarum* Cockerell. Common. Sept.–March. Nesting in old or abandoned burrows of *Dichragenia pulchricoma*, *Parachilus insignis* and *Ceramius lichtensteinii*. Cells constructed of leaves. (Gess & Gess, 1974: 204–206, Fig. 8; 1976a: 98; 1980c: 78).
- *** *Creightoniella dorsata* (Smith). Common. Nov.–March. Nesting in old or abandoned burrows of *Parachilus insignis*. Cells constructed of leaves. (Gess & Gess, 1976a: 98).

ANTHOPHORIDAE

- * *Tetralonia minuta* Friese. Uncommon. Nov.–Dec. Nesting in old or abandoned burrows of *Bembecinus cinguliger* and *Parachilus insignis*. (Gess & Gess, 1975: 40 and 1976a: 98). For account of nesting see also Rozen (1969a).

Category 3.

I. NESTING IN THE GROUND

(a) *In non-friable soils.*

(iii) *In pre-existing cavity not modified by the nester.*

CHRYSIDIDAE

- *** *Allocoelia bidens* Edney. Common. Nov. Parasitic in the nests of *Jugurtia confusa*. (Gess & Gess, 1980c: 76)
Allocoelia capensis Smith. Not yet recorded from Hilton but *highly likely* to occur there. Parasitic in the nests of *Ceramius lichtensteinii*. (Gess & Gess, 1980c: 76).
Allocoelia latinota Edney. Not yet recorded from Hilton but *highly likely* to occur there. Parasitic in the nests of *Ceramius capicola* and *Ceramius linearis*. (Gess & Gess, 1980c: 76).
*** *Octochrysis vansoni* (Brauns). Common. Nov.–Jan. Parasitic in the nests of *Parachilus insignis*. (Gess & Gess, 1976a: 97).
*** *Pseudospinolia ardens* (Mocsary). Uncommon. Nov.–Dec. Parasitic in the nests of *Parachilus insignis*. (Gess & Gess, 1976a: 97).

MUTILLIDAE

- * *Brachymutilla gynandromorpha* André. Rare. Oct. Found in nesting area of *Jugurtia confusa*.
* *Dasylabris stimulatix* (Smith). Rare. Nov.–Febr. Found in nesting areas of *Jugurtia confusa* and *Parachilus insignis*. (Also found in association with friable soils.)
*** *Dasylabroides caffra* (Kohl). Common. Oct.–May. Found in nesting areas of *Dichragenia pulchricoma*, *Parachilus insignis*, *Bembecinus oxydorcus*, *Jugurtia confusa* and *Ceramius lichtensteinii*. Reared from the cells of *C. lichtensteinii* in which parasitic. (Gess & Gess, 1980c: 76). (Rarely found in association with friable soils and vertical banks.)
* *Glossotilla specularix* (Smith). Rare. March. Found in nesting area of *Bembecinus oxydorcus*. (Very commonly found in association with friable soils.)
* *Mutilla scabrofoveolata* Sichel & Radoszkowski. Rare. Nov.–April. Found in nesting areas of *Dichragenia pulchricoma* and *Parachilus insignis*. (Also rarely found in association with vertical banks.)
* *Smicromyrme* sp. Rare. Found in nesting area of *Jugurtia confusa*.
* *Smicromyrme hecuba* (Péringuey). Common. Dec.–April. Found in nesting areas of *Parachilus insignis* and *Bembecinus cinguliger* and *B. oxydorcus*. Circumstantial evidence strongly indicates that parasitic in the nests of *Bembecinus* spp. (Common also in association with friable soils.)

POMPILIDAE

- *** *Ceropales punctulatus* Cameron. Rare. Nov.–March. Parasitic in the nests of *Dichragenia pulchricoma*. (Gess & Gess, 1974: 202, 204.)

MEGACHILIDAE

- ** *Coelioxys (Liothyrapis) lativentroides* Brauns. Rare. Dec. Circumstantial evidence very strongly indicates that this species is parasitic in the nests of Megachilidae (*Megachile* and *Creightoniella* spp.) nesting in old or abandoned burrows of *Parachilus insignis*.

Category 4.

I. NESTING IN THE GROUND

(b) *In friable soils.*

(i) In nest constructed entirely by the nester.

POMPILIDAE

- ** *Batozonellus fuliginosus sepulchralis* (Smith). Uncommon. Nov.–Apr. Observed searching for prey on *Acacia karroo* and dragging prey, *Caerostris* sp., across sandpit. Known to dig shallow, sloping one-celled nest and to provision cell with a single large argiopid spider. *Araneus* sp. or *Caerostris* sp. (Gess & Gess, 1980b).
- ** *Cyphononyx flavicornis antennatus* Smith. Common. Nov.–Mar. Observed dragging prey, *Palystes* sp. (Sparassidae) across ground.
- * *Tachypompilus ignitus* (Smith). Uncommon. Nov.–Febr. Known to dig nest in dry sand in sheltered situation and to provision cell with a single large sparassid spider, *Palystes natalius* Karsch (Gess & Gess, 1980b).

SPHECIDAE

- *** *Prionyx kirbii* (Van der Linden). Common. Nov.–May. In friable soils this species appears to dig its own nest. (In non-friable soils nests in old or abandoned burrows of *Parachilus insignis*.)
- *** *Podalonia canescens* (Dahlbom). Common. Aug.–May. Digs simple one-celled nest; cell provisioned with a single hairless caterpillar of the cutworm type (Noctuidae).
- *** *Ammophila beniniensis* (Palisot de Beauvois). Common. Oct.–Apr. Nesting in disturbed, loose and crumbly clayey soil.
- * *Ammophila bonaespei* Lepeletier. Rare. Dec., Mar. Known to provision with hairless caterpillars (Geometridae).
- * *Ammophila conifera* (Arnold). Uncommon. Nov.–Mar.
- *** *Ammophila ferrugineipes* Lepeletier. Very common. Oct.–May. Nesting in fine but consolidated sand. Digs a simple burrow terminating in single cell; cell provisioned with several hairless caterpillars (Geometridae) carried to nest in flight. Parasitized by Stylopidae (Strepsiptera).
- * *Ammophila insignis litoralis* (Arnold). Uncommon. Febr.–Apr.
- * *Ammophila vulcania* du Buysson. Rare. Nov. and Dec.
- * *Diodontus* sp. Rare. Oct. and Nov. Species of this genus are known to nest in soil and to provision with aphids. (Bohart & Menke, 1976: 178).
- *** *Astata fuscistigma* Cameron. Rare. Nov.–Apr. Nesting in compacted sand. *Astata* species are known to provision with bugs, especially Pentatomidae (Bohart & Menke, 1976: 211–212).
- * *Dryudella flavoundata* (Arnold). Rare. Dec. Prey known to be a “small heteropteran” (Arnold, 1924: 38).
- * *Liris* spp. (Some species may belong here, others may belong in category 2). Known to provision with crickets (Gryllidae).
- * *Tachytella aureopilosa* Brauns. Rare. Jan. Only species in genus; biology unknown. Presence in female of foretarsal rake and of pygidial plate indicative of sand-nesting. Provisioning likely to be with Orthoptera (*sensu lato*).
- * *Tachysphex aethiopicus* Arnold. Rare. Jan.
- *** *Tachysphex albocinctus* (Lucas). Common. Dec.–Mar. Digs simple one- or two-celled nest, each cell provisioned with 1–3 mantids (Mantidae), usually nymphs.
- *** *Tachysphex fugax* (Radoszkowski). Common. Sept.–May. Digs simple two-celled nest; each cell provisioned with several grasshoppers (Lentulidae), adults and nymphs.
- * *Tachysphex karroensis* Arnold. Uncommon. Dec.–Febr.

- *** *Tachysphex panzeri pentheri* Cameron. (= *caliban* Arnold). Common. Oct.–Mar. Digs simple two-celled nest; sealed cell examined contained two prey; grasshopper nymphs (Acrididae).
- * *Tachysphex schoenlandi* Cameron. Common. Dec.–Mar. Known to provision with nymphal mantids (Mantidae).
- * *Tachysphex sericeus* (Smith). Uncommon. Nov.–May.
- * *Parapiagetia vernalis* Brauns. Rare. Nov. Biology of genus largely unknown. Presence in female of foretarsal rake and of pygidial plate indicative of sand-nesting. Immature Acrydiidae recorded as prey of the Madagascan *P. longicornis* Arnold (Arnold, 1945: 94).
- *** *Kohliella alaris* Brauns. Common. Dec.–Mar. Digs shallow nest with one to several cells; each cell provisioned with several nymphs of the Tree Cricket, *Oecanthus capensis* Saussure (Gryllidae: Oecanthinae). Nesting described by Gess & Gess (1980a).
- *** *Palarus latifrons* Kohl. Common. Nov.–Mar. Unicellular nest dug in firm sand overlain by a layer of loose sand. Provisions with honey bees, *Apis mellifera* L. (Apidae). Brauns (1911: 117) in addition to honey bees recorded the following prey:
Mesa ♂ (cited as *Elis*) (Tiphidae), *Ceramius capicola* Brauns (Masaridae) and small bees. In South Africa known as the Banded Bee Pirate and is a nuisance to beekeepers (Mally, 1908: 206–213; Brain, 1929: 396; Taylor, 1939: 103; and Smit, 1964: 356).
- * *Palarus oneili* Brauns. Rare. Jan. and Febr. Prey known to include *Meria* ♀ (cited as *Myzine*) (Tiphidae) and small bees (Brauns, 1911: 117).
- * *Oxybelus acutissimus propinquus* Arnold. Rare. Nov.–Mar.
- * *Oxybelus aethiopicus* Cameron. Rare. Jan.
- * *Oxybelus imperialis* Gerstaecker. Rare. Nov.
- *** *Oxybelus lingula* Gerstaecker. Common. Nov.–Mar. Nesting in loose sand. Like all *Oxybelus* spp. provisions with adult Diptera. Prey recorded at Hilton: *Stomorhina lunata* (F.) (Calliphoridae) and *Musca* sp. (Muscidae). Other prey known for this species: *Sarcophaga* sp. (Calliphoridae).
- * *Oxybelus peringueyi* Saussure. Rare. Oct., Nov. and Mar.
- * *Oxybelus rubrocaudatus* Arnold. Uncommon. Oct.–Jan.
- * *Oxybelus ruficaudis* Cameron. Uncommon. Oct., Nov. and Jan.
- * *Dienoplus vicarius karrooensis* (Brauns). Uncommon. Nov.–Mar. Species of the genus are known to dig simple nests in sandy soil. There may be from 2–15 cells per nest; cells are provisioned with Cicadellidae and Cercopidae (Bohart & Menke, 1976: 495).
- * *Oryttus kraepelini* (Brauns). Uncommon. Dec. and Mar. The well developed foretarsal rake in the female is indicative of nesting in friable soil. Species of the genus are known to provision with Cicadellidae and Fulgoroidea (Bohart & Menke, 1976: 507).
- ** *Hoplisoides aglaia* (Handlirsch). Uncommon. Oct.–Mar. Associated with sandy soil. Provisions with Membracidae.
- * *Hoplisoides thalia* (Handlirsch). Uncommon. Dec., Jan. and Apr.
- * *Stizus imperialis* Handlirsch. Rare. Dec., Jan. *Stizus* species are known to provision mostly with grasshoppers.
- *** *Bembecinus braunsii* (Handlirsch). Very common. Oct.–Apr. Nesting in loose dry fine sand. Digs one- or two-celled nest; each cell provisioned with numerous Cicadellidae (incl. *Macropsis octopunctatus* China and *Macropsis chinai* Metcalf), exceptionally with one or two Fulgoroidea in addition.
- * *Bembecinus dentiventris* (Handlirsch). Very rare. Nov., Dec.
- *** *Bembecinus haemorrhoidalis* (Handlirsch). Very common. Oct.–Apr. Nesting in loose dry fine sand. Digs one- or two-celled nest; each cell provisioned with numerous Cicadellidae (incl. *Coloborrhis corticina* Germar, *Exitianus nanus* (Distant), *Macropsis octopunctata* China, *Macropsis chinai* Metcalf, *Macropsis* sp. nov., *Idioscopus* sp. and *Batracomorphus subolivaceus* (Stal)), exceptionally with one or two Fulgoroidea or Membracidae in addition.

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- *** *Bembix albofasciata* Smith. Common. Nov.–Febr. Digs a one-celled nest in sandy soil; cell provisioned progressively with adult Diptera belonging to the following families: Stratiomyidae, Tabanidae (*Chrysops obliquefasciata* Macq.), Bombyliidae (several spp., incl. *Lomatia pictipennis* Wied.), Asilidae (several spp. incl. *Stenopogon dilutus* Walker), Conopidae (*Conops* sp.), Muscidae (2 spp. incl. *Musca lusoria* Wied.), Calliphoridae (incl. *Sarcophaga* sp. and *Chrysomyia* sp.) and Tachinidae.
- * *Bembix cameroni* Handlirsch. Uncommon. Nov.–Jan.
- * *Bembix capensis* Lepeletier. Uncommon. Dec., Jan. Single prey obtained was an adult fly (Tachinidae).
- * *Bembix fuscipennis* Lepeletier. Rare. Mar.
- *** *Bembix melanopa* Handlirsch. Uncommon. Dec.–Febr. Both nests located were in steeply sloping firm and compacted sand. Known to provision with adult Diptera (incl. Muscidae).
- * *Bembix sibilans* Handlirsch. Uncommon. Nov.–Mar.
- * *Philanthus loefflingi* Dahlbom. Rare. Nov., Dec.
- *** *Philanthus triangulum* Fabricius. Uncommon. Oct.–Jan. Nesting in clayey yet friable soil. Provisioning with honey bees, *Apis mellifera* L. (Apidae) captured at their foraging flowers.
- *** *Cerceris* sp. A. Rare. Dec. Nest excavated in disturbed clayey soil. Shallow multicellular nest; each cell provisioned with numerous Pteromalidae.
- * *Cerceris amakosa* Brauns. Rare. Dec.–Mar. Associated with sandy soil.
- * *Cerceris armaticeps caffrariae* Empey. Very rare. Febr.
- * *Cerceris diodonta diodonta* Schletterer. Rare. Dec.
- * *Cerceris discrepans discrepans* Brauns. Very rare. Nov.
- * *Cerceris dominicana* Brauns. Very rare. Nov., Dec.
- * *Cerceris erythrosoma* Schletterer. Very rare. Dec. Associated with sandy soil. Known to provision with Curculionidae.
- *** *Cerceris holconota holconota* Cameron. Common. Nov.–Apr. Nesting in sandy soil; provisioning cells with Hymenoptera of various families (Braconidae, Bethyliidae, Tiphidae, Mutillidae, Formicidae and Halictidae).
- * *Cerceris hypocritica* Brauns. Rare. Dec.–Febr. Associated with sandy soil.
- *** *Cerceris languida languida* Cameron. Very common. Oct.–Apr. Nesting in sandy soil; provisioning cells with Phalacridae (*Olibrus* sp.).
- *** *Cerceris latifrons latifrons* Bingham. Very common. Nov.–Mar. Nesting in sandy soil in very deep nests; provisioning cells with Scarabaeidae (Melolonthinae: Hopliini).
- *** *Cerceris lunigera* Dahlbom. Uncommon. Dec.–Mar. Nest excavated in disturbed clayey soil; provisioning cells with Halictidae.
- * *Cerceris nasidens obscura* Schletterer. Uncommon. Nov., Dec., Mar. and Apr. Associated with sandy soil. Known to provision its cells with Scarabaeidae (Melolonthinae).
- * *Cerceris nigrifrons nigrifrons* Smith. Uncommon. Nov.–Febr. Associated with sandy soil. Known to provision its cells with Buprestidae (Brauns, 1926a: 320).
- *** *Cerceris oraniensis* Brauns. Uncommon. Dec.–Mar. Nesting in sandy soil in deep nests; provisioning with Curculionidae (*Protostrophus* sp.) (Fig. 17).
- * *Cerceris pearstonensis pearstonensis* Cameron. Common. Dec.–Apr. Nest excavated in disturbed clayey soil. Known to provision its cells with Curculionidae.
- * *Cerceris pictifacies* Brauns. Rare. Dec.
- *** *Cerceris ruficauda ruficauda* Cameron. Uncommon. Oct.–Apr. Nesting in disturbed clayey soil; provisioning with Chrysomelidae.
- *** *Cerceris rufocincta polychroma* Gribodo. Very common. Nov.–Apr. Nesting in sandy soil; provisioning with Tiphidae and Mutillidae.
- *** *Cerceris spinicaudata spinicaudata* Cameron. Common. Nov.–Mar. Nesting in sandy soil; provisioning with Halictidae.

Ethological notes concerning above *Cerceris* spp. given in Gess (1980a).

COLLETIDAE

- * *Colletes* sp. Uncommon.

HALICTIDAE

- * *Halictus* sp. A. Common. Oct.–Apr. Associated with sandy soils.
* *Halictus* sp. B. Common. Nov.–Mar. Associated with sandy soils.
* *Lasioglossum* spp. Uncommon. Associated with sandy soils.
*** *Nomiodes ?halictoides* Blüthgen. Common. Oct.–Mar. Nesting in sandy soil.
*** *Nomia* sp. Common. Nov.–Febr. Nesting in sandy soil.

Category 5.

I. NESTING IN THE GROUND

- (b) *In friable soils.*
(ii) In pre-existing cavity modified by the nester.
-

SPHECIDAE

- * *Liris* sp. Uncommon. May belong here or in category 4. Known to provision with crickets (*Gryllidae*).
*** *Megachile (Eutricharaea) semiflava* Cockerell. Common. Sept.–Mar. Frequently seen flying low over the ground in the sandpit carrying green leaf-discs; on several occasions seen to be nesting in holes on the floor of the sandpit. Identity of original excavator of holes not established.

Category 6.

I. NESTING IN THE GROUND

- (b) *In friable soils.*
(iii) In pre-existing cavity *not* modified by nester.
-

CHRYSIDIDAE

A total of seven species was recorded in association with sandy soils—in the sandpit. Of these, six species (*Chrysidea africana* Mocsary, *Hedychrum coelestinum* Spinola, *H. gonomaculatum* Edney, *Octochrysis laminata* (Mocsary), *O. mucronifera* (Mocsary) and *Pyriachrysis stilboides* (Spinola)) were rare and were mostly more commonly found associated with vertical banks.

One species, however, was both restricted to and common in the sandpit, namely:

Hedychrum sp. (near *comptum* Edney). Nov.–Mar. Associated with the nests of *Bembecinus braunsii* and *B. haemorrhoidalis* and believed to be parasitic in them.

TIPHIIDAE

A total of seventeen species was recorded in areas of friable, mostly sandy soil in and around the sandpit. Sixteen of these species (*Anthobosca* sp., *Meria* spp. (10), *Mesa* spp. (2) and *Tiphia* spp. (3)) are believed to be predaceous upon soil-inhabiting larvae of Scarabaeidae. The remaining species was:

Methocha mosutoana Péringuey. Rare. Jan. *Methocha* spp. are known to be predaceous upon the burrow-inhabiting larvae of tiger-beetles (*Cicindelidae*). The prey of the present species is certain to be *Cicindela brevicollis* Wied., adults of which are present in very large numbers in the sandpit throughout the summer months and well into the autumn or even early winter.

MUTILLIDAE

Fourteen species of Mutillidae were collected in association with the friable sandy soil of the sandpit. The most common species by far was *Glossotilla specularix* (Smith) (46 females and 67 males collected) followed by *Smicromyrme hecuba* (Péringuey) (29 females and 11 males collected), *Mimecomutilla renominanda* Bischoff, *Dasylabris* sp. nr. *danae* (Péringuey) and *Dasylabris mephiitis* (Smith). Also recorded but uncommon were *Antennotilla phoebe* (Péringuey), *Dasylabris* sp. nr. *bassutorum* (André), *Dasylabris* sp. nr. *cryentocincta* André, *Dasylabris stimulatix* (Smith), *Dasylabris thais* (Péringuey), *Dasylabroides caffra* (Kohl), *Labidomuilla tauriceps* (Kohl), *Psammotherma flabellata* (Fabricius) and *Viereckia* sp.

With the exception of *Dasylabroides caffra* which is a species characteristic of clayey rather than sandy areas and *Smicromyrme hecuba* which is common in both sandy and clayey areas, all the above listed species, with the exception of *Antennotilla phoebe*, were more common in the sandy areas than elsewhere and many appeared restricted to such areas.

Glossotilla specularix is highly characteristic of the sandy areas and in contrast to the larger numbers caught in the sandpit only two specimens were collected in bare patches in clayey areas. Though not reared from any nests circumstantial evidence indicates that the species is parasitic in the nests of *Bembecinus* species though other species nesting in the same situations are doubtless also parasitized. Its flight period is from December to April.

Smicromyrme hecuba appears like *Glossotilla specularix* to be associated with *Bembecinus* species and the two species of mutillid are usually found together within the areas occupied by *Bembecinus* pseudocolonies in the sandpit. Its flight period is similarly from December to April.

SCOLIIDAE

Eleven species of Scoliidae, believed to be associated with friable soils, were collected, many on flowers. By far the most common species was *Cathimeris capensis* (Saussure) (28 males and 13 females collected) which was present in the sandpit from September to May. Less common or rare were *Campsomeriella* sp., *Micromeriella* spp. (2), and *Scolia* spp. (7). All are believed to be pre-*daceous* upon soil-inhabiting larvae of Scarabaeidae.

SPHECIDAE

- * *Nysson braunsi* Handlirsch. Rare. Nov.–Jan. Species of *Nysson* are known to be cleptoparasitic in the nests of various gorytin genera including *Oryttus*, *Dienoplus* and *Hoplisoides* (Bohart & Menke, 1976: 468). Representatives of these genera associated with friable soils at Hilton are *O. kraepelini*, *D. vicarius karroensis*, *H. thalia* and *H. aglaia* and it may be assumed that the present species of *Nysson* is associated with one or more of these potential host species.

HALICTIDAE

- *** *Sphecodes* sp. Common. Sept.–Febr. In the sandpit frequently observed inspecting holes in the ground and entering them. Found associated with *Nomia* sp. which species is believed to have been the excavator of the nests concerned and thus to be the host of this *Sphecodes* sp. The genus *Sphecodes* is known to be cleptoparasitic in the nests of other Halictidae (*Halictus* and *Lasioglossum*) (Michener, 1944: 250) and also certain Andrenidae and Colletidae (Krombein *et. al.* 1979: 1974).

MEGACHILIDAE

- * *Coelioxys (Lyothyraxis) bruneipes* Pasteels. Very rare. Jan. Possibly parasitic in the nests of *Megachile (Eutricharaea) semiflava* Cockerell.

ANTHOPHORIDAE

- * *Epeolus amabilis* Gerstaecker. Uncommon. Oct.–Apr. The species of *Epeolus* are known to be parasitic in the nests of *Colletes* (Michener, 1944: 279) and of *Tetralonia* and *Colletes* (Arnold, 1947: 218). Mostly collected in the sandpit where it probably parasitizes the *Colletes* sp.
- * *Thyreus* sp. A. Uncommon in sandpit, more usually found associated with "sandstone" bank. In sandpit female observed inspecting holes in the ground.

Category 7.

II. NESTING IN OR ON VERTICAL BANKS

A. IN VERTICAL BANKS

(i) In nest constructed entirely by the nester.

POMPILIDAE

- ** *Dichragenia jacob* (Arnold). Uncommon. Apr.–May. Nine females, three with prey caught, at the “sandstone” bank with which this species, which was not found elsewhere, was definitely associated. No nests located but females seemed to be coming and going to and from a small cave so situated on the bank that it could not be reached by the author. Assumed to construct its nest itself as do other *Dichragenia* species. Prey: lycosid spiders.

SPHECIDAE

- *** *Chalybion (Hemichalybion) spinolae* (Lepelletier). Rare. Nov.–May. Nesting in the “sandstone” bank, circumstantial evidence indicates that the wasp excavates cavities itself, rather than utilizing pre-existing ones. Nesting cavity mud-lined. Prey: known to be small spiders.

MEGACHILIDAE

- *** *Hoplitis anthodemnion* Michener. Common. Nov.–Feb. Nesting in the “sandstone” bank. Nest consists of excavated inclined burrow terminated by a single excavated cell containing a cell constructed from discs cut from petals (including those of *Barleria pungens*). Nest closure, occupying space between provisioned cell and nest entrance, consists of tightly packed sand. Nesting described in detail by Michener (1968).

ANTHOPHORIDAE

- *** *Anthophora* sp. Common. Oct., Nov. and Mar. Nesting in sand bank and “sandstone” bank. Probably the most common species at the “sandstone” bank, and its old and abandoned nests are probably those used most often by species nesting in this situation in pre-existing cavities (that is species of category 8).

Category 8.

II. NESTING IN OR ON VERTICAL BANKS

A. IN VERTICAL BANKS

(ii) In pre-existing cavity modified by the nester.

POMPILIDAE

- * *Auplopus carinigena* Cameron. Rare. Apr.–May.
* *Auplopus ferruginea* (Magretti). Rare. Apr.–May.
** *Auplopus personata ornatcollis* (Cameron). Uncommon. Apr. Prey known to consist of errant spiders of the families Clubionidae, Salticidae and Sparassidae.
All three species were collected on the face of the “sandstone” bank. *A. personata* was observed hunting, boldly entering and searching crevices containing spider-spinnings, at times pushing its way through veils of spinings at the entrance of the spiders’ lairs; a prey-carrying female was furthermore seen entering a pre-existing cavity and it is consequently believed that this species (and the other two) may nest in such cavities. Support for this belief comes from Taylor (1968:72) who recorded *Auplopus mazoensis* (Arnold) nesting in a trap-nest and using mud to form cell partitions.

EUMENIDAE

A number of species, collected in association with vertical banks, is included in the present section, some having been observed nesting in pre-existing cavities, others being suspected of doing so. The species include:

- *** Eumenid A. Uncommon. Nov. Nesting in pre-existing cavities in the "sandstone" bank, in cracks within and between the layers of the near-horizontally bedded shale of the shale bank, and in trap-nests inserted into larger crevices in the latter. Nest entrance furnished with a lacy downturned mud turret, nest a linear series of cells separated by mud partitions, each cell provisioned with numerous small bright green caterpillars (Pyrilididae).
- * *Anterhynchium natalense* (Saussure). Rare. At "sandstone" bank.
- * *Antodynerus radialis oogaster* (Gribodo). Rare. Feb.–Apr. At "sandstone" bank.
- * *Euodynerus euryspilus* (Cameron). Rare. Nov.–Feb. At "sandstone" bank. Recorded in a later category (17) nesting in trap-nests tied to *Acacia karroo*.
- *** *Rynchium marginellum sabulosum* (Saussure). Uncommon. Feb. Nesting in trap-nests inserted into crevices in the "sandstone" bank and thus highly likely to be nesting in pre-existing cavities in the bank itself. Nest a linear series of cells separated by mud partitions; each cell provisioned with several (4–13) caterpillars (Pyrilididae). Known in Grahamstown to nest in cut culms of *Arundo donax* used for vegetable frames.
- *** *Tricaridynerus guerini* (Saussure). Uncommon. Jan. and Feb. Nesting in pre-existing cavities in sandbank, "sandstone" bank and shale bank as also in a trap-nest inserted into a larger crevice in the latter. Nest entrance furnished with a downturned mud turret (Fig. 28), nest a linear series of cells separated by mud partitions; each cell provisioned with several caterpillars, probably Tortricidae. *Anthrax ?tetraspilus* Hesse (Bombyliidae) reared from cells.

SPHECIDAE

- * *Chalybion (Chalybion) tibiale* (Fabricius). Rare. Nov.–Apr. Circumstantial evidence strong that this species nests in pre-existing cavities in the "sandstone" bank. Nesting described in a later category (17).
- * *Pison allonymum* Schultz. Uncommon. Dec.–May. Nesting recorded and described in previous category (2).
- * *Pison montanum* Cameron. Rare. Oct.–Mar. Nesting recorded and described in a later category (17).
- * *Trypoxylon* sp. Rare. Oct.–Mar. Nesting recorded and described in later category (17).

MEGACHILIDAE

- *** *Anthidiellum (Pygnanthidiellum) kimberleyanum* Friese. Uncommon. Oct. and Nov. Nesting in "sandstone" bank.
- *** *Branthidium braunsii* (Friese). Uncommon. Oct., Nov. and Apr. Nesting in "sandstone" bank.
- *** *Chalicodoma (Pseudomegachile) schulthessi* (Friese). Uncommon. Sept. and Oct. Nesting in "sandstone" bank. Nest entrance furnished with a small mud collar, nest a linear series of cells separated by mud partitions, final closure also of mud.
- * *Heriades ?freygessneri* Schletterer. Uncommon. Nov., Dec., Apr. and May. Thought to nest in "sandstone" bank. *H. freygessneri* is known to nest readily in trap-nests (Taylor, 1962b, 1965 and 1968).
- *** *Immanthidium junodi* (Friese). Common. Nov.–Apr. Nesting in "sandstone" bank. A carder bee. Nesting described by Michener (1968), Skaife (1950) and Taylor (1962a).
- *** *Megachile (Eutricharaea) gratiosa* Gerstaecker. Uncommon. Oct.–Mar. Nesting in trap-nests inserted into crevices in the shale bank and presumably also in cracks within and between layers of the shale. Nest a linear series of cells constructed of pieces cut from green leaves. Parasitized by *Zonitoschema eborina* (Fabr.) (Meloidae). Nesting described by Taylor (1963, 1965 and 1968).

- *** *Megachile (Paracella) spinarum* Cockerell. Uncommon. Oct.–Apr. Nesting in “sandstone” bank and also in trap-nest inserted into crevice in the above. Nest a linear series of cells constructed of pieces cut from green leaves of *Maytenus heterophylla*.

Category 9.

II. NESTING IN OR ON VERTICAL BANKS

A. IN VERTICAL BANKS

(iii) In pre-existing cavity *not* modified by the nester.

CHRYSIDIDAE

Seven of the eight species of cuckoo wasps collected on the vertical banks are believed to be associated with wasps nesting in the banks. The seven species, none of which was common, are: *Chrysidea africana* (Mocsary), *Chrysidea ghiliani* Gribodo, *Chrysis antiqua* Brauns, *Chrysis capitalis* Dahlbom, *Hedychrum coelestinum* Spinola, *Octochrysis laminata* (Mocsary), and *Octochrysis mucronifera* (Mocsary). Hosts are known for two species:

- * *Chrysidea africana* Mocsary. Known to be parasitic in the nests of *Trypoxylon* (see category 18).
 *** *Octochrysis laminata* (Mocsary). Reared from the nests of *Tricarinydnerus guerinii* (Saussure) (2 specimens).

MUTILLIDAE

Six species of Mutillidae were collected on the vertical banks, namely *Antennotilla phoebe* (Péringuey), *Dasylabroides caffra* (Kohl), *Mimecomutilla renominanda* Bischoff, *Mutilla scabrofoveolata* Sichel & Radoszkowski, *Ronisia trispilota* (Radoszkowski) and *Stenomutilla* sp. No species was common and no species can be said to be typical of this situation. One species only was definitely associated with a wasp nesting in the bank, namely

- *** *Stenomutilla* sp. Reared from the nest of Eumenid A. constructed within open crack in shale bank. (1 specimen).

SAPYGIDAE

- * *Sapyga (Sapygina) simillima* Arnold. Uncommon. Oct., Nov. and Apr. Known to be parasitic in the nests of *Heriades* sp. (see category 18. Possibly to be associated with *Heriades ?freygessneri* Schletterer nesting in “sandstone” bank.
 * *Sapyga (Sapygina) undulata* Gerst. Rare. Apr.

MEGACHILIDAE

- ** *Euaspi abdominalis* (Fabricius). Very rare. Nov. Circumstantial evidence indicates that this parasitic bee may be associated with the nests of *Chalicodoma schulthessi* (Friese) in the “sandstone” bank.
 * *Coelioxys (Coelioxys) lucidicauda* Cockerell. Very rare. Febr.
 * *Coelioxys (Lyothyraxis) bruneipes* Pasteels. Very rare. Nov. Possibly parasitic in the nests of *Megachile (Paracella) spinarum* Cockerell.
 ** *Coelioxys (Lyothyraxis) lativentris* Friese. Rare. Oct., Nov. Recorded as associated with an *Anthophora* sp. and as probably parasitic in its nest (Rozen, 1969b: 55). In the present community thus probably also associated with *Anthophora*.
 ** *Coelioxys (Lyothyraxis) lativentroides* Brauns. Rare. Oct.–Dec. Seen entering and leaving nests of *Chalicodoma schulthessi* (Friese) and therefore believed to be parasitic in the nests of this species. Supporting evidence for this belief supplied by Brauns (1930) who recorded this species as a parasite of *Chalicodoma latitarsis* Friese.

ANTHOPHORIDAE

- * *Thyreus* sp. Common. Nov.–May. A species of *Thyreus* was recorded as parasitic in the nests of an *Anthophora* species (Rozen, 1969b) and the same association may exist in the present community.

Category 10.

II. NESTING IN OR ON VERTICAL BANKS

B. ON VERTICAL BANKS

(i) In nest constructed entirely by the nester.

EUMENIDAE

* *Synagris abyssinica* Guérin. Rare. Feb. and Apr. Flying about in front of "sandstone" bank. Known to make aerial nests of mud and to provision with caterpillars.

* *Synagris analis* H. de Saussure. Rare. Mar. and Apr. As above.

*** *Eumenes lucasius* Saussure. Rare. Dec. & Apr. Urn-shaped mud cells found in sheltered positions on shale bank. Prey: caterpillars. Parasite: *Osprynchotus violator* (Thunberg) (Ichneumonidae).

VESPIDAE

*** *Ropalidia* sp. A. Rare. One nest with foundress female found (Jan.) in a fist-sized cavity in the sand bank. Nest aerial, constructed of wood pulp ("wasp paper") and in the form of a naked paper comb suspended from the roof of the cavity by a short pedicel. Social species: larvae fed directly on macerated insects and nectar.

SPHECIDAE

*** *Sceliphron spirifex* (L.) One nest with female found (Apr.) in a fist-sized cavity in the "sandstone" bank and several found on shale bank. Nest aerial, constructed of mud and consisting of several cells arranged parallel to one another and covered with a common envelope of mud applied after the last cell has been sealed. Each cell provisioned with numerous small spiders. Parasite: *Osprynchotus violator* (Thunberg) (Ichneumonidae).

Category 11.

II. NESTING IN OR ON VERTICAL BANKS

B. ON VERTICAL BANKS

(ii) In pre-existing cavity modified by the nester.

EUMENIDAE

*** *Eumenid* A. Rare. Nov. Nesting in old urn-shaped mud cells of *Eumenes lucasius* Saussure found in sheltered positions on the shale bank. Prey: Pyralididae (caterpillars).

Category 12.

II. NESTING IN OR ON VERTICAL BANKS

B. ON VERTICAL BANKS

(iii) In pre-existing cavity *not* modified by the nester.

CHRYSIDIDAE

*** *Chrysis* sp. One specimen reared from the urn-shaped mud cell of *Eumenes lucasius* Saussure found in a sheltered position on the shale bank.

MUTILLIDAE

* *Stenomutilla* sp. Rare. Known to be parasitic in the nests of *Eumenid* A. (see category 9).

Category 13.

III. NESTING ON STONES

(i) In nest constructed entirely by the nester.

POMPILIDAE

- *** *Auplopus rossi nigricornis* (Arnold). Rare. One nest was found, consisting of nine contiguous mud cells attached to the underside of a large flat stone where there was a shallow space between it and the ground on which it rested. One of the cells when opened was found to have been provisioned with a single spider of the family Lycosidae. Two male wasps and a female emerged from the cells during Sept.-Oct.

MEGACHILIDAE

- *** *Hoplitis jansei* (Brauns). Uncommon. Nests constructed upon the exposed portions of partially buried quartzite stones and boulders. Nests consist of independent cells closely grouped together and constructed of small, irregularly shaped pebbles of quartzite cemented in a matrix of resin. Emergence of adult bees from Aug.-Nov. Brauns (1926b: 220) recorded the species foraging on low composites at Willowmore.

Category 14.

III. NESTING ON STONES

(ii) In pre-existing cavity modified by the nester.

MEGACHILIDAE

- *** *Megachile (Eutricharaea) gratiosa* Gerstaecker. On one occasion was found to have utilized old open cells of *Hoplitis jansei* (Brauns) for purposes of nesting. Old *Hoplitis* cells each contained a single *M. gratiosa* cell constructed of pieces cut from green leaves. A male reared from such a cell emerged during Nov. *M. gratiosa* nests more commonly in pre-existing cavities associated with vertical banks and with woody plants (categories 8 & 17).

Category 15.

III. NESTING ON STONES

(iii) In pre-existing cavity *not* modified by the nester.

MUTILLIDAE

- *** *Antennotilla phoebe* (Péringuey). Rare. Parasitoids in the cells of *Auplopus rossi nigricornis* (Arnold). Three males reared from these cells emerged during early November.

Category 16.

IV. NESTING IN OR ON PLANTS

A. IN PLANTS

- (a) *Within woody stems.*
 (i) In nest constructed entirely by the nester.
-

ANTHOPHORIDAE

- * *Xylocopa caffra* L. Rare and all sightings confined to the riverine bush. Old abandoned galleries found in dead trunks and branches of *Rhus* and *Pinus* located in the riverine bush believed to have been those of this species. Known to nest in dead branches and structural timbers of *Pinus* spp.
 * *Xylocopa divisa* Klug. Rare and all sightings confined to riverine bush. Known to nest in dead branches.
-

Category 17.

IV. NESTING IN OR ON PLANTS

A. IN PLANTS

- (a) *Within woody stems.*
 (ii) In pre-existing cavity modified by the nester.
-

EUMENIDAE

- *** *Euodynerus euryspilus* (Cameron). Rare. Found nesting (Nov., Febr.) in four trap-nests tied to *Acacia karroo*. Nest a linear series of cells, cell partitions and closing plug composed of mud. Each cell provisioned with 7-13 caterpillars of family Pyralidae, in two nests *Loxostege frustalis* Zeller, the Karroo Caterpillar, a pest of *Pentzia incana*.

SPHECIDAE

- *** *Ampulex* sp. (near *cyanura* Kohl) (Fig. 36). Uncommon. Found nesting (Nov.-March) in thirty trap-nests tied to *Acacia karroo*. Examination of dead finger-thick branches of this shrub or small tree revealed that the natural pre-existing cavities used by this wasp were abandoned larval galleries of *Ceroplesis hottentota* (Fabricius) (Cerambycidae, Coleoptera) (Fig. 35). In both natural and artificial nesting cavities nest consists of a single cell plugged with loosely compacted detritus. Each cell provisioned with a single large nymph or apterous female of *Bantua dispar* (Burmeister) (Blattidae) (Fig. 36).
 *** *Ampulex denticollis* Cameron. Rare. Found nesting (Febr.) in one trap-nest tied to *Acacia karroo*. Nest single-celled, plugged with detritus and provisioned with a single blattid nymph.
 *** *Chalybion (Chalybion) tibiale* (Fabricius). Rare. Found nesting (Jan. and Febr.) in three trap-nests tied to dead tree-stump in riverine bush. Nest a linear series of cells; cell partitions and closing plug composed of mud; outer surfaces of partitions and closing plug whitened with uric acid from bird droppings. Each cell provisioned with 14-34 small spiders of the families Argiopidae (*Araneus*, *Argiope*, *Caerostris*, *Cyclosa*, *Isoxya* and *Nephila*), Thiridiidae (*Rhomphaea*) and Zodariidae. Nesting described by Gess & Gess (1980d).
 *** *Isodontia pelopoeiformis* (Dahlbom). Common. Found nesting (Jan.-Feb.) in over eighty trap-nests tied to *Acacia karroo*, *Maytenus linearis* and *Rhus lancea* in thorn scrub and riverine bush. Nest a linear series of cells; cell partitions constructed of plant "fluff" derived from fruiting inflorescences of *Lasiospermum bipinnatum* and *Senecio* spp.; preliminary plugs and closing plugs of the above

materials as well as clods of earth and debris (Fig. 32). Each cell provisioned with several katydids—Tettigoniidae: Phaneropterinae (*Terpnistria zebata* nymphs, *Eurycorypha prasinata* nymphs, and *Phaneroptera* spp.—nymphs and adults). Nesting of this species in Rhodesia described in Smithers (1958).

- * *Isodontia simoni* (du Buysson). Rare. Nov. & Dec. Not found nesting.
- *** *Isodontia stanleyi* (Kohl). Uncommon. Found nesting (Dec.–Febr.) in eighteen trap-nests similarly situated to those of *I. pelopoeiformis*. Nest a linear series of cells; cell partitions constructed of short lengths of grass leaf blades transversely arranged; preliminary plugs and closing plugs of grass inflorescences, transversely coiled and longitudinally arranged respectively (Fig. 33). Grasses used: *Danthonia curva*, *Diplachne fusca*, *Eragrostis* sp. (probably *E. curvula*), *Melica racemosa* and *Sporobolus* sp. (probably *S. fimbriatus*). Each cell provisioned with several katydids, apparently the same species taken by *I. pelopoeiformis* but smaller (younger) individuals. One cell in addition contained two tree crickets (*Oecanthus capensis* Saussure (Gryllidae: Oecanthinae)).
- *** *Holotachysphex turneri* (Arnold). Rare. Found nesting (Dec.–Febr.) in five trap-nests tied to *Acacia karroo* and *Salix mucronata*. Nest a linear series of cells; cell partitions constructed of coarse detritus and clayey earth; closing plug of coarse detritus. Each cell provisioned with a variable number (4–32) of *?Pyrgomorphella* sp. nymphs (Pyrgomorphidae, Acridoidea). Nesting described by Gess (1978).
- *** *Pison montanum* Cameron. Rare. Found nesting (Dec.–Febr.) in eight trap-nests tied to *Acacia karroo* and *Maytenus linearis*. Nest a linear series of cells; cell partitions and closing plug constructed of mud. Each cell provisioned with a variable number (7–47) of small spiders of the family Argiopidae.
- *** *Trypoxylon* sp. Common. Found nesting (Oct.–Febr.) in twenty-five trap-nests tied to *Acacia karroo* and *Rhus lancea*. Nest a linear series of cells; cell partitions and closing plug constructed of mud. Each cell provisioned with a variable number (5–11) of small spiders of the following families: Lycosidae (incl. *Hippasa* sp.), Pisauridae (*Euphrostenops* sp.), and Argiopidae (incl. *Araneus* spp., *Larinia* sp.).

COLLETIDAE

- *** *Hylaeus braunsi* (Alfken). Rare. Dec. Found nesting in two trap-nests tied to *Acacia karroo*. Nest a linear series of cells; cell partitions and nest closure of very shiny and thin transparent “cellophane”-like material.
- * *Hylaeus* spp. (at least two others).

MEGACHILIDAE

- *** *Immanthidium junodi* (Friese). Common. Nov.–May. Commonly found nesting in trap-nests tied to *Acacia karroo*. A carder bee constructing cell partitions and closing plug of cottonwool-like material. Nesting of this species described or commented upon by Skaife (1950), Taylor (1962a) and Michener (1968).
- *** *Heriades* sp. Rare. Oct. Found nesting in one trap-nest tied to *Maytenus linearis*.
- *** *Chalicodoma (Pseudomegachile) fulva* (Smith). Rare. Found nesting (Dec.) in two trap-nests tied to *Acacia karroo*. Nest a linear series of mud cells.
- *** *Chalicodoma (Pseudomegachile) sinuata* (Friese). Rare. Found nesting (Jan., Febr.) in three trap-nests tied to *Acacia karroo*. Nest a linear series of mud cells. Parasitized by *Zonitoschema eborina* (Fabr.) (Meloidae).
- *** *Megachile (Eutricharaea) gratiosa* Gerst. Common. Found nesting (Dec.–Feb.) in trap-nests tied to *Acacia karroo*. Nest a linear series of cells constructed of pieces cut from green leaves. Parasitized by *Zonitoschema eborina* (Fabr.) (Meloidae).
- *** *Megachile (Paracella) spinarum* Cockerell. Common. Found nesting in many trap-nests tied to *Acacia karroo*. Nest a linear series of cells constructed of pieces cut from green leaves of *Maytenus heterophylla*.

Category 18.

IV. NESTING IN OR ON PLANTS

A. IN PLANTS

(a) *Within woody stems.*

(iii) In pre-existing cavity *not* modified by the nester.

CHRYSIDIDAE

- *** *Chrysidea africana* Mocsary. Uncommon. Parasitic in the nests of *Trypoxylon* sp. nesting in trap-nests. (Seven females reared.)
- *** *Chrysis* sp. (near *purpuripyga* Edney). Uncommon. Parasitic in the nests of *Trypoxylon* sp. nesting in trap-nests. (Nine individuals reared.)
- *** *Chrysis inops* Gribodo. Rare. Parasitic in the nests of *Pison montanum* Cameron nesting in trap-nests. (Three males and a female reared.) Previously recorded as parasitic in the nests of *Pison transvaalensis* Cameron in Natal (Taylor, 1968).
- *** *Octochrysis hoplites* (Mocsary). Rare. Parasitic in the nests of *Euodynerus euryspilus* (Cameron) nesting in trap-nests. (Six individuals reared.)

SAPYGIDAE

- *** *Sapyga (Sapygina) simillima* Arnold. Rare. Parasitic in the nest of *Heriades* sp. nesting in a trap-nest. (One individual reared.)

MEGACHILIDAE

- *** *Coelioxys (Coelioxys) penetratrix* Smith. Rare. Parasitic in the nests of *Megachile (Paracella) spinarum* Cockerell nesting in trap-nests. (2 females and one male reared.)

Category 19.

IV. NESTING IN OR ON PLANTS

A. IN PLANTS

(b) *Within pithy stems.*

(i) In nest constructed entirely by the nester.

EUMENIDAE

- * *Raphiglossa natalensis* Smith. Very rare. March. Not found nesting. Recorded at Willowmore (as *R. flavo-ornata* Cameron) as excavating its cells in dry pithy stems (chiefly those of Liliaceae) and provisioning its cells with small caterpillars (Lepidoptera) (Meade-Waldo, 1913: 45 and Bequaert, 1918: 29-30).

SPHECIDAE

- * *Dasyproctus bipunctatus* Lep. & Brullé (incl. the colour forms *bipunctatus* Lep., *lugubris* (Arnold) and *simillimus* (Smith)). Flight period: Oct.-March. Common. Known to nest in the inflorescence stems of Amaryllidaceae, Iridaceae and Liliaceae (Bowden, 1964: 425-437) and to provision with adult Diptera.
- * *Dasyproctus dubiosus* (Arnold). Very rare. Dec., Jan.
- * *Dasyproctus immitis* (Saussure). Rare. Oct.-March.
- * *Dasyproctus ruficaudis* (Arnold). Rare. Dec.-Febr.
- *** *Dasyproctus westermanni* (Dahlbom). Common. Oct.-March. Found nesting during Dec. and Jan. in inflorescence stems of *Urginea altissima* (Liliaceae); nest a linear series of cells in an ascending and

a descending gallery; cells provisioned with numerous small adult Diptera (Simuliidae, Stratiomyidae, Bombyliidae, Empididae, Syrphidae, Otitidae, Chamaemyiidae). Parasites: *Perilampus* sp. (Perilampidae, Chalcidoidea, Hymenoptera) and Phoridae (Diptera). Evidence of nesting by *Dasyproctus* spp. (unidentified) also in inflorescence stems of *Gasteria* spp. (Liliaceae) and in stems of *Berkheya decurrens* Compositae).

Nesting of *Dasyproctus* spp. (especially *D. westermanni*) described by Gess (1980b).

ANTHOPHORIDAE

- *** *Xylocopa* (*Gnathoxylocopa*) *sicheli* Vachal. Common. At Hilton found nesting exclusively in dry but still attached inflorescence stems of *Aloe ferox* (Liliaceae) (Fig. 30). Nest consists of a descending gallery and an ascending gallery, both unbranched and subdivided serially into a number of cells each sealed with a pithy plug made of material rasped from the gallery walls. Bees are present throughout the year; nesting takes place during the summer. Parasite: *Coelopenecyrtus* sp. (Encyrtidae, Chalcidoidea). Cleptoparasites: *Gasteruption robustum* Kieffer (Gasteruptionidae) and *Synhoria hottentota* Péringuey (Meloidae).
- *** *Ceratina* sp. A. Common. Commonly found nesting in the thinner branches of dry but still attached inflorescence stems of *Aloe ferox* (Liliaceae), less commonly nesting in the stems of *Gasteria* spp. (Liliaceae) and infrequently in stems of *Datura stramonium* (Solanaceae). Nest plan like that of *X. sicheli* but all dimensions much smaller. Bees are present throughout the year; nesting takes place during the summer.
- *** *Ceratina* sp. B. Eleven further species known to occur at Hilton. *C. sp. B* found nesting in inflorescence stem of *Aloe ferox* (1 nest); One male of *C. sp. C* found sheltering in bored dry stem of *Berkheya decurrens* (Compositae); one female and two males of *C. sp. D.* found sheltering in bored dry inflorescence stem of *Apicra* sp. (Liliaceae).

Category 20.

IV. NESTING IN OR ON PLANTS

A. IN PLANTS

(b) *Within pithy stems.*

(ii) In pre-existing cavity modified by the nester.

SPHECIDAE

- *** *Isodontia stanleyi* (Kohl). Three nests found within old galleries of *Xylocopa sicheli* in inflorescence stems of *Aloe ferox* (Fig. 38). (For details of nesting of this wasp see previous entry for this species in category 17.)
- *** *Trypoxylon* sp. Nests found within old galleries of *Ceratina* sp. A. in inflorescence stems of *Aloe ferox*, within old galleries of *Ceratina* and *Dasyproctus* spp. in inflorescence stems of *Gasteria* sp., and within galleries of *Dasyproctus westermanni* in inflorescence stems of *Urginea altissima* (Gess, 1980b). (For details of nesting of *Trypoxylon* see previous entry for *Trypoxylon* sp. in category 17.)

ANTHOPHORIDAE

- *** *Allodape rufogastra* Lep. & Serv. OR *Allodape exoloma* Strand. Nests found within old galleries of *Dasyproctus* sp. in stems of *Berkheya decurrens*. Bee nest characterized by lack of cell partitions and by the eggs being cemented to the gallery wall.

MEGACHILIDAE

- *** *Capanthidium capicola* (Friese). Two nests found within old galleries of *Ceratina* sp. A. in inflorescence stem of *Aloe ferox*. A carder bee constructing cell partitions of cotton-wool-like material.

- *** *Immanthidium junodi* (Friese). Nests found within old galleries of *Ceratina* sp. A. in inflorescence stems of *Aloe ferox*, within old galleries of *Ceratina* and *Dasyproctus* spp. in inflorescence stems of *Gasteria* sp., and within old galleries of *Ceratina* sp. in stems of *Datura* sp. (For details of nesting of this bee see previous entry for this species in category 17.)
- *** *Heriades spiniscutis* (Cameron). Two nests found within old galleries of (?) *Dasyproctus* sp. in stems of *Berkheya decurrens* and one nest found within old gallery of *Dasyproctus* sp. in inflorescence stem of *Gasteria* sp. Nest in linear series of cells; cell partitions (when present) and closing plug of dark resin-like substance. Cell provisioned with bright yellow, rather dry pollen. The nesting of *H. spiniscutis* has been described in detail by Michener (1968).
- *** *Chalicodoma (Pseudomegachile) sinuata* (Friese). Six nests found within old abandoned galleries of *Xylocopa sicheli* in inflorescence stems of *Aloe ferox* (Fig. 40). Nest in linear series of mud cells.
- *** *Megachile (Paracella) spinarum* Cockerell. Six nests found within old abandoned galleries of *Xylocopa sicheli* in inflorescence stems of *Aloe ferox* (Fig. 39). Nest a linear series of cells constructed of pieces cut from green leaves of *Maytenus heterophylla*. Parasites: *Leucospis africana* Cameron (Leucospidae) (three females reared from above nests) and a species of Cleridae (?*Trichodes aulicus* Klug) (one larva found in one of the above nests). Also *Coelioxys (Coelioxys) penetratrix* Smith (see below).

Category 21.

IV. NESTING IN OR ON PLANTS

A. IN PLANTS

(b) *Within pithy stems.*

(iii) In pre-existing cavity *not* modified by the nester.

No species were recorded in this category from the above nests within pithy stems and branches of non-woody plants. However, parasites recorded from the nests of species nesting in trap-nests may be expected to occur also in the nests of the same host species nesting in pithy stems and branches. The following species are thus listed on the strength of this assumption:

CHRYSIDIDAE

Chrysidea africana Mocsary. Parasitic in the nests of *Trypoxylon* sp.

Chrysis sp. (near *purpuripyga* Edney). As above.

MEGACHILIDAE

Coelioxys (Coelioxys) penetratrix Smith. Parasitic in the nests of *Megachile (Paracella) spinarum* Cockerell.

Category 22.

IV. NESTING IN OR ON PLANTS

A. IN PLANTS

(c) *Within hollow stems.*

(i) In nest constructed entirely by the nester.

ANTHOPHORIDAE

- *** *Xylocopa caffrariae* Enderlein. Common. Nesting exclusively in dry but still attached hollow culms of *Phragmites australis* (Gramineae), "Common Reed", growing along the course of the New Year's River and immediately within the retaining wall of the earthen dam. Nest consists of a descending

and an ascending gallery subdivided serially into a number of cells each sealed with a pithy plug made of material rasped from the gallery walls. Access to the hollow internode is through an entrance hole cut by the bee through the 1 mm thick side wall of the culm (Fig. 31). Bees are present throughout the year; nesting takes place during the summer. Cleptoparasite: *Gasteruption robustum* Kieffer (Gasteruptionidae).

Category 23.

IV. NESTING IN OR ON PLANTS

A. IN PLANTS

(c) *Within hollow stems.*

(ii) In pre-existing cavity modified by the nester.

SPHECIDAE

*** *Isodontia stanleyi* (Kohl.) Two nests found within old galleries of *Xylocopa caffrariae* in bored hollow culms of *OHHRAGMITES AUSTRALIS*. (For details of nesting of this wasp see previous entry for this species in category 17).

*** *Holotachysphex turneri* (Arnold). Two nests found within old galleries of *Xylocopa caffrariae* in bored hollow culms of *Phragmites australis*. (For details of nesting of this wasp see previous entry for this species in category 17, Gess (1978) and Gess & Gess (1980a: 52)).

*** *Trypoxylon* sp. A few nests found within old galleries of *Xylocopa caffrariae* in bored hollow culms of *Phragmites australis*, a few others found in hollow culms of the same plant bored by lepidopterous larvae. (For details of nesting of *Trypoxylon* see previous entry for *Trypoxylon* sp. in category 17).

MEGACHILIDAE

*** *Chalicodoma (Pseudomegachile) sinuata* (Friese). One nest found within old gallery of *Xylocopa caffrariae* in bored hollow culm of *Phragmites australis*. Nest a linear series of mud cells.

Category 24.

IV. NESTING IN OR ON PLANTS

A. IN PLANTS

(c) *Within hollow stems.*

(iii) In pre-existing cavity *not* modified by the nester.

No species were recorded in this category from the above nests within hollow stems of hollow-stemmed plants. However, parasites recorded from the nests of species nesting in trap-nests may be expected to occur also in the nests of the same host species nesting in hollow stems. The following species are thus listed on the strength of this assumption:

CHRYSIDIDAE

Chrysidea africana Mocsary. Parasitic in the nests of *Trypoxylon*.

Chrysis sp. (near *purpuripyga* Edney). As above.

Category 25.

IV. NESTING IN OR ON PLANTS

- B. ON PLANTS (Irrespective of whether woody, pithy or hollow-stemmed).
 (i) In nest constructed entirely by the nester.
-

EUMENIDAE

- *** *Eumenes lucasius* Saussure. Rare. Urn-shaped aerial mud cell found under loose bark of fallen tree. Provisioned with caterpillars. A few other aerial mud nests constructed by Eumenidae were found but in all cases they were old, the wasps having already emerged, and identification of the species involved was not possible.

MASARIDAE

- * *Celonites capensis* Brauns. A rare species at Hilton; not found nesting. Known to construct small aerial mud cells. Provisions with a mixture of pollen and nectar.

VESPIDAE

- *** *Polistes smithii* Saussure. One nest (with foundress female) found (Nov.) attached to branches of *Lycium* overhanging "sandstone" bank. Nest aerial, constructed of wood pulp ("wasp paper") and in the form of a naked paper comb suspended from the branch by a short pedicel. Social species; larvae fed directly on macerated insects and nectar. Adult males occasionally stylopized.
- *** *Ropalidia* sp. B. One nest (with foundress female) found (Nov.) attached to branches of *Cadaba aphylla* overhanging "sandstone" bank. Form of nest similar to that of *Polistes smithii*. Adult males likewise occasionally stylopized.

SPHECIDAE

- * *Sceliphron quartinae* (Gribodo). Rare. Nov., Febr. Not found nesting at Hilton. Known to construct its cells of cow dung or clayey mud and to attach them singly or in twos to grass culms or other plant stems at some height above the ground. Provisioning is with small spiders. (Brauns, 1911: 119 and Jacot Guillarmod, *pers.comm.*) At Hilton found at puddles, presumably collecting mud for nest-building purposes.

Category 26.

IV. NESTING IN OR ON PLANTS

- B. ON PLANTS (Irrespective of whether woody, pithy or hollow-stemmed.)
 (ii) In pre-existing cavity modified by the nester.
-

No representatives recorded for this category.

Category 27.

IV. NESTING IN OR ON PLANTS

- B. ON PLANTS (Irrespective of whether woody, pithy or hollow-stemmed.)
 (iii) In pre-existing cavity *not* modified by the nester.
-

No representatives recorded for this category.

DISCUSSION

Evaluation of the completeness and representativeness of the sample

The classification of the aculeate wasps and of the bees of the study area on the basis of their ethology encompasses an annotated list of a total of 241 species. The strengths of the specific representation of the families involved are shown in Table 1.

TABLE 1.

The strengths of the specific representation of the families included in the annotated list.

Family	No. of spp.	Family	No. of spp.
Chrysididae	19	Vespidae	3
Tiphidae	17	Pompilidae	11
Mutillidae	20	Sphecidae	91
Scoliidae	11	Colletidae	3
Sapygidae	2	Halictidae	6
Masaridae	6	Megachilidae	25
Eumenidae	16	Anthophoridae	11

It is inevitable that in a survey of the present kind not all the species present in a given area (in the present instance, the farm Hilton) will be collected and identified and that it will not be possible to allocate to any particular nesting association those species for which ethological information is lacking.

It is axiomatic, however, that in any area, the most common species are the most likely to be noticed and recorded—that is most likely to be collected and most likely to be found nesting or at least intimately associated with a particular nesting association (e.g. a particular type of soil) in which nesting may be assumed to take place. It may therefore be expected that the present account of the ethology of the aculeate wasps and the bees of Hilton includes amongst the 241 species listed most if not all of the common and therefore most important species occurring there. Judged on the basis of the inclusion in the sample of these common and important species the sample may therefore be considered as representative of the entire community of the above defined insects.

Although further study of the whole area of Hilton would undoubtedly swell the lists of some if not all the various categories of the present classification with further species, it is believed that this quantitative change would not be accompanied by a qualitative change of any real importance.

For some families at least it is possible to obtain some indication of how representative the number of species listed above is of the total number of species occurring at Hilton. For example, with respect to the Sphecidae, the predominant family of the sample, the 91 species listed are believed to represent 80–90% of the total number of species of the family present at Hilton, and the five and six species listed respectively for the Vespidae and the Masaridae are believed to represent 60% and 100% of their total numbers, however; the nineteen listed species of Chrysididae are believed to represent only 45% of their total number.

An evaluation of the classification of the aculeate wasps and the bees of the study area on the basis of their ethology.

In the classification of the aculeate wasps and the bees of the study area on the basis of their ethology 27 categories are recognized. When the 241 species are allocated to these cate-

gories it is found that 209 species occur in only one category each and 32 in more than one category each. If, however, those species which construct their nests entirely by themselves are considered, it is found that of the 118 species in this category only one (0,85%) occurs in two categories, both of which offer the species in question, *Eumenes lucasius*, an aerial nester, a support for its nest.

The species which modify pre-existing cavities and therefore do not have to excavate their cavities themselves show, as one would expect, less specificity. Of the 44 species involved 13 species (29,5%) occur in more than one category. Of these 13 species 10 nest only above the ground either in vertical banks or in plants and of these three were restricted to plants. One species, *Megachile semiflava*, was restricted to cavities in the ground regardless of the nature of the soil.

Of the 79 species which nest in pre-existing cavities which they do not themselves modify 17 (21,5%) occur in more than one category, however, these species, belonging to the Chrysididae, Mutillidae, Sapygidae and Megachilidae such as *Coelioxys*, are "parasitic" in one way or another and the categories in which they occur are therefore determined by those of their hosts. These species are therefore 100% restricted on the basis of host.

It is clear that each community determined by habitat is characterized by those species which construct their nests entirely by themselves but that there is, not surprisingly, overlap in species using pre-existing cavities and a resultant overlap in species which are hosted by the latter.

Having established the validity of the ethological classification nesting in the four main habitat categories; ground, vertical banks, stones and plants; will be discussed.

Discussion of nesting in the four main habitat categories.

The Ground

Soils may be divided into two different types—friable and non-friable. By definition, the word "friable" means easily crumbled and a friable soil therefore is one in which it is easy to dig, the individual particles being relatively loosely aggregated and not difficult to part from one another. "Non-friable" means not easily crumbled and a non-friable soil is therefore one in which it is difficult to dig, the individual soil particles being closely aggregated and difficult to part from one another. The character of a non-friable soil may, however, vary greatly with the amount of moisture which it contains, a wet non-friable soil being more easily worked than a dry one.

At Hilton the friable soil is mostly sandy in nature and is derived from the weathering of Witteberg Quartzite and the non-friable soil is clayey in nature and is derived from the weathering of Witteberg Shale. In certain small areas recent disturbance during farming activities has broken down the structure of the clayey soil and has temporarily rendered it partially friable.

At Hilton, the number of species recorded as nesting in the ground exceeds the number recorded from the three other situations combined: 167 species as against 74. Of the 167 species recorded from the ground, 126 (75,5%) were associated only with friable soil, 35 (21%) were associated only with non-friable soil and 6 (3,5%) were associated with both friable and non-friable soils.

On account of the species which were recorded in both soil types, the number of species/substrate associations exceeds the actual number of species by 6 and therefore totals 173. An analysis of this figure according to the degree of participation of species of wasps and of bees in the construction of their nests is given in Table 2 and is shown graphically and in greater detail in the Pie-diagram (Fig. 16).

TABLE 2.

Number of species of aculeate wasps and of bees nesting in the ground.

	In nests constructed entirely by the nesters themselves	In modified pre-existing cavities	In unmodified pre-existing cavities
In non-friable soils	15	12	14
In friable soils	76	2	54

It may be seen immediately that with respect to those species which excavate their nests themselves there are many more (76 as against 15) that do so in friable soils than in non-friable soils. It should be noted that this marked difference in the numbers of species nesting in the two soil types is not a reflection of the extent of the availability of these soils for nesting, the density of nesting in areas of friable soil being far greater than in areas of non-friable soil with readily available water sources. Furthermore this discrepancy is not a peculiarity of the Hilton population but bears out the picture which emerges from a consideration of ground-nesting aculeate wasps as a whole.

It can be clearly seen from the Pie-diagram (Fig. 16) that, at Hilton, at the family level the composition of the communities of species which construct their nests themselves are strikingly different in friable and non-friable soils. Whereas in friable soils the vast majority of species, 67 (88%), are members of the family Sphecidae in non-friable soils this family is only represented by two (13%) of the species. The majority of species, 11 (74%), in non-friable soils are members of the Vespoidea, five species of Masaridae and six species of Eumenidae. There are no representatives of the Vespoidea nesting in friable soils. Species of Pompilidae excavate their nests in both soil types. Whereas the two species of *Dichragenia* appear to be the only pompilids associated in this way with non-friable soils, the number of species, 3, recorded for friable soils is in all probability too low. Bees represented, albeit poorly, amongst the nest excavators in friable soil are absent amongst those in non-friable soil.

The construction of nests in the two very different soil types clearly demands different excavation techniques and therefore differences in the structure and behaviour of the wasps involved.

Characteristic of the species excavating nests in friable soil is that there is no modification of the physical nature of the substrate by the addition of water. Excavation of the nests is by digging, the organs involved being the mandibles, the fore-legs and in some species the pygidium.

Initial loosening of the soil at the working face of the excavation is frequently done with the mandibles. These may be used simply to bite away the soil but in some species nesting in compacted soil they are aided in their work by the wasp's manipulation of its flight mechanisms which produces vibrations transmitted by the mandibles to the substrate. Evidence of this method of loosening the soil was the very noticeable buzzing sound that could frequently be heard being made by excavating females of the sphecids *Podalonia canescens* and *Ammophila ferrugineipes*. Frequently this buzzing sound emanating from the ground was the first indication that nest excavation by one of these species was under way in the immediate vicinity.

Removal of the loosened soil may be effected in several ways, on the basis of which Olberg (1959) divided the digger wasps into "rakers", "pullers", "carriers" and "pushers". A

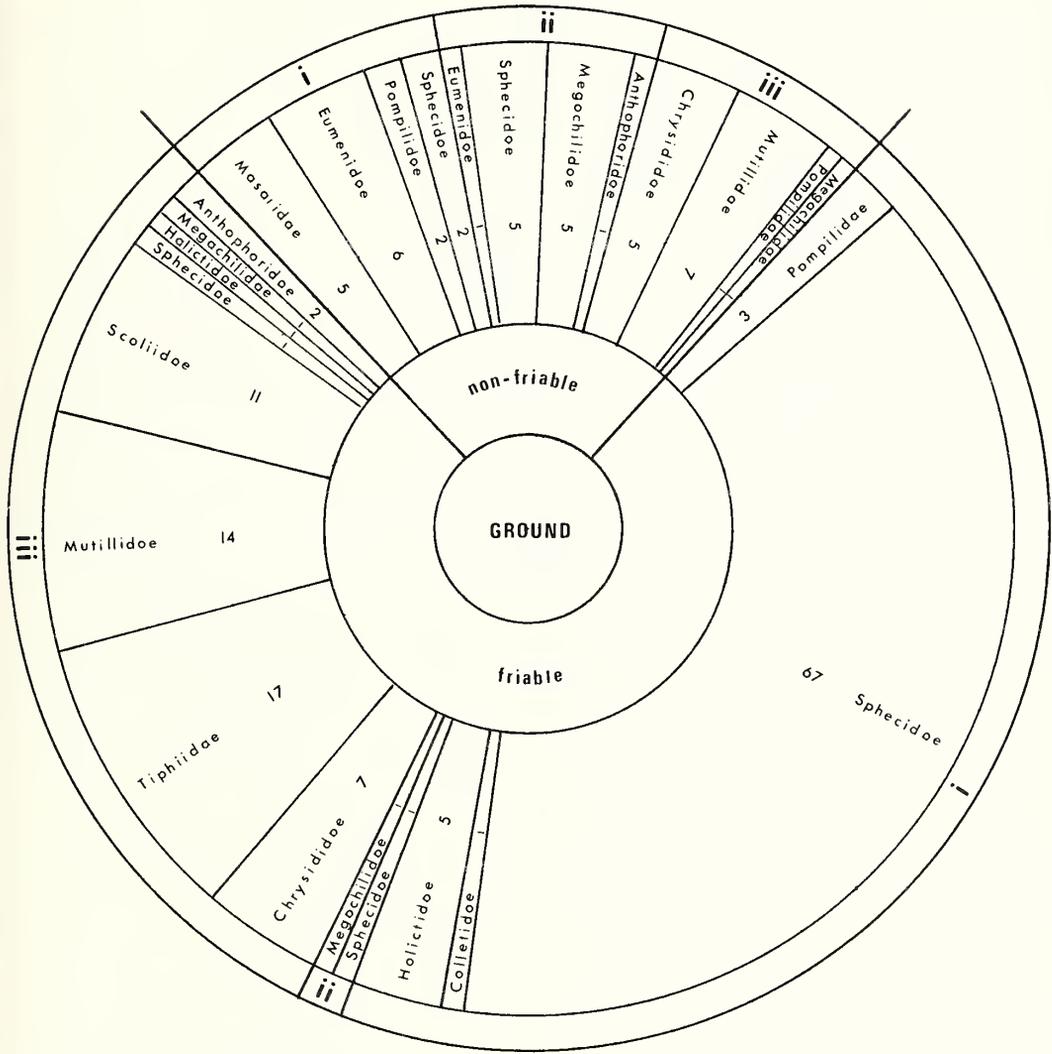


Fig. 16. Diagram showing the structure of the communities of the aculeate wasps and the bees nesting in the ground in the study area. Numbers accompanying the family names represent numbers of species. The numbers (i, ii, iii) in the outermost ring correspond to the same numbers in the classification of the aculeate wasps and the bees of the study area on the basis of their ethology. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester.

good account of the different modes of digging based upon the above division is given by Evans and Eberhard (1970) and will only be briefly outlined here, with the addition of examples drawn from the present study.

The "rakers", constituting the majority of the fossorial wasps, are characterized by having a strongly developed series of stout spines on the front tarsus, forming the so-called "tarsal comb" or "sandrake". In digging, the fore tarsi which are bent towards the midline of the body are moved repeatedly backwards and forward, each backstroke throwing back a load of soil which passes beneath the upheld abdomen to behind the body. By walking backwards whilst so raking, loose soil can rapidly be swept from the excavation. Many of the species observed nesting in friable soil at Hilton are included in the "rakers", for example *Batozonellus fuliginosus* (Pompilidae) (Gess and Gess, 1980b), *Tachyphex* spp., *Kohliella alaris* (Gess and Gess, 1980a), *Palarus latifrons*, *Bembecinus braunsii*, *Bembecinus haemorrhoidalis* and *Bembix albofaciata* (Sphecidae). In some species the two front legs move alternately (e.g. *Batozonellus*), in other species synchronously (e.g. *Bembix*). By virtue of the fact that it is not possible to rake or sweep loose sand vertically upwards, all the burrows of "rakers" examined at Hilton were found to be inclined, often at a fairly small angle with the horizontal (for example see nest plans of *Kohliella alaris*—Gess and Gess, 1980a: Figs 4 and 5).

The "pullers" like the "rakers" use the fore legs to remove the loosened soil from the excavation. However, instead of raking out the soil, the latter is gathered together to form a load held between the underside of the head and prothorax and the basal parts of the fore legs and, the wasp walking backwards, this soil is then pulled out of the excavation and deposited at its entrance. At Hilton a common "puller" is *Podalonia canescens*. However, this wasp does also act as a "raker" for the small heap of excavated soil pulled to the nest entrance is from time to time dispersed by raking. Raking of soil is also practised in nest closure. Soil pulling unlike soil raking does not necessarily require the burrow to be inclined and the burrow of *Podalonia canescens* is frequently subvertical, at least initially.

The "carriers" are like the "pullers" in their mode of removing the loosened soil from the excavation. However, unlike the "pullers" they do not deposit the soil at the nest entrance but drop it at a distance from the nest entrance, having transported it there either on foot or in flight. At Hilton the most common carrier nesting in friable soil is *Ammophila ferrugineipes* which carries the soil to a distance of 1–1.5 m from the nest before dropping it. Generally each load of soil is dropped in the same area, mostly into a low bush. Despite the fact that each load is dropped in the same place, the discarded sand is not noticeable for, being dropped from a height into a bush by a wasp which is moving in flight, it is well scattered and concealed. Like the burrow of *Podalonia canescens*, the burrow of *Ammophila ferrugineipes* is initially subvertical. The "pushers" differ from the "rakers", "pullers" and "carriers" in their use of the end of the abdomen in clearing soil from their excavations. Soil loosened by the mandibles and fore legs is moved back by the legs to behind the wasp which then backs up its burrow pushing the soil before it, in an action comparable to that of a piston in its cylinder. The common "pushers" in friable soil at Hilton are the many species of *Cerceris* which for the purpose of pushing soil with the end of the abdomen have a well developed pygidial plate. Characteristic of *Cerceris* burrows is that they are vertical or subvertical and that the excavated soil in the form of "sand sausages" forms a conical heap surrounding and surmounting the nest entrance (Fig. 17). The length of the "sand sausage" indicates that this method of nest excavation allows a great amount of loosened material to be brought to the surface at any one time—more than can be moved at any one time by a "puller". It is therefore an efficient and time-saving method of excavation and allows the construction of nests of great depth. At Hilton, *Cerceris latifrons*, for example, constructs a burrow far deeper than that of any other species examined there—at a depth of 600 mm, the reach of the excavator's arm, the burrow still continues downwards.

Characteristic of those species constructing original nests in non-friable soils is that excavation of the nest is affected by the use of water used to soften the soil thus rendering it workable. The water, collected by the nesting female from a water source, usually a pool or



Fig. 17. Nest entrance of *Cerceris oraniensis* showing excavated soil in the form of "sand sausages". (× 1)

puddle in the vicinity of the chosen nesting site, is carried to the nesting site in the crop. The mechanics of excavation consist of the regurgitation of a droplet of water from the crop onto the working face of the excavation, the working of this water into the soil by the mandibles, and the formation of the resultant mud into a pellet which is carried from the excavation by means of the mouthparts. Several such pellets may be formed from a single crop-full of water: when the supply is depleted the wasp returns to the water source for a further crop-full. Whilst the above outlined method of softening the soil is unique to those wasps nesting in non-friable soils, the use of the mandibles for carrying out the pellets of mud from the excavation involves the same behaviour as shown by many nesters in friable soils which may use their mandibles for carrying out pebbles and other objects from their excavations though their digging is otherwise done by raking or pulling the soil. Another facet of behaviour shared by certain excavators in both friable and non-friable soils is the use of vibrations generated by the manipulation of the flight mechanisms and transmitted by the mandibles to the substrate for the purpose of loosening the latter. Recorded above with respect to the sphecids *Podalonia canescens* and *Ammophila ferrugineipes* ("pullers" and "carriers" respectively), it is a feature also of the excavating behaviour of the sphecid *Bembecinus cinguliger* (and probably also *Bembecinus oxydorcus*).

The use of water for nest excavation has been described in detail for several species of wasps nesting in clayey soils at Hilton: *Dichragenia pulchricoma* (Arnold) (Gess and Gess, 1974) and *Dichragenia neavei* (Kohl) (Gess and Gess, 1976b) (both Pompilidae); *Parachilus insignis* (Saussure) (Gess and Gess, 1976a) (Eumenidae); *Ceramius capicola* Brauns, *Ceramius lichtensteinii* (Klug), *Ceramius linearis* Klug and *Jurgurtia confusa* Richards (Gess and Gess, 1980c) (all Masaridae); *Bembecinus cinguliger* (Smith) and *Bembecinus oxydorcus*

(Handlirsch) (Gess and Gess, 1975) (both Sphecidae). In addition to these species a further five species, all Eumenidae, have been recorded using this method of nest excavation: included are *Antepipona scutellaris* Giordani Soika, *Parachilus capensis* (Saussure) and *Pseudepipona erythrospila* (Cameron).

The above species, in marked contrast to those excavating their nests in friable soils, make no use of the fore-legs in manipulating the nesting substrate and these limbs are consequently devoid of any modifications such as "sandrades" used for digging. This is particularly striking with respect to the sphecid genus *Bembecinus*, represented at Hilton by four very common species, *B. braunsii* and *B. haemorrhoidalis* nesting in friable soil (in the sandpit) and *B. cinguliger* and *B. oxydorcus* nesting in non-friable, clayey soil. Typically the members of this large cosmopolitan genus are sand-raking and have the fore-tarsi furnished with long spines for this purpose as in *B. braunsii* and *B. haemorrhoidalis*. In *B. cinguliger* and *B. oxydorcus*, by contrast, these spines forming the "sandrade" are totally absent, the fore-tarsi having instead a dense row of short spines (Figs 18 and 19).

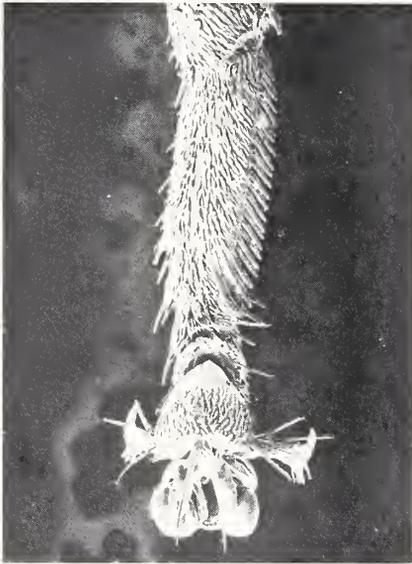


Fig. 18. Left fore-tarsus of *Bembecinus cinguliger* showing dense row of short spines. ($\times 32$)

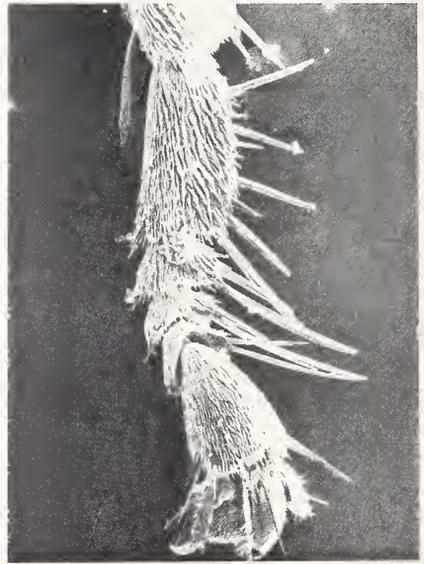


Fig. 19. Left fore-tarsus of *Bembecinus haemorrhoidalis* showing long spines forming "sandrade". ($\times 32$)

Within the Pompilidae, the unmodified fore-tarsi of the two species of *Dichragenia* nesting in non-friable soil may similarly be contrasted with the modified fore-tarsi of *Batozonellus fuliginosus* nesting in friable soil (Figs 20 & 21).

It might be expected with respect to the clay-nesters that as all work associated with the manipulation of the substrate and of the excavated material (mud pellets) is performed by the mouthparts, principally the mandibles, some modifications associated with these organs might be present. This does indeed appear to be the case in the two *Dichragenia* species, females of which possess a brush of long, stiff, forwardly directed bristles emitted from the base of the

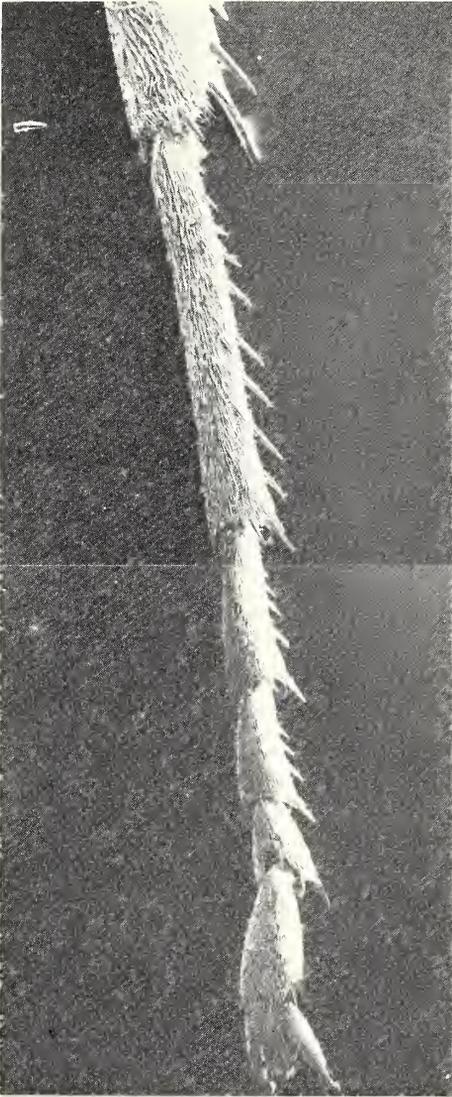


Fig. 20. Left fore-tarsus of *Dichragenia pulchrcoma* showing very short spines not forming a "sand-rake". ($\times 28$)

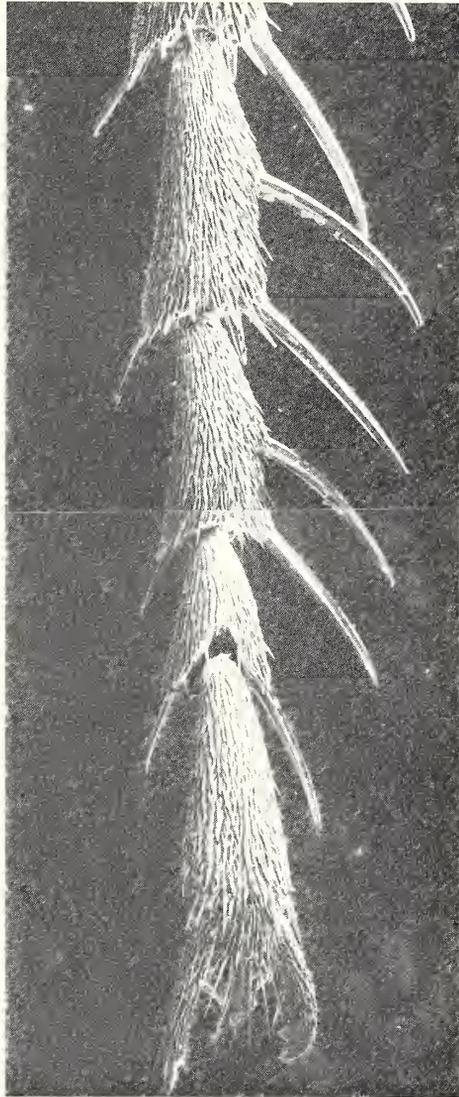


Fig. 21. Left fore-tarsus (distal four joints only) of *Batozonellus fuliginosus* showing long spines forming "sandrake". ($\times 24$)

mentum (Figs 22 & 23 and Arnold, 1934: Figs 1, 1a). It is believed that these bristles may by supporting it from below aid the mandibles in holding and manipulating a mud pellet. Support for this belief may be drawn from two aulopodine genera closely allied to *Dichragenia*—*Phanagenia* and *Auplopus* which possess similar brushes of mental bristles and which use mud pellets to construct aerial mud cells.



Fig. 22. Underside of head of *Dichragenia pulchricoma* showing stiff, forwardly directed bristles emitted from the base of the mentum. ($\times 56$)

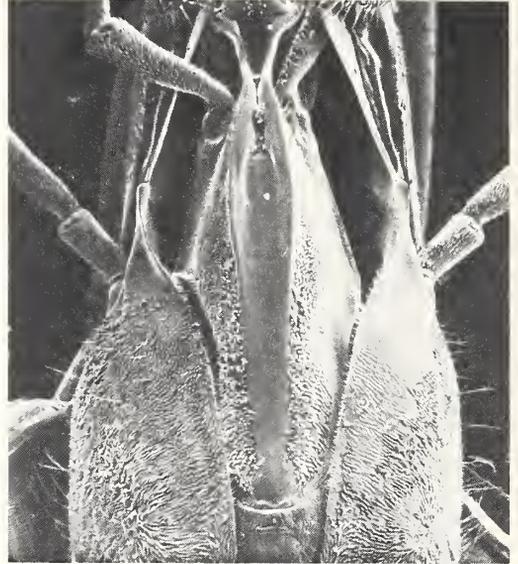


Fig. 23. Underside of head of *Batozonellus fuliginosus* showing absence of forwardly directed bristles. ($\times 24$)

In the brief outline given above of the excavating methods used by nesters in friable soils, it was shown that whereas soil raking allowed the construction only of inclined burrows, soil pulling and the development of soil pulling—soil carrying—allowed the construction of vertical burrows. As the species excavating their nests in non-friable soils all remove the excavation spoils in the form of mud pellets held by the mandibles it follows that they may be considered soil carriers and it is not surprising that the nests excavated are without exception vertical or subvertical (Gess and Gess, 1974: Figs 2–5; 1975: Figs 10–17; 1976a: Figs 1–4; 1976b: Figs 1–2; 1980c: Figs 1–5). The genus *Bembecinus* may once again be used as an illustration, in this instance to show the differences in the nest plan resulting from different excavation techniques employed in the two substrates. Thus, whereas the nest of several sandraking species has been described by Evans (1966: 137–138) as being without exception oblique, a description also fitting the nests of *B. braunsii* and *B. haemorrhoidalis*, the nest of the mud pellet-carrying *B. cinguliger* and *B. oxydorcus* is vertical or subvertical. The distinction can be clearly seen by comparison between Evans (1966: Fig. 76) and Gess and Gess (1975: Figs 10–17). The same picture emerges from a comparison of the nest plan of *Batozonellus fuliginosus* (Gess and Gess, 1980b: 5) with those of the two *Dichragenia* species.

Characteristic of all the species recorded excavating their nests in non-friable clayey soil is that at least some of the excavated material—in the form of mud pellets—is used to build an aerial superstructure encircling and surmounting the nest entrance. Among the species involved, the two *Dichragenia* species are unique in that all the pellets removed from their burrows are added to the superstructures. All other species stop adding pellets to the superstructure once this has attained a certain size, and further pellets are discarded at varying distances from the nest, depending upon the species.

Each species builds a superstructure of definite form so that the identity of the builder may readily be established from the style of its architecture.

The largest and most striking superstructures are constructed by the two Pompilidae: that of *Dichragenia pulchricoma* is retort-shaped (Gess and Gess, 1974: 195-196, Pls 5-8 and 1976b: Fig. 3) whereas that of *D. neavei* is funnel-shaped (Gess and Gess, 1976b: Pl. 1 and Figs 1 and 2).

The nest superstructures of the Eumenidae are all of a single basic type or developments thereof: a low collar encircling the nest entrance in *Parachilus insignis* (Gess and Gess, 1976a: 88, Fig. 1 and Pls 3-8) and in *Pseudepipona erythrospila*; a very low turret with a downwardly recurved lip in Eumenid sp. G; a short vertical flared tube in *Antepipona scutellaris*; and a vertical funnel-shaped turret in *Parachilus capensis*.

The four Masaridae studied all construct nest superstructures in the form of cylindrical turrets. That of *Jugurtia confusa* is characteristically very short (Gess and Gess, 1980c: 66, Figs 1 and 7) whereas those of the three species of *Ceramius* are longer: those of *C. linearis* (Gess and Gess, 1980c: 66, Fig. 3) and *C. lichtensteinii* (Gess, 1973: 117, Pl. 2; and Gess and Gess, 1980c: 66, Figs 4, 5 and 9) are initially vertical or subvertical but may, if of any considerable length, curve over and that of *C. capicola* (Gess, 1973: 117, Pl. 1; and Gess and Gess, 1980c: 66, Figs 2 and 8) is always downcurved and may continue in a horizontal plane close to the ground but always free from it.

The nest superstructures of the two Sphecidae though superficially very different are on closer examination clearly of similar plan and may readily be homologized (Gess and Gess, 1975: 33): that of *Bembecinus cinguliger* is elongated and is applied to the surface of the ground (Gess and Gess, 1975: Figs 6-9 and Pls 5 and 6) whereas that of *B. oxydorcus* is shortened and raised above the ground (Gess and Gess, 1975: Figs 2-5 and Pls 7-13).

A feature common to the nest superstructures of the Pompilidae, Eumenidae and Masaridae enumerated above is that of radial symmetry, at least in the initial stages of their construction. Whereas radial symmetry is characteristic of the completed superstructures of all the Eumenidae and of *Jugurtia confusa* as well as of large superstructures of *Dichragenia neavei*, it is lost in those of the *Ceramius* species and in large superstructures of *D. pulchricoma*. The nest superstructures of the two species of *Bembecinus* (Sphecidae), however, are never radially symmetrical even initially.

In *Ceramius lichtensteinii* at least, it has been established (Gess, 1973: 117) that experimental removal of a completed nest turret is followed by its replacement by the nesting wasp with a new one of similar design to and size as the first. The response by *D. pulchricoma* to a damaged nest superstructure is different and has been described in detail by Gess and Gess (1974: 196).

That the possession of an aerial superstructure surmounting the nest entrance is of survival value to species excavating their nests in non-friable clayey soils is evident by the fact that all the species listed as belonging to this category of ground nesters construct such superstructures. This is all the more striking when it is considered that the species involved belong to four different families and that the technique of nesting in clay has evolved independently in the Pompilidae, Eumenidae-Masaridae, and Sphecidae. Ways in which these superstructures may be of value to the wasps constructing them will be discussed later.

All the species of wasps excavating their nests in the ground exhibit the same behavioural elements. Differences in the nesting behaviour result from differences in the sequence in which these behavioural elements are performed and from the repetition in some species of the performance of one or more of the behavioural elements within the sequence.

The basic and most primitive ethological type found in nest-excavating wasps is characterized by the sequence:

Hunting—Paralysis of the prey (by stinging)—Transportation of the prey—Excavation of

the nest (consisting of an entrance burrow and a cell)—*Oviposition*—*Closing of the cell and of the nest.*

This basic type is found amongst species excavating their nests in friable soils and is typical of the vast majority of Pompilidae, examples at Hilton being *Batozonellus fuliginosus* and probably *Tachypompilus ignitus* (Gess and Gess, 1980b). A few Sphecidae such as the noctuid-caterpillar-hunting *Podalonia canescens* also exhibit this primitive nesting type.

The wasp after transporting the prey into the vicinity of the chosen nesting site, often close to the point of prey capture, is forced temporarily to deposit the former on the ground or in some place of concealment—frequently under a leaf or in a small weed—while a shallow burrow for its reception is rapidly excavated. Despite the fact that the wasp may frequently interrupt her digging to check upon the prey, the latter is subject to misadventure and may either be carried away by other insects such as ants or may be oviposited upon by cleptoparasitic insects such as the pompilid *Ceropales*.

Excavation of the cell having been completed the wasp retrieves the prey, transports it into the cell, oviposits upon it and then closes the cell by filling the burrow leading to it with some of the previously excavated soil.

In the behaviour of the wasps belonging to this basic ethological type characterized by the fact that hunting precedes nest excavation there is never any repetition of a behavioural element within a single sequence and it therefore follows that not only is a cell provisioned with only a single prey but each nest consists of only a single cell. With the closure of the cell the association with the nest is ended and capture of a further prey by the wasp is followed by the excavation of a new nest.

More specialized ethological types found amongst species excavating their nests in the ground are all characterized by the fact that hunting and nest excavation have been transposed in the sequence in which the behavioural elements are performed—that is nest excavation now precedes hunting. Of immediate benefit to all wasps having this more advanced sequence is that the prey may be taken directly into the cell with greatly reduced risks of its being stolen or furnished with an egg by a cleptoparasite.

Nest excavation preceding hunting is the sequence common to the majority of those wasps recorded at Hilton as excavating their nests in friable soil and is characteristic of all those species excavating their nests in the non-friable clayey soil.

As has been noted above, wasps which hunt before excavating nests construct these close to the site of capture of the prey. With the adoption of the new sequence of nest excavation before hunting, the nest site is not chosen as a matter of expediency but on the basis of its overall suitability and as a consequence there is a tendency for successive nests excavated by a wasp to be localized in one area which may moreover be removed from the hunting area.

The grouping by a wasp of successive nests in the same nesting area is clearly pre-adaptive for a labour and time saving shortcut in which there is a substitution of a smaller number of nests with two or more cells for a larger number of nests each with a single cell. This change from single-celled to two-celled or multi-celled nests is brought about within the new sequence of nest excavation before hunting by a delay in carrying out the final element of the sequence—that of nest closure (as opposed to cell closure) and by a repetition after cell closure of all the preceding elements in the sequence other than the initial one—the excavation of the entrance burrow.

The amended sequence may be expressed as:

Excavation of the nest entrance burrow—[*Excavation of the cell*—*Hunting*—*Paralysis of the prey*—*Transportation of the prey*—*Oviposition*—*Cell closure*]ⁿ—*Nest closure.*

(The portion of the sequence in square brackets is that subject to repetition “n” times.)

At Hilton, examples of wasps belonging to this ethological type are the two pompilids excavating their nests in clayey soils—*Dichragenia pulchricoma* and *D. neavei* (Gess and Gess,

1974 and 1976b, respectively). In both these species the final nest closure has never been found to occur and it therefore seems that it is not only delayed but is omitted altogether.

The sequence of nest excavation preceding hunting is pre-adaptive for the substitution in the provisioning of a cell of several smaller prey for a single large one. This is clearly of advantage with respect to prey transport, it being easier to transport several small prey, one at a time, than a single large prey. The advantage can easily be seen with respect to wasps provisioning their cells with spiders (Table 3). Like all Pompilidae, *Batozonellus fuliginosus* and *Tachypompilus ignitus* (Gess and Gess, 1980b) provision each cell with a single spider, which on account of its weight relative to that of the wasp transporting it—up to around eight times—cannot be transported other than by being dragged laboriously over the ground. Frequently the wasp has difficulty in overcoming the obstacles on the way to the nest. By contrast, in the Sphecidae *Chalybion tibiale* (Gess and Gess, 1980d) and *Pison montanum* provision each cell with numerous small spiders, which on account of their light weight—for each individual a mere fraction (about one-third) of that of the wasp—are able to be transported effortlessly, rapidly and directly to the nest by the wasp in flight.

TABLE 3

The relationship for some species of Pompilidae and Sphecidae between the weight of the spider or spiders forming the provision of a cell and the weight of the female wasp provisioning the cell.

Wasp family & species	Size of sample	No. of prey/cell (range)	No. of prey/cell (average)	Provision weight wasp wt. (range)	Provision weight wasp wt. (average)	Individual prey wt. wasp wt. (average)
POMPILIDAE						
<i>Batozonellus fuliginosus</i>	2	1	1	2,25–7,61	4,93	4,93
<i>Tachypompilus ignitus</i>	16	1	1	1,00–8,52	4,2	4,2
SPHECIDAE						
<i>Chalybion tibiale</i>	3	15–21	17,4	4,65–6,52	5,87	0,37
<i>Pison montanum</i>	20	7–23	14,5	2,5–7,0	4,9	0,33

The substitution of several smaller prey for a single large one, like the substitution of two-celled or multi-celled nests for single-celled nests discussed above, is achieved by repetition of some of the elements of the behavioural sequence—in this case the elements concerned with hunting, paralysis of the prey, and transport of the latter to the nest.

It is clear that though the number of prey introduced as provision into a single cell may be increased from one to several or many, oviposition within the cell must be limited to a single egg and cannot automatically follow the introduction of each prey into the cell. However, whereas multiple oviposition is universally suppressed, there is variation in the point in time during the provisioning of a cell when oviposition of the single egg occurs. Oviposition may be fixed to be either on the first prey to be introduced into the cell or may be on the last (as in *Cerceris* species) or it may not be determined by order of prey introduction at all but rather by the size or some other particular attribute of one of the prey. This appears to be the case in the sand-nesting sphecid *Kohliella alaris* for which size of prey appears to be a factor in the determination of the prey chosen for oviposition (Gess and Gess, 1980a: 52).

Oviposition upon the first prey to be introduced into a cell may be followed by two distinct forms of provisioning differing in the time span during which the subsequent provisioning (that is introduction of additional prey) is performed. Thus, if rapidly performed, the cell may

be fully provisioned and sealed before the larva hatches from the egg (= mass provisioning). However, if subsequent provisioning is delayed, the larva may hatch before provisioning is completed. Whereas this may be the consequence of a shortage of prey or of weather unfavourable for hunting, some wasps habitually practise delayed provisioning even under optimal conditions. In this case, introduction of the second prey into the cell is delayed until the young larva has at least partially consumed the first (on which the egg was laid) and subsequent prey are similarly introduced only when the larva is ready to consume them (= progressive provisioning). Such is the case in the nesting of *Bembix albofasciata*, at Hilton excavating its one-celled nests in sandy soil.

Whereas oviposition in all the ethological types hitherto discussed has been upon the provision and has thus followed the introduction of one or more prey into the cell, some of the more specialized wasps exhibit transposition of hunting and oviposition and oviposit into an empty cell.

This behaviour is uncommon in the Sphecidae but is known in the genus *Bembecinus*, amongst others, and at Hilton has been described for *B. cinguliger* and *B. oxydorcus* (Gess and Gess, 1975). Oviposition into an empty cell is, however, typical of all Vespoidea and amongst the ground nesting wasps of Hilton has been described for the eumenid *Parachilus insignis* (Gess and Gess, 1976a) and for masarids of the genera *Jugurtia* and *Ceramius* (Gess and Gess, 1980c).

Oviposition into an empty cell, like oviposition onto the first prey to be introduced into a cell, allows either mass or progressive provisioning. Both options are shown by the above wasps. The two *Bembecinus* species practise progressive provisioning at least initially (Gess and Gess, 1975: 38–39) whereas *Parachilus insignis* practises mass provisioning. Mass provisioning is the method used by the Masaridae studied. The contrary belief held by some authors in the past that one of these species (*Ceramius lichtensteinii*) practises progressive provisioning has been exhaustively discussed and shown (Gess and Gess, 1980c: 80–81) to have been based upon incorrect interpretation of delayed provisioning due to external causes. In passing it may be mentioned that the Masaridae are unique amongst the wasps in that (with the exception of one genus) all provision not with insect or spider prey but with a mixture of pollen and nectar. In this facet of their behaviour the Masaridae therefore parallel the bees.

The nesting of the solitary bees recorded excavating their nests in the ground: *Colletes* (Colletidae), *Halictus*, *Lasioglossum*, *Nomioides* and *Nomia* (Halictidae) is similar in many respects to that of the more specialized wasps and follows a sequence of behaviour found also amongst the latter. Nesting is initiated by the excavation of an entrance burrow and of a cell. Provisioning of the cell (with a mixture of pollen and nectar) follows and is completed before oviposition on or near the provision takes place; thereafter the cell is sealed and the next cell is excavated. It will be noted that the relative order of provisioning and ovipositioning in these bees and in the pollen and nectar provisioning wasps (Masaridae) is reversed.

When the nesting of the relevant species of wasps recorded at Hilton is considered with respect to the foregoing account of the ethological types represented in the nesting of the wasps and bees excavating original nests in the soil, an interesting distinction between those species associated with friable and non-friable soils may be discerned. Whereas a wide range of ethological types from the most basic (hunting before nest excavation) to the most advanced is found amongst those species associated with friable soils, only the more advanced types are found amongst those species associated with non-friable soils. Illustrative of this is that in all the species associated with non-friable soils hunting is preceded by nest excavation and that two-celled or multi-celled nests are the rule (though *Bembecinus* and *Parachilus* may occasionally fail to excavate the second cell). Furthermore that in all the species, with the exception of the two *Dichragenia* species, provisioning of each cell is with numerous prey and that oviposition in the empty cell is practised.

It must therefore be postulated that, amongst the wasps and bees excavating their nests in the soil, the association with friable soil is the original one and is primitive and that the association with non-friable soil is secondary and is derived and advanced.

Certainly, the difficulties attendant upon the excavation of nests in non-friable soil precludes those species doing so from possessing the sequence of behavioural elements (hunting before nest excavation) characteristic of the basic or primitive ethological nesting type. On the other hand, the more advanced ethological nesting types seen amongst the species nesting in friable soil are pre-adaptive in overcoming the difficulties imposed by nesting in non-friable soil.

With respect to the relative sequence in which hunting and nest excavation are performed, the primitive sequence (hunting preceding nest excavation) is possible only if the delay in the introduction into the nest of the prey, already at hand and waiting, can be kept to a minimum. This is possible if the nest is being excavated in friable soil in which digging is easy and therefore rapid. However, in non-friable soil where excavation is difficult and therefore slow and furthermore involves the periodic absence of the wasp from the site when fetching water the prey would be exposed for a longer period which would increase the possibility of desiccation, theft or parasitism. Nest excavation preceding hunting is therefore a prerequisite for nesting in non-friable soils.

The change from single-celled to two-celled or multi-celled nests sharing a single entrance burrow common to both or all the cells, though in terms of saved energy and time advantageous to nesters in friable soils, is of even greater advantage to nesters in the more difficult non-friable soils, and must be considered pre-adaptive to nesting in the latter substrate.

Similarly, the substitution in the provisioning of each cell of several smaller prey for a single large one, besides being of importance with respect to ease of transport, must be seen as bringing about a saving in energy and time expended in nest excavation in that the bore of the entrance burrow and the overall size of the cell can thereby be reduced. This again is of greatest advantage to excavators in non-friable soil and can be seen as pre-adaptive to nesting in this substrate.

A comparative reduction in the bore of the entrance burrow and in the size of the excavated cell is achieved also by the two species of *Dichragenia* despite the fact that, like in all Pompilidae, provisioning of each cell is with but a single large spider. In this case reduction of the dimensions of the nest is made possible by the amputation of the legs of the prey. This habit of amputation of the legs of the prey, characteristic of the pompilid tribe Auplopodini, like the change seen in more highly evolved wasps from a single large prey to several smaller ones per provisioned cell, probably serves the primary purpose of greater ease of prey transport but is also pre-adaptive for nesting in non-friable soils.

A prime requisite for the nesting of all nest-excavating wasps, whether nesting in friable or non-friable soils, is the presence of areas of soil partially or totally denuded of plant cover. Thus, at Hilton the most favoured areas for ground-nesting are those which have been modified by man's activities and take the form of paths, car-tracks, a sand-pit, and tracts once denuded of their original plant cover (by ploughing and cultivation) and subsequently only partially covered by mostly pioneer species.

Over the decade during which the nesting of wasps and bees has been studied at Hilton, it has been noticeable that available nesting sites both in friable and in non-friable soils have shrunk due to an increase of plant cover, a trend which, if it continues, will eventually lead to a marked reduction in the size of the nesting communities.

It is obvious that the nest-excavating species associated with friable, sandy soil are able to excavate their nests in this substrate where ever bare patches of it occur within a given area. Species associated with non-friable, clayey soil, however, have no such freedom but are restricted to bare patches of this substrate in those parts of a given area that lie within a certain

maximum distance of a source of water required for soil softening. This distance, which may vary from one species to another, is determined by how far it is economical, in terms of expenditure of energy and time, for a wasp to have to fly to collect this water. In effect, it has been observed at Hilton to limit the nesting areas of the species concerned to tracts of clayey soil in fairly close proximity to water sources (Gess and Gess, 1974: 192; 1975: 24; 1976a: 86; 1976b: 131; 1980c: 64). Other tracts of bare clayey soil, apparently identical in all respects to the above but further removed from water sources are notable for the absence of any nesting wasps.

The water sources most commonly used at Hilton by excavators in non-friable clayey soils are temporary in nature and consist of pools formed after rain in small depressions, in erosion gullies and in a man-made furrow flanking the chief nesting area (Gess and Gess, 1974: Pls 1-4). Infrequent use is made of small puddles left in the river bed but the larger and more permanent water bodies, the dams, are unused. It follows therefore that nesting is dependent upon the occurrence of rain and of run-off filled water holes and that it can continue only for as long as the water supply lasts. In contrast therefore to those wasps excavating their nests in friable sandy soil, which as a community may be found in any one year to nest continuously over a long period, from early spring to late autumn, the wasps excavating their nests in non-friable clayey soil and requiring water for nest excavation are as a community in any one year frequently restricted to a very much shorter nesting period, or have an interrupted nesting period, determined by the time and abundance of rainfall and by the availability of water in temporary pools. Though these wasps individually and as a community have the potential for a long nesting period, like that seen in the sand nesters, it is frequently not realized and in several summer seasons it has been seen to have been arrested at or near its height by the failure of the water supply. This is particularly noticeable with respect to *Bembecinus cinguliger*.

In the light of the physical difficulties attendant upon the excavation of nests in non-friable clayey soils and the spatial and temporal restrictions imposed upon nesting in such soils due to the requirement that water be available to the wasps where and when nesting is undertaken, it must be asked what led certain groups of wasps to leave a friable substrate in favour of a non-friable one.

The answer must be postulated to lie on the one hand in a response to the pressure of interspecific competition for available nesting sites and prey with respect to one substrate and on the other hand in a response to the existence of another, unexploited substrate with its associated community of unexploited potential prey species.

The ability of certain wasps to adapt to excavating nests in the previously unexploited non-friable clayey soils allowed the spread of ground-nesting wasps into tracts of country which had such soils and from which the latter had hitherto been debarred. Moreover, in situations as at Hilton where both soil types occur in close proximity a given area including both soil types can support a greater number of soil-excavating species than could the same area if only one soil type were included.

The presence at Hilton of both soil types must be seen as the key to the co-existence there of large nesting populations of four species of *Bembecinus*, two, *B. cinguliger* and *B. oxydorcus*, associated with non-friable soil and two, *B. braunsii* and *B. haemorrhoidalis*, associated with friable soils. Whereas it is immediately apparent that there is no competition between the two pairs of species for nesting sites, there is likewise no competition for prey. Examination of the prey recovered from the cells of the four wasps shows that whereas provisioning by all the species is with numerous species of (mostly) Cicadellidae and that both nymphs and adults, males and females, large and small individuals are utilized, the specific composition of the prey of the two pairs of *Bembecinus* species is completely different though within a pair of species it is similar. This situation is a reflection of the observed fact that the two soil types support

different plant communities which in turn have feeding upon them different complexes of Cicadellidae and furthermore that the *Bembecinus* species do not hunt at any great distance from their nests and therefore exploit those prey found on vegetation growing on the soil type to which they (the wasps) are themselves restricted.

Whereas the use for nest excavation of non-friable soils appears to have been adopted only very rarely and sporadically by the Pompilidae and the Sphecidae, it is typical of almost all the ground-nesting Eumenidae and of all the ground-nesting species of the allied Masaridae. This has in effect freed the Vespoidea from competing with the vast majority of the Pompilidae and Sphecidae for nesting sites in the ground.

Of interest are those Eumenidae which, atypically, do excavate their nests in friable, sandy soil—species of *Pterocheilus*, divided by Bohart (1940) into a number of subgenera. These sand-nesting Eumenidae, unlike the sand-nesting Pompilidae and Sphecidae, do not possess sandrakes on the fore-legs, which limbs do not differ in structure from those of the clay-nesting and water-utilizing *Parachilus insignis*. Instead, for the removal of the burrow of the sandy material loosened by the mandibles, the wasp possesses a "sand basket" formed by long hairs fringing the outer edges of the mandibles and by others fringing the second and third segments of the long pendulous labial palps (Evans and Éberhard, 1970: Fig. 55).

It must be postulated that the Vespoidea evolved from forms associated with friable soils, that at an early stage in their evolution they forsook nesting in that soil type in favour of nesting in non-friable soil and that forms such as *Pterocheilus* now found nesting in friable soil secondarily returned to that substrate. However, the Eumenidae having as a group earlier lost any fore-tarsal digging organs, removal of excavation spoils by the sand-nesting species is by means of the mouthparts as in the pellet-carrying, water-utilizing, clay-nesting species from which the sand-nesters are probably derived.

It has been shown above that the substitution in the provisioning of each cell of several smaller prey for a single large one was advantageous in terms of greater ease of transport of the prey and greater economy of labour consequent upon the construction of nests of smaller dimensions. However, a disadvantage introduced with the substitution is that cell closure has to be delayed until after the last of several or many prey has been placed in the cell and that the partially provisioned cell is left unattended by the wasp during the time the latter is away hunting for additional prey. During this time, the open, partially provisioned cell is in danger of attention by parasites of one sort or another unless some means are employed to exclude them.

This exclusion of at least a certain proportion of parasites is effected by many of the species excavating their nests within friable soil by the maintenance of a temporary closure at the nest entrance. In the present study, this is described for the sphecid *Kohliella alaris* (Gess and Gess, 1980a: 52) which rakes sand respectively into or out of the nest entrance each time it leaves or returns to the nest.

So easy and quick a way of closing and opening a nest is clearly possible only in friable soil and it must be asked how those wasps nesting in non-friable soil have solved the matter of the exclusion of parasites. The answer may be sought in a comparative study of certain aspects of the nesting of a genus including both sand- and clay-nesters—in the present instance the genus *Bembecinus*.

All four species of *Bembecinus* studied at Hilton construct temporary nest closures but the frequency with which these are fashioned differs between the sand-nesting and clay-nesting species.

In the sand-nesting *B. braunsii* and *B. haemorrhoidalis* temporary nest closures are maintained throughout the wasps' working day whenever the wasps are not within their nests. In the clay-nesting *B. cinguliger* and *B. oxydorcus*, however, temporary closures, in the form of mud plugs sited in the entrance shafts (and in *B. oxydorcus* at the turret opening as well) (Gess

and Gess, 1975: Figs 11 and 16), are constructed only at the end of each working day and the first action by the wasps on returning to the nesting sites at the beginning of the following working day is to remove these mud plugs. Therefore, whereas the nests of *B. braunsii* and *B. haemorrhoidalis* are open only for short periods during which the wasps are introducing prey, those of *B. cinguliger* and *B. oxydorcus* are open for the full duration of the wasps' working day, whether the wasps are present in the nests or not. As it is not an unreasonable assumption that parasite pressure on *Bembecinus* should be similar in the two nesting substrates—indeed at Hilton species of Mutillidae, notably *Smicromyrme hecuba*, are commonly found associated with all four species—the lack of a temporary closure during the working day of *B. cinguliger* and *B. oxydorcus* must be compensated for by some other factor. In the absence at the time of cell provisioning of any other behavioural difference between the two pairs of species, the factor can only be an additional difference in the physical nature of the nest, namely the presence in those species omitting the temporary closure of the mud superstructures surmounting the nest entrances. The hypothesis is therefore put forward that in *Bembecinus* at least, the mud superstructures serve as a protection against the entry of parasites into the nest.

Possibly a similar rôle may be assigned to the nest superstructures built by at least some of the other species. Oldroyd (1964: 132) has pointed out that Bombyliidae seen hovering close to the ground are not always looking for flowers but may be actively egg laying, the egg being dropped near the burrow of a solitary bee or wasp. Furthermore, Painter (1932, as reported by Clausen, 1940: 377) recorded experiments in inducing oviposition by a hombyliid, *Villa* sp., which develops in the cells of solitary bees. The eggs were reported to be "readily projected into glass vials buried in the soil to simulate the nest openings of the host". It would appear that the stimulus to oviposit by the hovering fly is visual and consists of the sight of a small, dark, round hole in the ground. It does not seem unreasonable therefore to suggest that the removal of the stimulus to oviposit by the concealment of the dark hole in the ground would be of survival value to those wasps which leave their nest entrances open—that is, those wasps that nest in clayey soils. In many of these wasps concealment from above of the burrow entrances is effectively achieved by covering them with curved turrets and it is therefore postulated that these superstructures are a defence against parasitization by Bombyliidae. It is perhaps significant that the only bombyliid larva found during the course of the excavation of very many nests of a variety of species nesting in clayey soils was in a cell of *Parachilus insignis* (Gess and Gess, 1976a: 97), a species which surmounts its nest entrance not with a curved turret but with a low collar which does not conceal the "dark, round hole".

In addition to the probable value of at least some nest superstructures in excluding certain categories of parasites, it is certain that all superstructures, even those consisting only of a low collar surrounding the nest entrance serve to prevent loose, powdery clay soil and other fine wind-blown debris from entering the nest shafts. This may well be of value to wasps which lack both the physical equipment (tarsal sand rakes) and the behaviour requisite for the removal of fine, loose material from their burrows.

Finally, the more extensive of the superstructures covering nest entrances serve to protect the nests against flooding for upon being well wetted by rain or surface run-off the superstructures collapse upon the nest entrances, effectively blocking them. The nest collar of *Parachilus insignis* is clearly too small to serve this function. However, as described in detail by Gess and Gess (1976a: 99) the wasp nevertheless protects its nest from flooding by blocking the nest shaft with its own body and by allowing a plug of water-borne mud to form above it.

Among the 167 species of ground-nesting wasps and bees recorded during the survey at Hilton, thirteen species were found to nest not in burrows of their own excavation but in pre-existing cavities which they, however, modify by the construction within them of a cell or cells. The thirteen species concerned are listed in the annotated list of species under categories

2 and 5. Four families were represented: Eumenidae (1 species), Sphecidae (6 species), Megachilidae (5 species) and Anthophoridae (1 species).

A necessary pre-condition for the nesting of these species is the presence in the ground of pre-existing cavities of a bore suited to their individual requirements. The pre-existing cavities most often used are burrows excavated for nesting purposes by other, nest excavating, aculeates. Usually these burrows are no longer being used by their excavators but are newly excavated burrows that have been abandoned for some reason or another (such as the death of the builder) or are old burrows, excavated in a previous nesting season, from which the wasps that developed within them have emerged. There is very little evidence that competition for burrows occurs between the original burrow excavators and the users of pre-existing cavities—that is, burrows do not appear to be usurped if still in use.

It will be seen from Table 2 and from the Pie-diagram (Fig. 16) that, whereas in non-friable soil the number of species nesting in modified pre-existing cavities approximates the number of species excavating original nests, in friable soil the number nesting in modified pre-existing cavities is very low indeed. This is all the more striking on account of the far greater number of species excavating original nests in friable soil than in non-friable soil.

The reason for the difference which is clearly substrate-determined is probably due largely to the fact that a burrow excavated in non-friable clayey soil is stable and long-lasting whereas one excavated in friable sandy soil tends if it is not maintained to collapse or fill with loose material after even a short time. This is of particular relevance to old burrows from which wasps or bees have emerged. With respect to newly excavated but abandoned burrows, it must be remembered that wasps excavating in friable soil frequently maintain a temporary closure at the nest entrance which would render such burrows inaccessible to seekers of pre-existing cavities even when the original "owners" of such nests had suffered some misadventure during hunting or foraging. The opposite would pertain to burrows excavated in non-friable soil particularly where the clay nest superstructures are incomplete or broken.

It appears that the thirteen species recorded as making use of pre-existing cavities (burrows) in the ground may be divided into those for which such behaviour is obligatory and those for which it is facultative.

Among the former are the five megachilid bees belonging to the genera *Megachile* and *Creightoniella*. One of these bees, *Megachile semiflava*, has been recorded as making use of pre-existing burrows in both the non-friable clayey soil and the friable sandy soil and there seems no reason why the other species should not show a similar lack of restriction to a particular soil type. All five species construct their cells within the pre-existing cavities with foreign materials—green leaves or in the case of *M. meadowaldoi* the petals of low-growing flowers.

Other species for which nesting in pre-existing cavities is obligatory are the sphecid *Pison allonymum* and an unidentified eumenid known only by its turret which it had constructed surmounting that of *Bembecinus oxydorcus*, the burrow of which species it was using. Both species are probably derived from forms which used water to excavate nests in non-friable soils. Though the ability to excavate nests has been lost, both species remain associated with clayey soils due to their use of mud in modifying the burrows in which they nest.

The nesting of all the above species involves the modification of the chosen pre-existing cavities by the introduction into them of foreign materials for cell construction prior to the gathering and introduction of provision.

Very primitive in comparison is the presumed nesting behaviour of *Ampulex mutilloides* which though not actually found nesting is included in the present category on considerable circumstantial evidence.

Ferruginous and metallic blue and thus atypical in colouration, this *Ampulex* looks very mutillid-like (as attested by its specific epithet), a similarity that is enhanced by the fact that in

the experience of those who have seen the species in the field (the present author and the late C. F. Jacot-Guillarmod—*pers. com.*) it is only met with on the ground. The fact that the Hilton specimen, a freshly emerged female, had clayey soil adhering to her head strengthens the view that this species nests in the ground. Probable prey is *Pilema thoracica*, a cockroach excavating burrows in clayey soils in the area in which the wasp was found walking on the ground.

In common with other species of *Ampulex*, nesting would be commenced with hunting which would be followed by the introduction of the single prey into an unmodified pre-existing cavity which would then be closed with detritus. If the above interpretation of the nesting of *A. mutilloides* is correct, this wasp would be restricted to nesting in clayey soils as it is there that its prey occurs. Furthermore, it is possible that the pre-existing cavities used by the wasp are the burrows excavated in the soil by the cockroach.

Species for which nesting in pre-existing cavities in the ground appears to be facultative and determined by the nature of the substrate are *Prionyx kirbii*, *Tachysphex* sp. near *modestus* and possibly *Tachysphex modestus* itself (all Sphecidae) and *Tetralonia minuta* (Anthophoridae).

Prionyx kirbii and *Tachysphex* sp. near *modestus* both have well developed tarsal sand rakes and may therefore be expected to excavate original burrows in friable soil. This indeed is the case with the common *P. kirbii* which has been observed at Hilton to excavate original burrows in the sandpit. *Tetralonia minuta* also is probably capable of excavating original burrows. Though this is not actually stated it may be inferred from the account of the nesting of this bee given by Rozen (1969a).

What are these species doing then in pre-existing cavities? The only explanation is that these species have some plasticity of behaviour and that, in non-friable soil, burrow excavation is initiated not at the surface of the soil but at the bottom of a pre-existing cavity: the old or abandoned burrows of *Parachilus insignis* in the case of *P. kirbii* and *T. sp. near modestus*; the old or abandoned burrows of *Parachilus insignis* or of *Bembecinus cinguliger* in the case of *T. minuta*. In some instances at least (as with *P. kirbii* and *T. sp. near modestus*) the pre-existing cavity may already approximate in dimensions the burrow excavated in friable soil so that little additional excavation need be done. With respect to *T. minuta* which appears to make deeper and more complex nests than do the two sphecids it is probable that the initial use of a pre-existing cavity enables the bee to start its own excavation at a depth at which the soil may be moister and consequently softer and where it is therefore easier to excavate.

In all cases, the use of pre-existing cavities as a starting point for nest excavation allows these species to extend their distribution into areas of non-friable soil where nesting in the manner normal to them would be precluded or would at best be very difficult. That the use of pre-existing cavities by these species is simply a short cut in nest excavation adopted in hard clayey soil and does not represent any radical change of behaviour is shown by the fact that both *P. kirbii* and *T. sp. near modestus* do remove considerable quantities of soil from the bottom of the pre-existing cavity. *P. kirbii* arranges the material removed from the cavity in a circle around the burrow opening (Fig. 24); *T. sp. near modestus* places it only to one side of the opening (Fig. 25). Both species prepare the burrow before hunting and *P. kirbii* carefully positions three or four small clods of earth as a temporary closure at the entrance of the modified pre-existing cavity before she leaves to hunt.

Sixty-four of the 167 species of ground-nesting wasps and bees recorded during the survey at Hilton are listed, under categories 3 and 6, as developing within pre-existing cavities which they do not themselves modify. Ten species were recorded from non-friable soils, 50 species were recorded from friable soils and four species, all Mutillidae, were recorded from both friable and non-friable soils. It must be pointed out, however, that the above figures pertaining to the two soil types are not directly comparable for, whereas all 14 species listed for non-

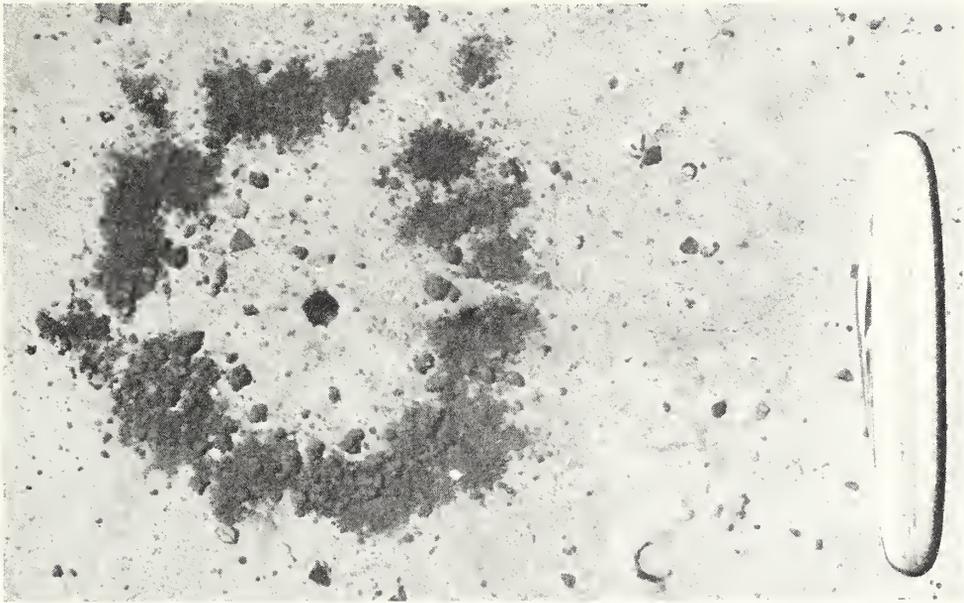


Fig. 24

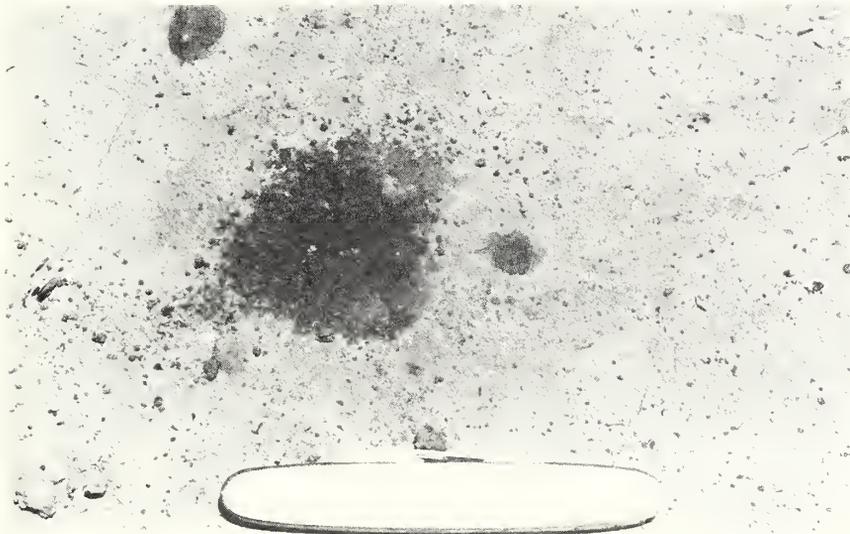


Fig. 25

Figs 24 and 25. Entrances of old burrows of *Parachilus insignis* used for nesting by *Prionyx kirbu* (Fig. 24) and by *Tachysphex* sp. near *modestus* (Fig. 25), showing arrangement of material removed from the pre-existing cavities by these wasps. ($\times 0,7$)

friable soils are "parasitic" in one way or another in what are to them pre-existing cavities—cells constructed and provisioned by other wasps and bees and occupied by the eggs or immature stages of these species, this is true of only 26 of the 54 species listed for friable soils. The remaining 28 species listed for friable soils are associated with the larvae of Coleoptera, with one exception (*Methocha mosutoana*) those of Scarabaeidae, which are sought for and attacked in their burrows, often deep in the ground, where, after they have been oviposited upon, they are usually left *in situ*.

Those species which are "parasitic" in the cells of other aculeate Hymenoptera and are therefore dependent upon the occurrence of the latter for their own presence belong primarily to the families Chrysididae (12 species) and Mutillidae (17 species). A few other families are represented as well, namely Pompilidae (*Ceropales punctulatus*), Sphecidae (*Nysson braunsi*), Halictidae (*Sphedes* sp.), Megachilidae (*Coelioxys bruneipes* and *C. lativentroides*) and Anthophoridae (*Epeolus amabilis* and *Thyreus* sp.).

TABLE 4.

Secondarily cleptoparasitic ground-nesting species and their established or presumed hosts. (For authorities see annotated list.)

CLEPTOPARASITE		HOST	
Genus & Species	Family	Genus & Species	Family
<i>Ceropales punctulatus</i>	Pompilidae	<i>Dichragena pulchricoma</i>	Pompilidae
<i>Nysson braunsi</i>	Sphecidae Nyssoninae	<i>Oryttus kraepelini</i>	Sphecidae Nyssoninae
		OR <i>Dienoplus vicarius karrooensis</i>	Sphecidae Nyssoninae
		OR <i>Hoplisoides aglaia</i>	Sphecidae Nyssoninae
		OR <i>Hoplisoides thalia</i>	Sphecidae Nyssoninae
<i>Sphecodes</i> sp.	Halictidae	<i>Nomia</i> sp.	Halictidae
<i>Coelioxys bruneipes</i>	Megachilidae	<i>Megachile semiflava</i>	Megachilidae
<i>Coelioxys lativentroides</i>	Megachilidae	<i>Megachile</i> sp.	Megachilidae
		OR <i>Creightoniella</i> sp.	Megachilidae
<i>Epeolus amabilis</i>	Anthophoridae	<i>Colletes</i> sp.	Colletidae
<i>Thyreus</i> sp.	Anthophoridae	?	?

Ethologically the species belonging to families other than Chrysididae and Mutillidae are possibly the most interesting for all are derived from non-parasitic forms and the cleptoparasitism now practised by them is therefore secondary or derived. As may be seen from Table 4 most of the species are related to their hosts and in each case host and cleptoparasite must therefore have a common origin.

In all cases the cleptoparasitic way of nesting has been arrived at by a reduction in the number of elements in the behavioural sequence performed by the parasite, the "missing" elements being supplied by the host. For example, the pompilid *Ceropales punctulatus*, recorded as cleptoparasitic in the nests of *Dichragenia pulchricoma* (Gess & Gess, 1974: 202, 204) and assumed to behave like other species of its genus, restricts its nesting activity to hunting and oviposition. Hunting, however, is not for a free active spider but for one already captured and stung by the host pompilid and oviposition (inside the booklungs) takes place before the host has installed the spider in its cell. There the *Ceropales* egg hatches before that of its host and the young foreign larva after destroying the latter feeds upon the spider. In the case of *Ceropales* most of the labour involved with nesting is therefore supplied by its host, *Dichragenia*, namely construction of the cell, hunting of the spider prey, stinging of the prey, transport of the prey to the cell, and closure of the cell.

The cleptoparasitic bees behave similarly in so far that all the labour involved in nest construction and provisioning is supplied by their hosts. Concomitant with the adoption of a cleptoparasitic way of life has been the secondary loss of the pollen-collecting apparatus and therefore the ability to provision cells. The search for cells already provisioned with a mixture of pollen and nectar by the host bees therefore replaces the search for flowers from which to obtain these substances and flower-visiting by cleptoparasitic bees is therefore restricted to the purpose of obtaining their own nutriment.

In contrast to the above discussed species, the species of Chrysididae and Mutillidae, all of which are "parasitic", are not related to their hosts.

The Chrysididae show similarities in their ethology to the cleptoparasitic Pompilidae, Sphecidae and Apoidea in so far that the majority of species develop on the provision stored by their hosts, the egg being introduced into the cell while this is being provisioned. Such appears to be the case with respect to *Octochrysis vansoni* which was recorded (Gess & Gess, 1976a: 97) as attending the open nests of *Parachilus insignis*, inspecting these when they were left unguarded and occasionally entering them, presumably in order to oviposit in the cells. In behaviour *O. vansoni* is therefore clearly cleptoparasitic.

The Mutillidae on the other hand do not develop on the stored provision but limit their attack to fully fed, diapausing larvae or pupae, the female mutillid breaking into a cell containing a cocoon into which she introduces her egg. Feeding upon the host within its cocoon is followed by the mutillid larva spinning its own cocoon within that of its host, as recorded (Gess & Gess, 1980c: 76) for *Dasylabroides caffra* in the cells of *Ceramius lichtensteini*. In behaviour *D. caffra*, like other Mutillidae, is therefore clearly a parasitoid. This term has been used (Evans & Eberhard, 1970: 9) with respect to a species which cannot be considered a true parasite (because it kills its host) nor a true predator (because it is confined to a single prey individual).

The remaining 28 species listed as developing within pre-existing cavities which they do not themselves modify are species of Tiphidae and Scoliidae. As already stated all are associated with the larvae of Coleoptera, the majority with those of Scarabaeidae. All were found in association with friable soil for it is only in such soil that the beetle larvae and the female wasps hunting them are able to dig. In no case was the nesting investigated and only one species was associated with its prey: *Methocha mosutoana* (Tiphidae) with *Cicindela brevicollis* (Cicindelidae).

Vertical banks

The vertical banks studied at Hilton are situated at the sandpit and in places along the course of the New Year's River. At the former locality the banks are man-made and constitute the actual walls of the sandpit whereas in the other localities they have been cut by the river and constitute the banks thereof. Mostly the latter are situated at a height above the river bed reached by water only during times of flood.

The banks of the sandpit and a section of the river bank near the confluence of the Iron Put River with the New Year's River are composed of firmly compacted very fine sand. Going downstream along the course of the latter river the physical nature of the banks changes, increasing amounts of clay being mixed with the sand. In places the mixture of sand and clay has apparently been affected by recent mineralization and has assumed the character of a weak and crumbly sandstone-like material. Still further downstream the western bank of the river is formed by the face of a low cliff cutting across roughly horizontally bedded shale.

Though the sand and shale banks clearly constitute very different substrates, those banks composed of mixtures of sand and clay and including both mineralized and unmineralized portions, cannot, on account of their variability, be placed in a single class. It seems preferable therefore not to attempt to further classify the banks on the basis of the physical nature of the materials of which they are composed but to deal with all banks together. However, where it is relevant, attention will be drawn to substrate-determined differences in the nesting of the wasps and bees concerned.

Wasps and bees which nest in association with vertical banks may be divided into those which nest within the banks and those which nest on the banks and use the latter solely as a raised support to which to attach their aerial nests.

At Hilton the number of species recorded as nesting in association with vertical banks totals 51, made up of 43 species nesting within the banks, 6 nesting in aerial nests on the banks and 2 nesting both in the banks and in aerial nests on the banks. On account of the latter species the number of species/substrate associations exceeds the actual number of species by 2 and therefore stands at 53. An analysis of this figure according to the degree of participation of species of wasps and of bees in the construction of their nests is given in Table 5 and is shown graphically in the Pie-diagram (Fig. 26).

TABLE 5.

Number of species of aculeate wasps and of bees nesting in or on vertical banks.

	In nests constructed entirely by the nesters themselves	In modified pre-existing cavities	In unmodified pre-existing cavities
In vertical banks	4	20	21
On vertical banks	5	1	2

With regard to the nesting of wasps and bees a vertical bank resembles level ground with respect to the nature of the substrate which it offers but differs with respect to the angle at which this substrate is presented.

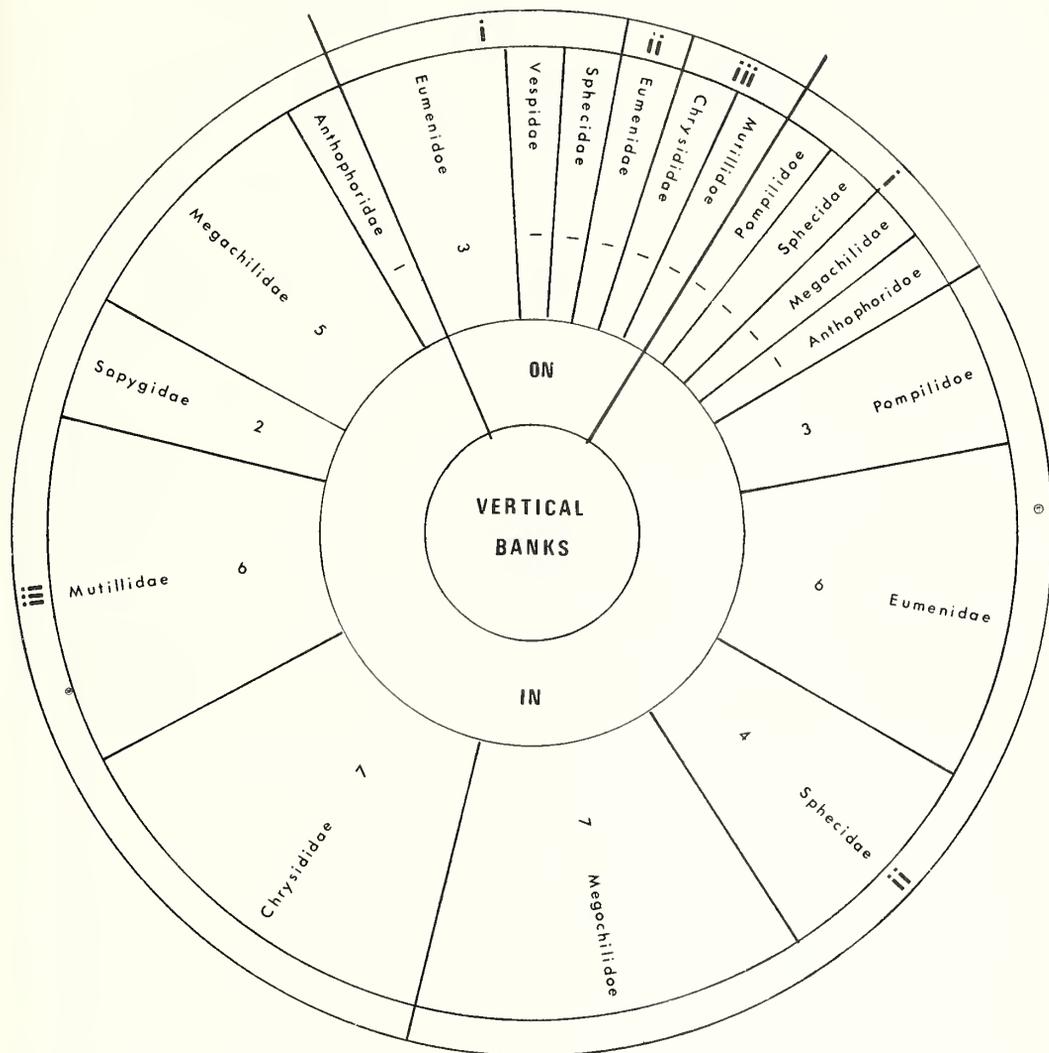


Fig. 26. Diagram showing the structure of the communities of the aculeate wasps and the bees nesting in or on vertical banks in the study area. Numbers accompanying the family names represent numbers of species. The numbers (i, ii, iii) in the outermost ring correspond to the same numbers in the classification of the aculeate wasps and the bees of the study area on the basis of their ethology. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester.

The difference in the angle of presentation of the soil surface—vertical as opposed to horizontal—has a very profound influence upon nesting. Illustrative of this is that, with the possible exception of *Pison allonymum*, there is no sharing of species between level ground and vertical banks. Indeed, both nesting situations are characterized by communities of species

unique to themselves. It is furthermore very noticeable that in the two nesting situations there is a marked difference between the proportion of species excavating their nests and those modifying pre-existing cavities. In level ground as has already been shown, nest excavators greatly outnumber nest modifiers (91 as against 14) whereas in vertical banks the opposite is true, nest excavators being outnumbered by nest modifiers (4 as against 20).

In view of the great dissimilarity between the communities nesting in vertical banks and in level ground, it is of interest that some points of similarity exist between the former community and that nesting within plant tissue, at least with respect to those species which do not excavate or hollow out their nests themselves but modify pre-existing cavities. Thus at Hilton at least seven species nesting in pre-existing cavities are shared between vertical banks and plant tissue, namely *Euodynerus euryspilus* (Eumenidae), *Chalybion* (*Chalybion*) *tibiale*, *Pison montanum* and *Trypoxylon* sp. (Sphecidae), and *Immanthidium junodi*, *Megachile gratiosa* and *Megachile spinarum* (Megachilidae). *Rynchium marginellum sabulosum* (Eumenidae) at Hilton found nesting in trap-nests inserted into crevices in the "sandstone" bank but known in Grahamstown to nest in cut culms of the reed *Arundo donax* used for vegetable frames may probably be added to the above listed species.

Furthermore, the preponderance of nest-modifiers over nest excavators characteristic of the vertical banks is evident also with respect to plant tissue.

Characteristic of the community nesting within the vertical banks studied is the dominant rôle played by bees, both in terms of number of species and number of individuals. Thus, of the four species of wasps and bees listed as excavating their nests in the vertical banks, only the two bees, *Hoplitis anthodemnion* (Megachilidae) and *Anthophora* sp. (Anthophoridae) are of any real importance. Common to the degree of being by far the most noticeable species, their presence is fundamental to the existence of a large part of the rest of the community as a whole, for it is their abandoned galleries that constitute the pre-existing cavities which are sought for and modified by a much larger number of diverse species of wasps and bees which do not excavate their nests themselves (Fig. 27). Furthermore, among the latter cavity-

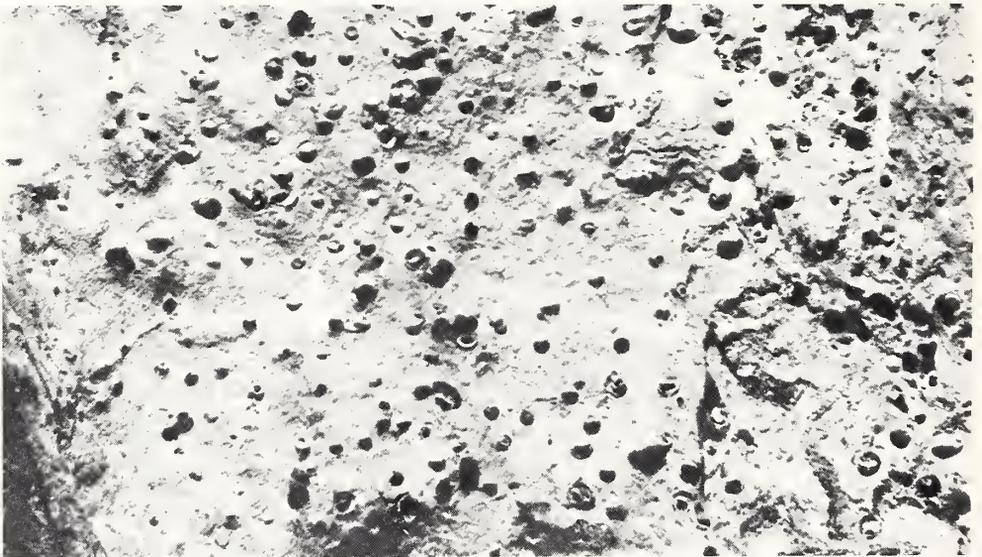


Fig. 27. Small portion of the surface of the "sandstone" bank showing the abundance of old nesting galleries available to nesters in pre-existing cavities.

modifying species, twenty in number, the Megachilidae with seven species is the best represented family. Involved are *Anthidiellum kimberleyanum*, *Branthidium braunsii*, *Chalicodoma schulthessi*, *Heriades ?freygessneri*, *Immanithidium junodi*, *Megachile gratiosa* and *M. spinarum*. Though in terms of numbers almost equally by the Eumenidae the bee family nevertheless considerably surpasses the latter in number of individuals. Bees are well represented also amongst those species which nest parasitically in the nests of other species, five Megachilidae, namely *Euaspid abdominalis*, *Coelioxys lucidicauda*, *C. bruneipes*, *C. lativentris* and *C. lativentroides*, and one species of Anthophoridae, *Thyreus* sp., being listed.

Taken altogether, bees represent 33% (15 out of 45) of the total number of species listed as nesting within vertical banks. Comparative figures for nesters within level ground and within plant tissue are 10% (17 out of 167) and 46% (18 out of 39) respectively. It may be seen that, gauged with respect to the relative numerical representation of species of bees and wasps in the different nesting substrates, vertical banks once again appear to have more in common with plant tissue than with level ground.

With regard to the different substrates offered by vertical banks at Hilton, that consisting of recently mineralized mixtures of sand and clay and referred to as "sandstone" supports the largest community, both in terms of number of species and number of individuals. This is on account of the fact that it is in this sandstone-like material that the principal nest excavators, *Anthophora* sp. and *Hoplitis anthodemnion*, are most active; indeed *H. anthodemnion* appears to be restricted to this substrate. *Anthophora* sp. on the other hand also nests in sand banks but not as commonly. Clearly no nest-excavators are able to nest in the shale bank.

Whereas many of the wasps and bees nesting in modified pre-existing cavities are restricted to the sand and in particular to the "sandstone" banks, probably on account of their dependence upon the presence of old abandoned galleries of the above two nest-excavating bees, a few species have in addition colonized the shale bank where they make use of pre-existing cavities in the form of open cracks between and within individual layers of the shale. Such is the case with respect to Eumenid A and *Tricarinydnerus guerinii* (both Eumenidae) and probably also *Megachile gratiosa*. At Hilton *T. guerinii* has been found nesting in vertical banks presenting all three major substrates and is possibly the most characteristic species of vertical banks (Fig. 28). Its nest which is furnished with a downturned mud turret is invariably sited in a protected situation such as under an overhang where it is protected from the weather and particularly from rain.

Protected situations are sought also by those species which nest not within banks but construct aerial nests upon them, as was demonstrated by the location of recorded nests: a naked comb made of "wasp paper" by *Ropalidia* sp. A. was sited in a fist-sized cavity in a sand bank; a mud nest of *Sceliphron spirifex* was built in a similarly sized cavity in the "sandstone" bank; and urn-shaped mud cells of *Eumenes lucasius* were found attached to the face of the shale bank under overhangs.

On stones lying upon the ground

At Hilton, stones lying upon the ground were found to represent the least used of all four nesting situations with only four of the 241 species included in the annotated list associated with it. It is clear therefore that this nesting situation is of very little importance with respect to the nesting of the community as a whole. However, it must be taken into consideration that all nests associated with stones are aerial in nature and that a true assessment of the status of this nesting situation can therefore only be arrived at by comparison with the status of aerial nesting associated with other nesting situations. Thus it may be seen that the number of species (2) constructing original nests on stones though smaller is nevertheless comparable to the numbers of species constructing original nests on vertical banks (5) and on plants (5).

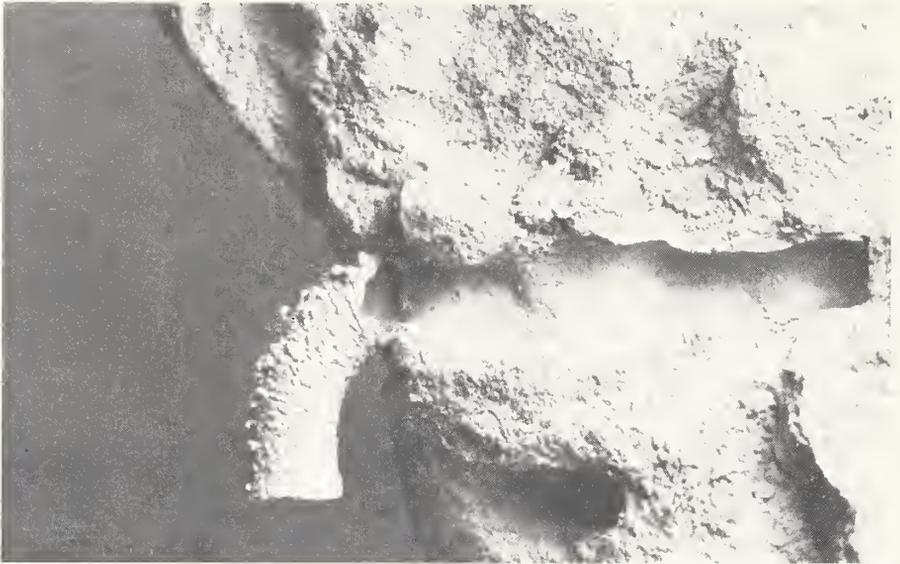


Fig. 28. Section through "sandstone" bank showing pre-existing cavity modified for nesting and furnished with a down-turned mud turret by *Tricarnodynerus guerinii*. ($\times 1,6$)

The two species constructing original nests on stones differ in the placement of their cells. Whereas *Auplopus rossi* (Pompilidae) builds its cells in a sheltered position on the underside of large stones lying loose upon the ground (Fig. 10), *Hoplitis jansei* (Megachilidae) builds its cells fully exposed on the upper surface of partially buried stones and boulders (Fig. 11). In the case of the former species a sheltered position for the placement of the cells is essential as these are made of dried mud, are thin-walled and fragile, and would consequently melt and collapse if exposed to rain. The cells of *Hoplitis*, by contrast, are made of plant resin in which are set numerous small pebbles and are consequently waterproof and of great mechanical strength.

The cells of *Hoplitis* being fully exposed on the upper surface of stones and boulders, are clearly potentially subject to extremes of temperature, both high and low, which might well be detrimental to the bee young within them. There may therefore be a good reason with respect to survival why the bee builds only on those stones which are partially buried in the ground for these stones by virtue of the fact that heat can be exchanged between them and the ground would not become as hot or as cold as similar stones lying loose upon the ground with as a consequence a reduced capacity for heat exchange.

The nesting of *Auplopus rossi* in aerial mud cells which though separate are built in close proximity to one another is of the most advanced and specialized ethological type exhibited by the Pompilidae. It has been shown by Evans (1953: 161) that this ethological type may be derived from that exhibited by those ground-nesting Pompilidae which prepare the cell before hunting. This advanced sequence of behaviour has already been discussed with reference to the two turret-constructing, clay-soil nesting *Dichrageria* species occurring at Hilton. The mastery of the technique of using water to work clayey soils shown by species such as the latter may be seen as presaging the eventual abandonment by some species of the ground as a nesting substrate in favour of nesting aerially. There is thus a change from mud being merely a

by-product of nest excavation to be used in turret construction to mud being purposively mixed to provide the material used for cell construction.

Only one species was found to modify pre-existing cavities associated with stones on the ground: *Megachile gratiosa* (Megachilidae) which constructed its own cells, made of pieces of leaves, within old, abandoned and therefore open resin and pebble cells of *Hoplitis jansei*.

Antennotilla phoebe (Mutillidae), a parasite, was reared from the unmodified cells of its host, *Auplopus rossi*.

Plants

Wasps and bees which nest in association with plants may be divided into those which nest within plants, in galleries within plant tissue, and those which nest on plants and use the latter solely as a raised support to which to attach their aerial nests.

With respect to those species which nest within plant tissue, it is necessary that the parts of the plants concerned should be thick enough to contain the nesting galleries and that the hollow parts should retain their physical structure for at least as long as it takes the species nesting within them to complete their development from egg to adult and to emerge from the nest. Parts of plants fulfilling these requirements are certain stems and, in the case of larger shrubs and trees, branches.

Just as soils are divisible on the basis of whether they are sandy or clayey, so plant stems may be divided on the basis of their internal cellular development and may be classified as woody, pithy or hollow. The nature of each stem determines which species may be able to prepare galleries within it and each of the three stem types therefore has associated with it species peculiar to itself. The internal nature of a stem or branch, however, has no direct bearing upon those wasps and bees using plants merely as sites to which to attach aerial nests. Therefore, whereas the nesting of those species nesting within plant tissue is dealt with with reference to the nature of the stems, the nesting of those species attaching aerial nests onto plants is dealt with irrespective of the natures of the plants concerned.

At Hilton, the number of species recorded as nesting in or on plants totals 44, made up of 39 nesting within plant tissue and 5 nesting in aerial nests on plants. Of those nesting within plant tissue, 17 (43,5%) were associated only with woody stems, 12 (31%) were associated only with pithy stems, and 1 (2,5%) was associated only with hollow stems. Nine species (23%) were associated with two or all three stem types.

On account of the species which were recorded in two or three stem types, the number of species/substrate associations exceeds the actual number of species by 14. The number of species/substrate associations with respect to those species nesting in plant tissue is therefore 53 and the total number of species/substrate associations for both those species nesting within and on plants is 58. An analysis of this figure according to the degree of participation of species of wasps and of bees in the construction of their nests is given in Table 6 and is shown graphically in the Pie-diagram (Fig. 29).

With respect to those species which themselves prepare galleries in plant stems there is complete specificity as regards stem type. Pithy stems are by far the most commonly utilized and the number of species recorded (nine) could probably be more than doubled. Besides the two species of *Ceratina* listed, approximately another ten species belonging to the genus are known to occur at Hilton.

Species preparing their galleries themselves belong chiefly to the Anthophoridae (*Xylocopa* and *Ceratina*; large and small carpenter bees, respectively) and the Sphecidae (*Dasyproctus*). *Raphiglossa natalensis* of the Eumenidae, known to occur at Hilton but to date not found nesting, is included among the gallery-excavators on the authority of Meade-Waldo (1913) and Bequaert (1918).

TABLE 6.

Number of species of aculeate wasps and of bees nesting in or on plants.

	In nests constructed entirely by the nesters themselves	In modified pre-existing cavities	In unmodified pre-existing cavities
In woody stems	2	18	6
In pithy stems	9	8	3
In hollow stems	1	4	2
On plants	5	—	—

In their choice of nesting substrates it appears that these bees and wasps exhibit marked ecological displacement. In the present study this can best be illustrated with reference to the nesting of the four species of large carpenter bees recorded at Hilton: *Xylocopa caffra*, *X. caffrariae*, *X. divisa* and *X. sicheli*.

X. caffra and *X. divisa* have been observed to be confined to thick riverine bush where as far as can be established they make their nests in dead, dry, woody branches of the trees occurring in that situation. As the two species are very different in size it is likely that each is confined for its nesting to branches of a certain thickness and interspecific competition between the two for nesting sites is therefore unlikely despite the fact that they occur in the same habitat.

X. caffrariae is also a riverine species but occurs not in thick bush but in open tracts along the banks of permanent and semi-permanent water bodies where it nests exclusively in the dry culms of *Phragmites australis*, a reed forming beds in such situation (Figs 14 & 15).

X. sicheli, by contrast is found only in open country and is associated with *Aloe ferox* growing on higher ground, especially on the north facing slope of the E-W ridge to the south of the study area. Nesting is restricted to the old, dry but still attached, inflorescence stems of this plant (Figs 13 & 30).

The small carpenter bees, *Ceratina* species, appear also to show considerable ecological displacement. One of these species, *Ceratina* sp. A. is most commonly found nesting with *X. sicheli* in *Aloe ferox* inflorescence stems. Though galleries of both bees frequently occur in the same inflorescence stems they never occupy the same parts: *X. sicheli* galleries are restricted to the thicker basal parts above and below the point where the inflorescence branches whereas *Ceratina* sp. A. galleries are restricted to the thinner terminal portions of the branches themselves. Maximum use is therefore made of the nesting substrate offered by the inflorescence stem without any interspecific competition for gallery space arising.

With respect to species of *Dasyproctus* it may be seen from the review of their known ethology (Gess, 1980b) that considerable specificity exists in their choice of pithy stems in which to nest. At Hilton *D. westermanni* was found to nest exclusively in galleries hollowed out within green inflorescence stems of *Urginea altissima*, which stems were, however, not utilized by any of the other four *Dasyproctus* species. Evidence of the nesting of the latter was, however, found in the form of old galleries in inflorescence stems of *Gasteria* species and in stems of *Berkheya decurrens* (Gess, 1980b).

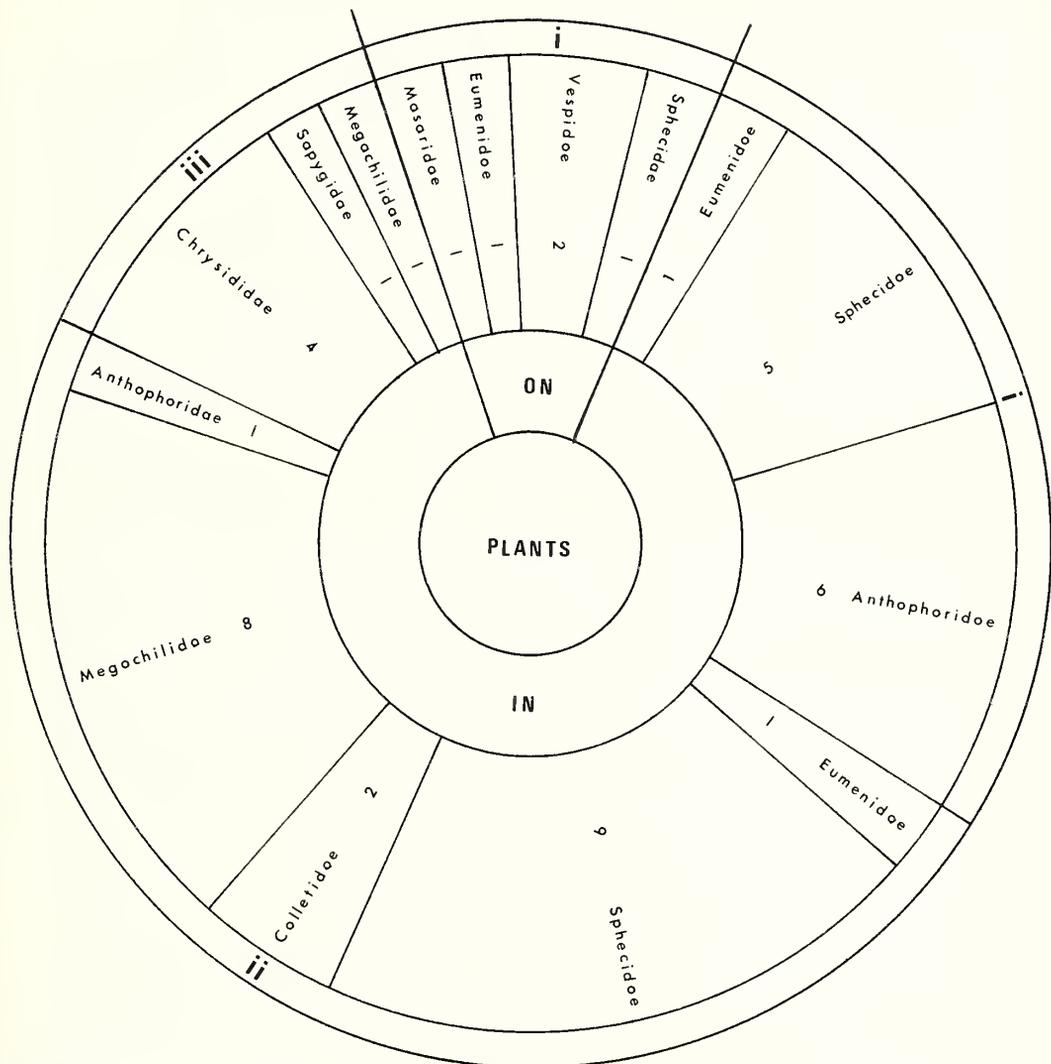


Fig. 29. Diagram showing the structure of the communities of the aculeate wasps and the bees nesting in or on plants in the study area. Numbers accompanying the family names represent numbers of species. The numbers (i, ii, iii) in the outermost ring correspond to the same numbers in the classification of the aculeate wasps and the bees of the study area on the basis of their ethology. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester.

Xylocopa, *Ceratina* and *Dasyproctus* share certain characteristics with respect to their nesting: all initiate nesting with the preparation of galleries within plant tissue, all construct multicellular nests the cells of which are serially arranged and mass provisioned, and all construct the cell partitions of materials derived from within the plant stem—plant tissue rasped

from the walls of the gallery. In no case is foreign nesting material introduced into a gallery from without.

Xylocopa caffrariae differs from the other species in that it does not itself hollow out a nesting gallery but makes use of the naturally formed hollow internode of *Phragmites*. The bee must nevertheless be classed with the nest constructors and not the tube renters in that it does not seek out broken off reeds in order to enter the internodes at an open end but habitually cuts an entrance hole through the hard wall of the culm and thus gains access to an intact internode from the side (Fig. 31). Once through the culm wall, however, it is spared the trouble of hollowing out a gallery as this already exists due to the natural breakdown and disappearance of the pith concurrent with the maturing of the culm.

The nesting by the genera *Xylocopa*, *Ceratina* and *Dasyproctus* in galleries constructed by themselves within plant tissue must be seen as advanced and derived from nesting in the ground. Supporting this view is the fact that most nest-constructing (that is, non-parasitic) Anthophoridae are ground-nesting (Krombein *et alia*, 1979: 2082) as are many of the more primitive genera of the Crabronini (the sphecid tribe of which *Dasyproctus* is an advanced genus) (Bohart and Menke, 1976: 371). These genera therefore substituted the excavation of galleries in plant tissue for the more basic excavation of burrows in friable soil, thereby both freeing themselves from competition for nesting sites in the soil and, more importantly, gaining the ability to invade previously unutilized habitats.

Dasyproctus differs from the Anthophoridae in so far that it hollows out its galleries in green plant tissue whereas this is not the case with respect to the two genera of bees. The statement by Brauns (1913: 117–118) repeated by Hurd and Moure (1963: 15 and 185) and by Hurd (1978: 1) to the effect that *Xylocopa sicheli* excavates its galleries in *Aloe* inflorescences which are still green and juicy could not be substantiated by the field work of the present author and must be recognized as being incorrect.

A danger inherent in nesting in green plant stems is that these stems with any nests contained within them may be ingested by browsing herbivores. The ways in which the nests of several *Dasyproctus* species, including that of *D. westermanni* in *Urginea altissima*, are protected by physiological or morphological attributes of the stems or by the protected habitats of the latter is discussed by Gess (1980b: 105).

Among the 39 species recorded at Hilton as nesting within plant tissue, 21 were found to nest not in galleries of their own excavation but in pre-existing cavities which they, however, modified by the construction within them of a cell or cells. The species concerned are listed in the annotated list of species under categories 17, 20 and 23. Four families were represented: Eumenidae (1 species), Sphecidae (9 species), Colletidae (2 species) and Megachilidae (9 species).

There seems little restriction by these insects to any one particular stem type, three of the species (*Holotachysphex turneri*, *Immanthidium junodi* and *Megachile spinarum*) having been recorded in two stem types each and another three species (*Isodontia stanleyi*, *Trypoxylon* sp. and *Chalicodoma sinuata*) in all three stem types each. Further field work would doubtless augment the number of species recorded in more than one stem type, all the more so as many of these species are not even restricted to plant stems but are found nesting also in pre-existing cavities in vertical banks (*Euodynerus euryspilus*, *Chalybion tibiale*, *Pison montanum*, *Trypoxylon* sp., *Immanthidium junodi*, *Megachile gratiosa* and *Megachile spinarum*).

Due to the catholicity which these wasps and bees exhibit with respect to the nature of the material in which the pre-existing cavities utilized by them occur, it is not surprising that they should readily accept trap-nests of the types described by Krombein (1967 and 1970).

With the exception of one species (*Isodontia simoni*), all the wasps and bees listed in category 17 as nesting in woody stems were in fact nesting in trap-nests tied to woody branches of trees such as *Acacia karroo*, *Maytenus linearis* and *Rhus lancea*. The fact that these trap-

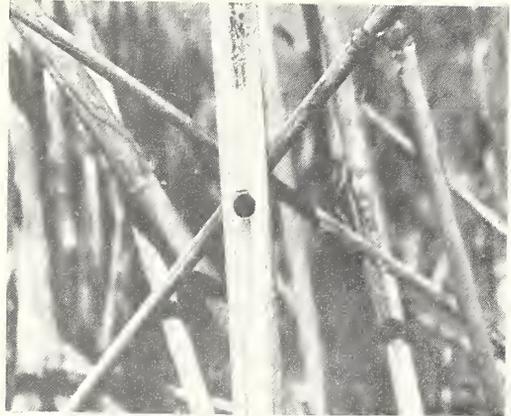
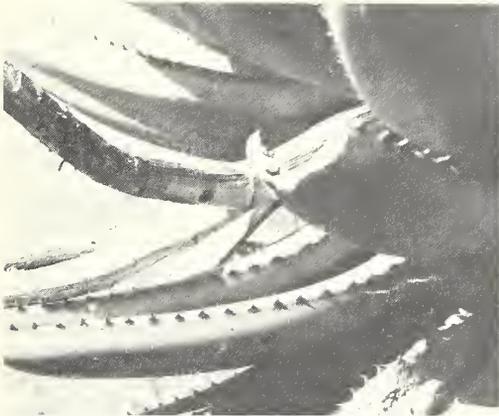


Fig. 30. Downcurved dry inflorescence stem of *Aloe ferox* showing nest entrance hole cut by *Xylocopa sicheli*.

Fig. 31. Dry culm of *Phragmites australis* showing nest entrance hole cut by *Xylocopa caffrariae*.

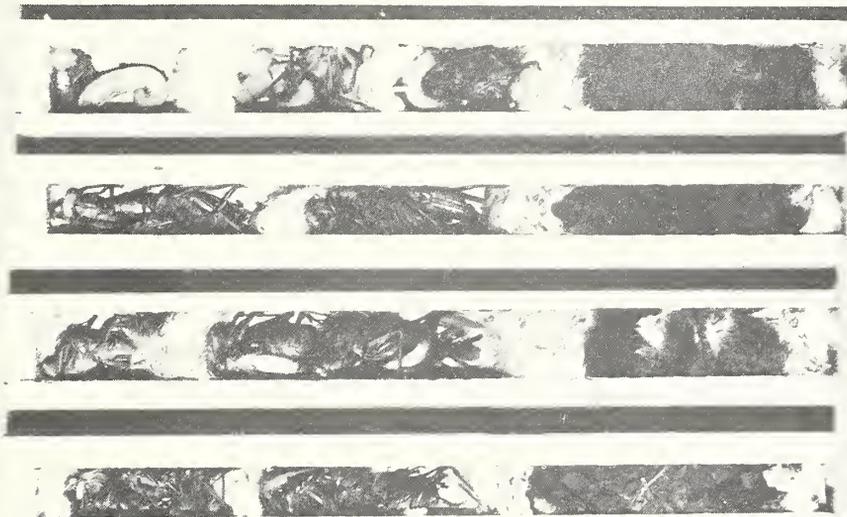


Fig. 32. Completed nests of *Isodontia pelopoeiformis* in trap-nests, showing prey, nesting materials and immature stages of wasp. ($\times 0,65$)



Fig. 33. Completed nest of *Isodontia stanleyi* in trap-nest, showing prey, nesting materials and immature stages of wasp. ($\times 0,52$)

nests were so readily and frequently made use of (for example, over a period of three summer seasons 85 trap-nests were occupied by *Isodontia pelopoeiformis* alone) shows that the woody branches to which they were attached were in fact being carefully searched for the presence of pre-existing cavities by the wasps and bees concerned. The inclusion of the trap-nests as extensions of the trees themselves is therefore validated. Further proof of the validity of the approach is furnished by the nesting of *Ampulex* sp. near *cyanura*. It having been noticed that the wasp nested only in those trap-nests tied to *Acacia karroo*, a careful physical investigation was made of this tree species which culminated in the discovery within its branches of nests constructed within naturally occurring pre-existing cavities.

All nests consisting of cells built within pre-existing cavities may immediately be recognized as such and may readily be distinguished from nests consisting of cells built within a gallery prepared by the nesting wasp or bee itself. This is possible due to the fact that all users of pre-existing cavities in plant tissue introduce foreign materials into the former for the construction of cell partitions and nest closures, whereas, as already noted above, species hollowing out galleries themselves utilize materials rasped from the gallery walls.

Of all the species nesting in pre-existing cavities in plant tissue at Hilton, the two species of *Ampulex*, *A.* sp. near *cyanura* and *A. denticollis* exhibit the most primitive behaviour. Nesting in both species is commenced with hunting. After the introduction of the single large prey (a cockroach) into the pre-existing cavity, oviposition onto the prey takes place after which the cavity is sealed with detritus. It follows that neither *Ampulex* ever introduces foreign nesting material into a cavity prior to the introduction of the prey. Preliminary plugs, as found at or near the blind ends of cavities used for nesting by many of the behaviourally more advanced wasps, are therefore unknown in the *Ampulex* nests. Furthermore, each nest consists of a single cell and where two or more cells are found within a single cavity these represent as many separate nests, not necessarily even made by the same female.

The great majority of species, however, are behaviourally advanced and commence nesting with the search for a suitable pre-existing cavity. Thereafter some foreign nesting material is frequently introduced in connection with cell construction. In the wasps, a preliminary plug at or near the inner end of the cavity may or may not be constructed to form the inner end-wall of the first cell as shown for *Holotachysphex turneri* (Gess, 1978: Fig. 1) and for *Chalybion tibiale* (Gess and Gess, 1980d: Fig. 1) and additional material may be used to form a temporary cell closure as in species of *Isodontia*. In at least some of the bees the introduced foreign materials may be used to fashion not merely an inner end-wall of a cell but a complete cylindrical cell within the walls of the cavity. Such is the case with the leaf-cutter bees, *Megachile gratiose* and *M. spinarum*, and the mason-bees, *Chalicodoma fulva* and *C. sinuata*. Only after some form of cell preparation has been undertaken does provisioning commence.

If the pre-existing cavity is of a length that allows it, several serially arranged cells are constructed. Successive provisioned cells are separated one from another by partitions of foreign material, the outer end-wall (i.e. the cell closure) of one cell forming the inner end-wall of that immediately succeeding it. Frequently the nest is completed by the construction near the cavity opening of a closing plug as shown for *Holotachysphex turneri* (Gess, 1978: Fig. 1).

Exceptionally no foreign nesting materials are introduced into the pre-existing cavity and there is therefore a complete absence of any cell partitions. Such is the case in the nests of *Allodape* sp. (*rufogastra* or *exoloma*) found at Hilton within old *Dasyproctus* galleries in *Berkheya decurrens* stems. This bee is unusual also in that it practises progressive provisioning of the larvae whereas all the other bees recorded at Hilton as nesting in modified pre-existing cavities in plant tissue practise mass provisioning of the cells, an egg being laid on the provision of each cell prior to the closure of the latter. The biology of species of *Allodape* and of related genera has been reported in detail by Michener (1971b).

The nesting of the species modifying pre-existing cavities in plant tissue, like that of the species excavating original galleries in this substrate may be seen as being derived from nesting in the ground. At Hilton this derivation is clearly reflected in those species for which the foreign material introduced into the pre-existing cavities in plant tissue consists wholly or partially of earth. The earth used is in all cases of a clayey nature and may be introduced into the cavity either in the form of mud or in the form of dry clods. In the latter instance small pieces of twig, bark and other detritus found lying upon the surface of the ground are utilized in addition.

Such is the case with *Holotachysphex turneri*, found nesting both in trap-nests tied to woody trees (Gess, 1978: 209) and in old abandoned galleries of *Xylocopa caffrariae* in the dry culms of *Phragmites* (Gess and Gess, 1980a: 52), which, as has been discussed by Gess (1978: 212-214), may be considered to have developed from a *Tachysphex*-like form. The species differs ethologically from typical *Tachysphex* species in that excavation of a nest in friable soil has been abandoned in favour of the utilization for nesting of a pre-existing cavity in plant tissue. Concomitant with this ethological change has been the secondary loss of both the foretarsal rake and the pygidial plate.

The nesting of *Tachysphex* sp. near *modestus* in pre-existing cavities (abandoned wasp burrows) in non-friable clayey soil, discovered since the publication of the account of the nesting of *Holotachysphex turneri* but described in some detail earlier in the present discussion, may be seen to represent an intermediate but very important pre-adaptive step that will have had to have been taken by the progenitor of *H. turneri*. Clearly, once the basic change had been made from the excavation of a nest in friable soil to the facultative use of a pre-existing cavity in non-friable soil (as in *Tachysphex* sp. near *modestus*) the way was open to a change to obligatory use of such a pre-existing cavity in the ground and for its eventual abandonment in favour of a pre-existing cavity above the ground in plant tissue. The use by *Holotachysphex turneri* of dry clods of clayey earth and pieces of detritus collected on the ground must therefore be interpreted as relict behaviour evolved in response to nesting in pre-existing cavities in non-friable clayey soils.

Dry clods of clayey earth and pieces of detritus (including bits of stick, vetch burs, insect remains and small mammal droppings) picked up off the ground are also the main foreign nesting materials introduced into pre-existing cavities in plant tissue by *Isodontia pelopoeiformis*, according to Bohart and Menke (1976: 121) one of the more structurally primitive species of the genus *Isodontia*. The same interpretation as that given to the use of these nesting materials by *Holotachysphex turneri* may be applied to their use by *Isodontia pelopoeiformis* which therefore is seen similarly as having evolved from a nester in pre-existing cavities in non-friable soils. It is therefore of interest that amongst the nesting situations recorded for species of *Isodontia* by Bohart and Menke (1976: 121) there should be that of abandoned bee burrows in the ground.

Isodontia pelopoeiformis, however, in addition to the above foreign nesting materials uses "fluffy" plant material, at Hilton derived from the fruiting inflorescences of the Composites *Lasiospermum bipinnatum* and *Senecio* species (including *S. leptophyllus*) (Fig. 32). Cell partitions are almost exclusively constructed of this material whereas preliminary plugs and nest closing plugs are constructed of earth, detritus and "fluff" in distinct layers. The "fluffy" plant material which is collected directly from the plant inflorescences represents "new" nesting material as opposed to the earth and the detritus which as has been shown to represent "old" or "relict" materials. Presumably pieces of this "fluff" were initially picked up off the ground like any other detritus but as the use of this particular nesting material became more established the wasp took to collecting it from its source.

Isodontia stanleyi, a structurally more advanced species, is also ethologically more advanced for it has abandoned the legacy of its past in the form of "old" or "relict" nesting

materials and uses only "new" materials (Fig. 33). These consist of short lengths of grass leaf blades and longer lengths cut from grass inflorescences including lengths of unbranched culm and the branched portions including the flower heads. The cell partitions are constructed of short lengths of grass leaf blades, transversely arranged; preliminary plugs and the inner parts of the closing plugs are composed of the longer lengths of grass inflorescences, transversely coiled; and the outer parts of the closing plugs are formed of the latter material arranged longitudinally, the stems lying parallel and projecting from the nest entrance as a broom-like tuft.

That the use of grass by *I. stanleyi* is homologous with the use of Composite "fluff" by *I. pelopoeiformis* is evident from the very occasional and exceptional use of lengths of very soft grass leaf blades by the latter species when its usual "new" nesting material is not available.

An interesting piece of behaviour practised by both *I. pelopoeiformis* and *I. stanleyi* is that of "buzzing" in the nesting cavity in order to consolidate the introduced materials forming the preliminary plug and the cell partitions. The "buzzing" is the same as that already commented upon in connection with other Sphecidae, the ground-nesting *Padalonia canescens* and *Ammophila ferrugineipes* which use it to loosen soil in the course of the excavation of their burrows. This behaviour may be seen as additional evidence for deriving the plant-nesting *Isodontia* species from ground-nesting, possibly nest-excavating, forms.

Earth in the form of mud for the construction of cell partitions and nest closures is introduced into pre-existing cavities in plant tissue by *Euodynerus euryspilus* (Eumenidae) and *Chalybion tibiale*, *Pison montanum* and *Trypoxylon* sp. (all Sphecidae).

The use of mud as the nesting material suggests that these wasps are derived from species which employed water to aid them in the excavation of original nests in non-friable clayey soils in the manner already described for other species of Eumenidae (*Parachilus*, *Pseudepipona* and *Antepipona*) and Sphecidae (*Bembecinus*). From the excavation of original nests in the ground to the use of pre-existing cavities in plant tissue two changes of behaviour would have been required—firstly the abandonment of the excavation of an original nest in the ground in favour of the use of pre-existing cavity in the same substrate, secondly the abandonment of nesting in this pre-existing cavity in the ground in favour of nesting in a similar pre-existing cavity above ground in plant tissue (or for that matter in a vertical bank). The use of mud for cell partitions and nest closures, initially a consequence of using water in nest excavation, is retained by those species nesting in pre-existing cavities and provides a continuous thread linking the three nesting types.

The three nesting types outlined above as necessary to the derivation may all be found to occur within the genus *Pison*. Thus, excavation with the aid of regurgitated water of an original burrow in non-friable soil has been reported for the South American *Pison chilense* (Janvier, 1928, as reported by Bohart and Menke, 1976: 335). Use of pre-existing cavities (abandoned burrows of bees and wasps) in clayey soils has been reported for the Micronesian *Pison nigellum* (Krombein, 1950: 139) and is recorded in the present account for *Pison allonymum* at Hilton. Use of pre-existing cavities in plant tissue has been reported for several species (see Bohart and Menke, 1976: 335) and is the habit at Hilton of *Pison montanum*, one of the species presently being discussed.

Great specificity is shown in the nature of the foreign materials introduced into pre-existing cavities in plant tissue by various pollen-collecting (that is, non-parasitic) bees. In the family Megachilidae, *Megachile gratiosa* and *Megachile spinarum* construct their cells of pieces of green leaves cut to definite shapes and sizes and arranged overlappingly (Fig. 39). Leaves of only one plant species are used by these two bees at Hilton, namely those of *Maytenus heterophylla* (Celastraceae) which would appear therefore to be those best suited for the purpose at that locality. Elsewhere *M. gratiosa* has been found to use not only green leaves but, less commonly, flower petals also (Taylor, 1963, 1965 and 1968). Other bees of the same family,

Capanthidium capicola and *Immanthidium junodi*, both so-called carder bees, use cotton wool-like plant down, *Heriades* species use plant resin, and *Chalicodoma fulva* and *Chalicodoma sinuata* use mud (Fig. 40).

Hylaeus species including *Hylaeus braunsi* (family Colletidae), by contrast, construct their cells not of materials which they have collected but of a cellophane-like material secreted by their salivary glands.

The construction by many of the bees of complete cells within the pre-existing nesting galleries as opposed to the construction only of cell end walls (that is cell partitions) as by the wasps is clearly linked to the nature of the provision. The damp nature of the pollen and nectar mixture clearly requires that it be protected not only from desiccation through loss of moisture to the nesting substrate but also that it be protected from contamination from the nesting substrate. The cell walls be they of leaves, plant down or mud thus serve to isolate the provision from the nesting substrate. This is of particular importance in the *Hylaeus* species the nectar-pollen mixture of which is very liquid and can only be protected and contained by the impermeability of the cellophane-like "bags" forming the cells. On the other hand the pollen stored by *Heriades* species, including *H. spiniscutis* at Hilton nesting in old *Dasyproctus* galleries in *Berkheya* and *Gasteria* stems, is very dry which may account for the fact that no cell walls are constructed and that the introduced nesting material, resin, is used only for the construction of cell partitions and nest closures.

It may be accepted that foreign materials for the construction of cells within pre-existing burrows were used already by the ground-nesting antecedents of the bees now nesting above ground and that the change in nesting situation was not accompanied by any change in the nature of the nesting materials. Certainly, there is no difference in the nature of the leaf cells constructed at Hilton by, on the one hand, the ground-nesting *Megachile semiflava* and *M. stellarum* and, on the other hand, the above-ground-nesting *M. gratiosa* and *M. spinarum*.

In passing it may be remarked that the apparently successful co-existence at Hilton of six species of *Megachile* must be due at least in part to the fact that the search for suitable pre-existing cavities in which to nest is not restricted to one situation but is divided between the ground (*M. aliciae*, *M. meadowaldoi*, *M. semiflava* and *M. stellarum*) and situations above the ground (*M. gratiosa* and *M. spinarum*). Within each of the two major nesting situations competition is probably further reduced by the fact that the species concerned are of different sizes and therefore seek pre-existing cavities of commensurate bore. For example, with respect to the two species nesting above the ground and thus found also in trap-nests, the 8 mm long *M. gratiosa* was found to be restricted to small bore (6,4 mm) trap-nests whereas the 13 mm long *M. spinarum* was found to use mostly larger bore (9,5 and 12,7 mm) trap-nests.

Six of the thirty-nine species recorded at Hilton as nesting within plant tissue were found doing so in pre-existing cavities which they themselves had not in any way modified. All were reared from cells constructed by other aculeate Hymenoptera and all may be classed as clepto-parasites as they feed upon the provision stored by their hosts.

Three families were involved, namely Chrysididae, Sapygidae and Megachilidae. The four cuckoo wasps and their hosts were: *Chrysidea africana* and *Chrysis* sp. (near *purpuripyga*), both in the cells of *Trypoxylon*; *Chrysis inops* in the cells of *Pison montanum*; and *Octochrysis hoplites* in the cells of *Euodynerus euryspilus*. *Sapyga simillima* (Sapygidae) and *Coelioxys penetratrix* (Megachilidae) developed in the cells of *Heriades* sp. and *Megachile spinarum* respectively.

All the above cleptoparasitic species appear to be highly host specific with regard to the nests in which they develop and their occurrence is therefore linked with that of their hosts. *Chrysidea africana*, besides being reared from *Trypoxylon* cells in trap-nests tied to bushes and trees, was found also in association with *Trypoxylon* nests in cavities in vertical banks. On the

face of the latter the cuckoo wasp was frequently seen walking about inspecting holes, then flying up and settling elsewhere after which the inspection of holes was resumed.

With respect to the association of *Coelioxys* with *Megachile* it is of interest that the two genera are closely related. It appears that both are probably derived from the same nest-constructing and pollen-collecting forms and that the cleptoparasitic behaviour of *Coelioxys* is secondary and specialized, being arrived at by the abandonment by this genus of nest construction and pollen collection in favour of the utilization for nesting of the nest constructed and provisioned by *Megachile*.

Five species, all wasps, were listed at Hilton as constructing aerial nests on plants, namely *Eumenes lucasius* (Eumenidae), *Celonites capensis* (Masaridae), *Polistes smithii* and *Ropalidia* sp. B. (Vespidae), and *Sceliphron quartinae* (Sphecidae).

The nesting of all these species, like those species constructing nests above ground but within plant tissue, may be seen as derived from nesting in the ground. In contrast to those species which nest within plant tissue and which in their nesting therefore are subject to the constraints imposed either by the availability of plant tissue suitable for gallery excavation or by the availability of pre-existing cavities of suitable dimensions, the species nesting on plants are free of such limitations and for their nesting require only that the plant should offer mechanical support for the nest. Despite this freedom with regard to the surface to which the nest may be attached, the species cannot nest anywhere for all are dependent upon the presence of water for the construction of their cells.

With respect to the four Vespoidea, water, collected in the crop and regurgitated from there, is required to transform dry clayey earth into mud and dry rasped-off wood fibres into wood pulp, materials used for cell building by *Eumenes* and *Celonites* and by *Polistes* and *Ropalidia* respectively. *Sceliphron quartinae*, in contrast to the above two water-collecting, mud-mixing species, probably behaves like the mud-daubing *Sceliphron spirifex* and related species which gather already existing mud from beside pools and puddles.

Nesting is therefore restricted to within a certain distance of water, and furthermore, in the case of those species making mud cells, to areas of clayey soils. However, *Sceliphron quartinae*, which has been reported by Brauns (1911: 119) to make its cells either of clayey mud or cow dung, will by its use of the latter material (when fresh and wet) be able to nest in areas where mud suitable for cell construction is unavailable, either because the soil is not of a clayey nature or because pools and puddles are absent, or both.

With respect to wasps and bees nesting within plant tissue, two associations between some species and certain plants are of particular interest. These associations will be dealt with in further detail in order to illustrate the primary rôle played by the plant in question and to show the chains of dependence existing amongst the insects constituting a community upon such a plant. It is obvious that such chains of dependence within a community are not the monopoly of those species nesting within plant tissue but are a feature of all communities whatever their nesting substrates and nesting situations. The present two examples are chosen as they have the added interest of having as the nesting substrate an additional living organism, the plant.

The first example pertains to a complex of three insect species associated with and restricted to the shrub or small tree, *Acacia karroo*, and concerns the nesting of the sphecid, *Ampulex* sp. near *cyanura*, listed in category 17 of the annotated list as being a modifier of pre-existing cavities in woody stems. As will be seen in Fig. 34 in which the association under discussion is diagrammatically portrayed the other two insects concerned are *Ceroplesis hottentota* (Cerambycidae) and *Bantua dispar* (Blattidae) (Figs 35 & 36).

First in the three-linked chain is the beetle, *C. hottentota*, the larvae of which in the course of their feeding bore galleries in finger-thick branches of *A. karroo*. The consequences of the activity of these larvae are three-fold and make possible the existence of the other two species in the chain. Firstly, damage to the living branches of the tree results in a copious amount of

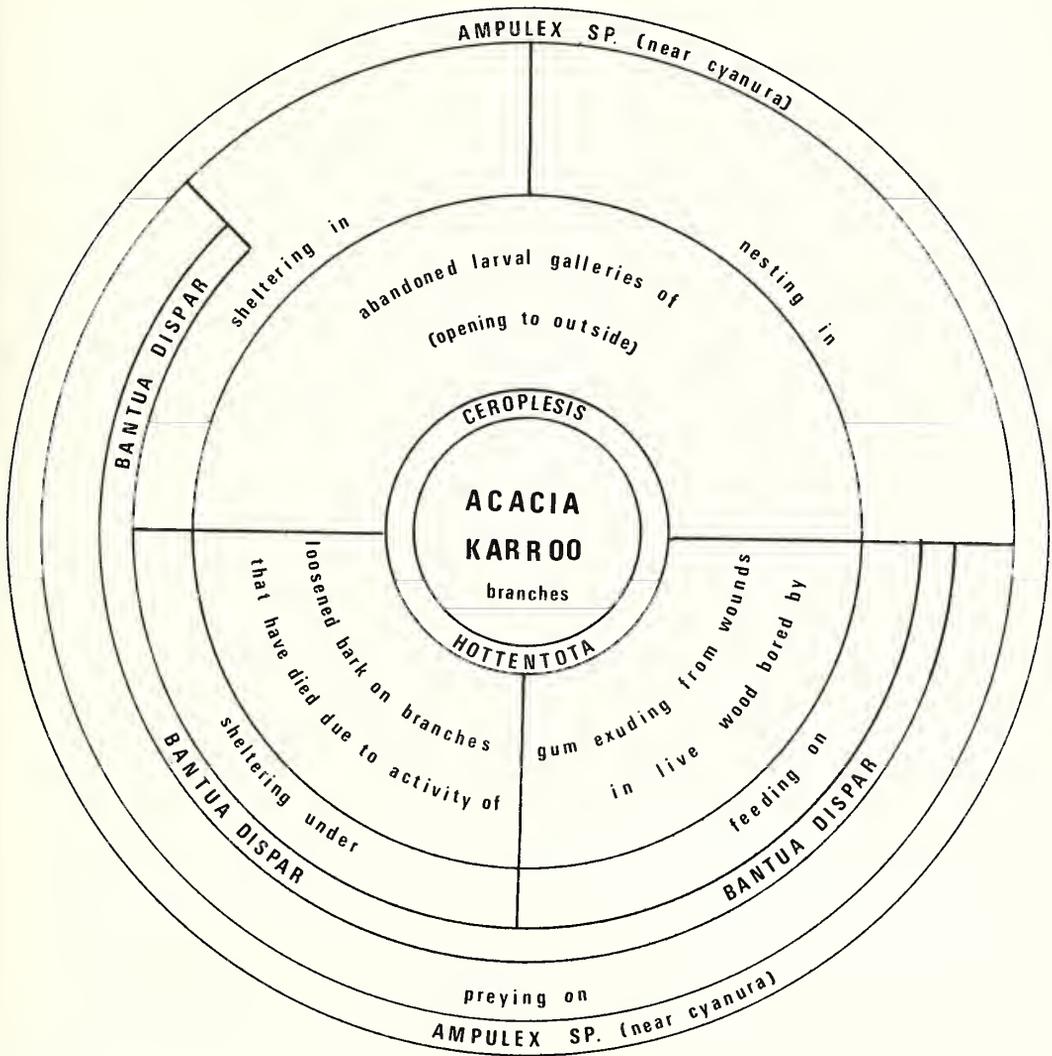


Fig. 34. Diagram showing the structure of a complex of three insect species, *Ceropales hottentota* (Cerambycidae), *Bantua dispar* (Blattidae) and *Ampulex* sp. near *cyanura* (Sphecidae) associated with and restricted to the shrub or small tree *Acacia karroo* (Leguminosae).

gum being exuded from the wounds. Secondly, and at a later stage, the bored branches die with the result that their bark separates from the wood. Thirdly, after the beetles have completed their larval feeding, have pupated and have metamorphosed into adults, they break out and abandon their galleries with the result that the latter become available for the use of other insects which cannot themselves hollow out such cavities.

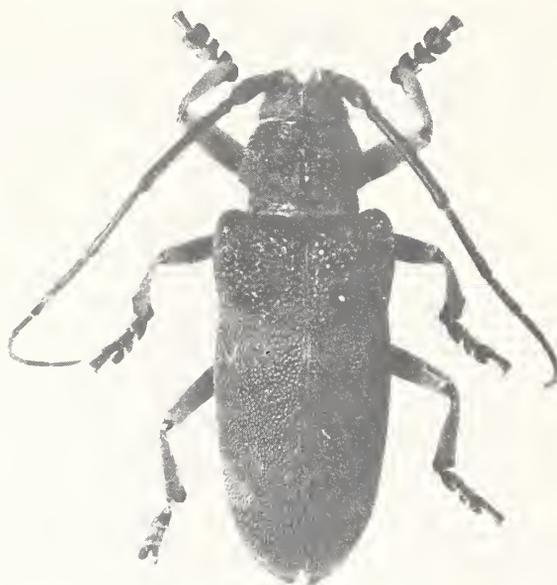


Fig. 35. *Ceroplesis hottentota*, the larvae of which bore galleries in finger-thick branches of *Acacia karroo*. ($\times 3$)



Fig. 36. *Bantua dispar* and *Ampulex* sp. near *cyanura*. The wasp having subdued the cockroach has cut off the end of an antenna (seen lying at bottom right-hand corner of photograph) and is malaxating prior to leading prey to nesting gallery. ($\times 3$)

Second in the chain of species is the cockroach, *B. dispar*, which appears to be restricted to those *A. karroo* shrubs and trees harbouring *C. hottentota*. A nocturnal species, it spends the day in hiding in old abandoned beetle galleries and under the loosened bark of dead branches and comes out at night to feed upon the gum exuding from living branches being bored by the beetle.

Third and last in the chain is the wasp, *Ampulex* sp., which preys exclusively upon *B. dispar* for which it may be seen hunting on foot on the branches of the tree. Having flushed a *B. dispar* from its hiding place, the wasp stings it and then, holding the subdued cockroach by one of its antennae, leads it to an old *C. hottentota* gallery (Fig. 36). Once arrived there the wasp installs the cockroach within the cavity, oviposits on it and then seals the gallery with detritus collected on or immediately under the tree.

The existence of *Ampulex* sp. near *cyanura* within any locality is therefore inextricably linked with the presence of not only its prey but also with that of the beetle and ultimately with that of *Acacia karroo*. As the wasp was never collected anywhere other than on *A. karroo* it would appear that its entire life is spent on this plant.

The second example, presented diagrammatically in Fig. 37, pertains to a community of species referable to categories 19, 20 and 21 of the annotated list and associated with the dry inflorescence stems of *Aloe ferox*.

The community differs from the complex of three species concerned in the first example in that the species at the core of the community are hymenopterous, not coleopterous. Furthermore, species are included that exhibit all three degrees of participation in nest construction: those which construct their nests entirely by themselves, those which modify pre-existing cavities (Figs 38, 39 & 40) and those which nest parasitically in pre-existing cavities which they do not themselves modify.

Most strikingly different, however, is the far looser association with the plant, only the two gallery excavators at the core of the community, *Xylocopa sicheli* and *Ceratina* sp. *A.* being apparently restricted to the aloes. However, even these species are dependent upon these plants only in so far that they offer a suitable pithy substrate in which nesting galleries may be excavated and in areas where *A. ferox* does not occur, inflorescence stems of other species of *Aloe* are known to be used. Foraging for pollen and nectar with which to provision the cells within the galleries takes place on other plants for at the time of nesting the aloes are not in flower.

At the level of those species which modify pre-existing cavities and are recorded as using the abandoned borings of the two gallery excavating bees there is no dependence on the presence of aloes at all nor on the presence of the bees. As has been shown species like *Isodontia stanleyi*, *Trypoxylon* sp., *Megachile spinarum*, *Chalicodoma sinuata* and *Immanthidium junodi* will nest in a variety of pre-existing cavities provided these are situated up above the ground. It is clear, however, that if these species are to nest in *Aloe* inflorescence stems then they can do so only in the presence of old *Xylocopa* and *Ceratina* borings.

At the level of those species which do not modify pre-existing cavities but nest parasitically the association is clearly with their hosts only and the occurrence of these species is therefore determined by that of their hosts.

Communities of loosely associated species of wasps and bees, as exemplified by the community nesting in *Aloe ferox* inflorescences, may be seen to exist in all four nesting situations—the ground, vertical banks, stones and plants and in the subdivisions of these primary nesting situations. It may therefore be concluded that the picture that emerges of the interaction of species of wasps and bees in a community such as that described above is typical of the entire population of these insects at Hilton.

Within any community individual species, as exemplified by *Ampulex* sp. near *cyanura* of the community nesting in *Acacia karroo* stems, may be associated not with other species of

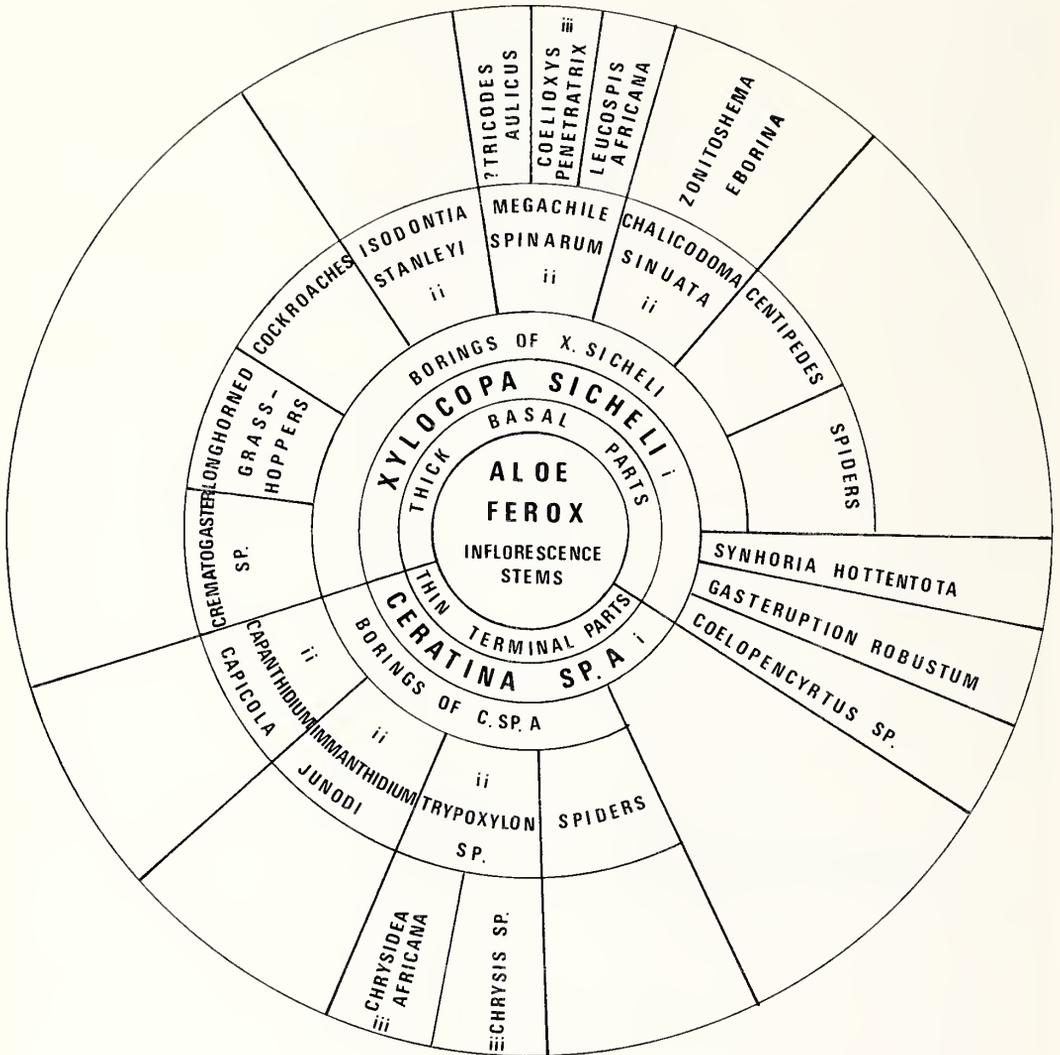


Fig. 37. Diagram showing the structure of a community of insects associated with the dry inflorescence stems of *Aloe ferox* (Liliaceae). With respect to the aculeate wasps and the bees the degree of participation in the construction of their nests is indicated by the numbers (i, ii, iii) as in the classification of these insects on the basis of their ethology. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester.



Fig. 38

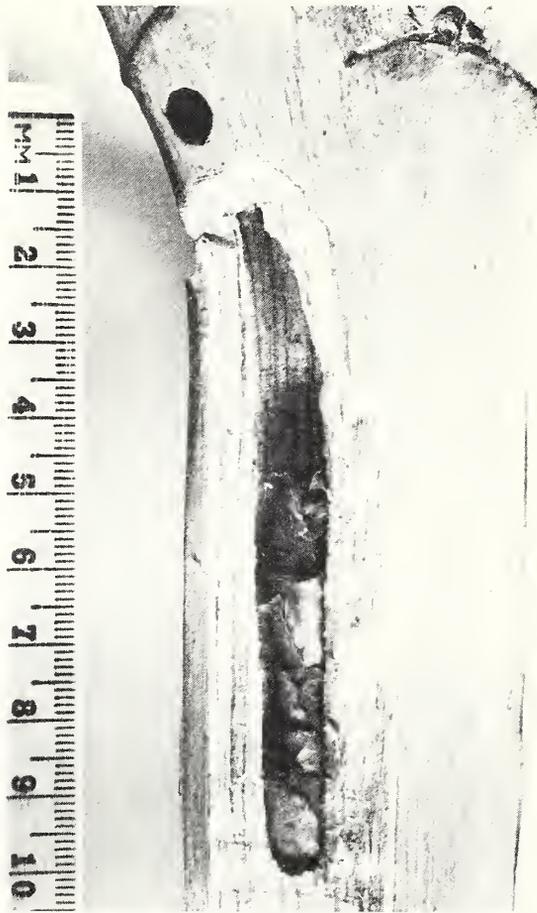


Fig. 39

Figs 38 and 39. Dry inflorescence stems of *Aloe ferox* cut longitudinally to show old galleries bored by *Xylocopa sicheli* and containing nests of *Isodonia stanleyi* (Fig. 38) and *Megachile spinarum* (Fig. 39).

wasps or with bees, except perhaps peripherally (e.g. in competition for pre-existing cavities), but may rather be part of the community by virtue of their association with non-hymenopterous species.

The circumscribed association of *Ampulex* sp. near *cyanura* with the beetle and the cockroach making up the three-species complex on *Acacia karroo* appears to be exceptional and no similar example was found during the course of the present study at Hilton.



Fig. 40. Dry inflorescence stem of *Aloe ferox* cut longitudinally to show old gallery bored by *Xylocopa sicheli* and containing nest of *Chalicodoma sinuata*.

The study of nesting ethology of the aculeate wasps and the bees of Hilton has apart from adding considerably to the knowledge of these groups in Africa provided a clear illustration of their remarkable propensity for behavioural adaptability which has led to the formation of communities of large numbers of sympatric species showing marked ecological displacement.

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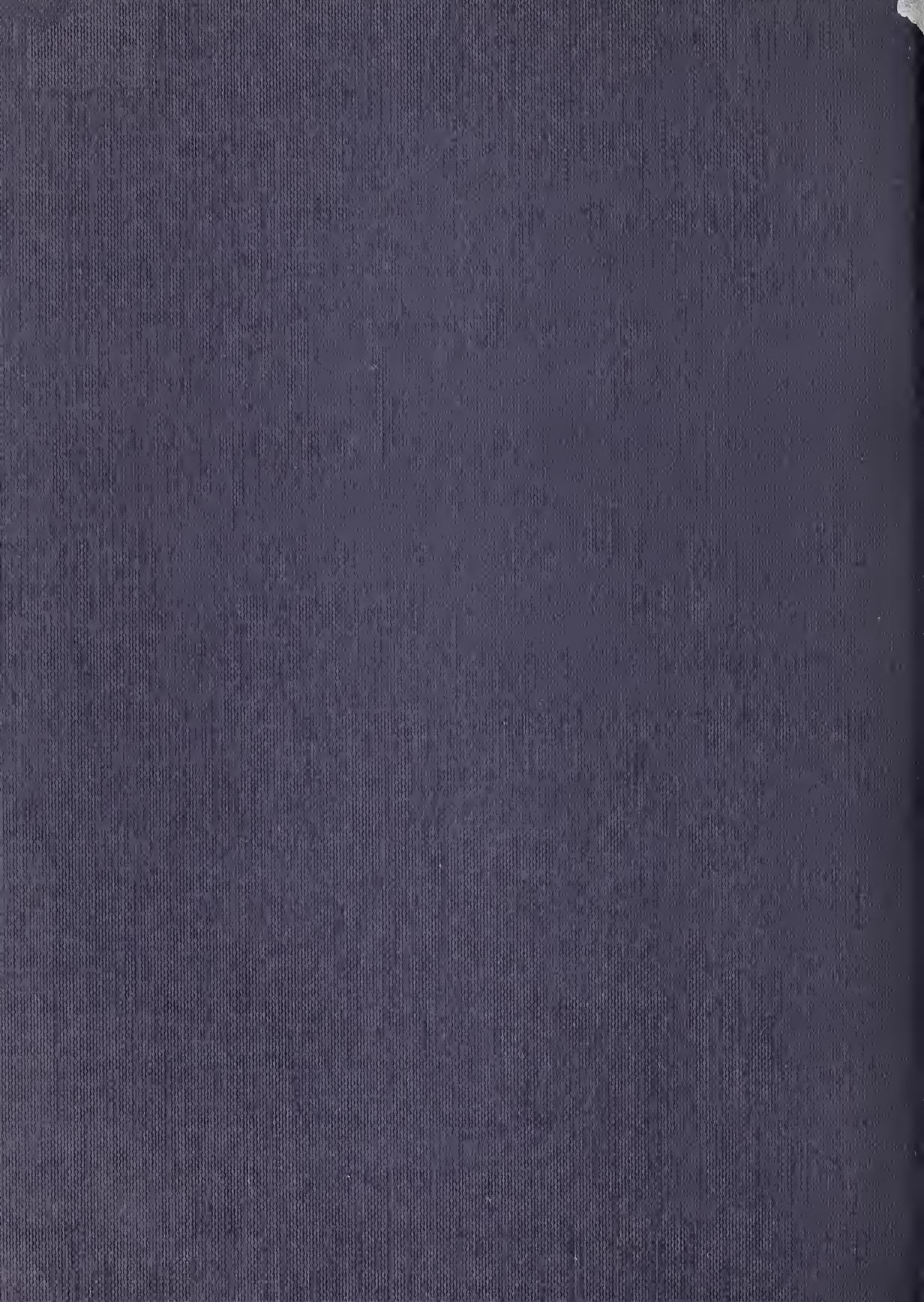
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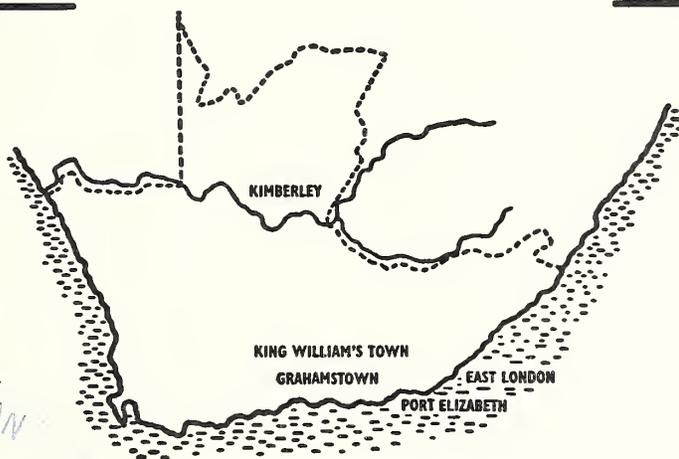


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A selected bibliography of literature on Odonata from Africa and adjacent islands Part 2

by

B. C. WILMOT and L. P. WILMOT

(Albany Museum, Grahamstown)

This bibliography, like the first compiled by Wilmot & Wilmot (1978), is intended to supplement that of Pinhey (1962) which included mostly systematic references to African Odonata up to December 1959. Though the vast majority of articles included in the present bibliography were published subsequent to 1959 a few earlier non-systematic references omitted by Pinhey and previously overlooked by the compilers have been included. All articles in which reference is made to Odonata have been included, whether of a systematic, ecological, zoogeographical, biological or bibliographical nature.

The geographical coverage of articles is indicated by a code letter or letters placed after each reference. The code letters and their meanings, after Scott & Scott (1969), are as follows:

- N. North Africa, i.e. Africa north of the Sahara, including oases.
- C. Africa south of the Sahara but north of the Zambesi. This is the largest area, including all the central African countries from the Sudan to Zambia and Senegal to Somalia.
- S. Southern Africa, i.e. Africa south of the Zambesi. This includes South Africa, Namibia, Zimbabwe, Lesotho, Swaziland, Botswana and the southern part of Mozambique.
- I. Islands off the coast of Africa with the exception of those in the Mediterranean Sea which are excluded.
- A. This indicates Africa as a whole and means that the article concerned covers the continent in general.

The relative importance of an article is indicated by the number of asterisks placed after the geographical code of that reference. Following Davies & Davies (1976) the ratings are as follows:

- * only passing reference made to Odonata;
- ** a part of the article deals with Odonata;
- *** the article deals exclusively with Odonata.

An article dealing exclusively with Odonata but with only passing reference to the African fauna is rated as single asterisk.

The abbreviations of publication titles cited follow the *World List of Scientific Periodicals* (1963–1965). Titles of publications for which there are no acceptable abbreviations are written out in full.

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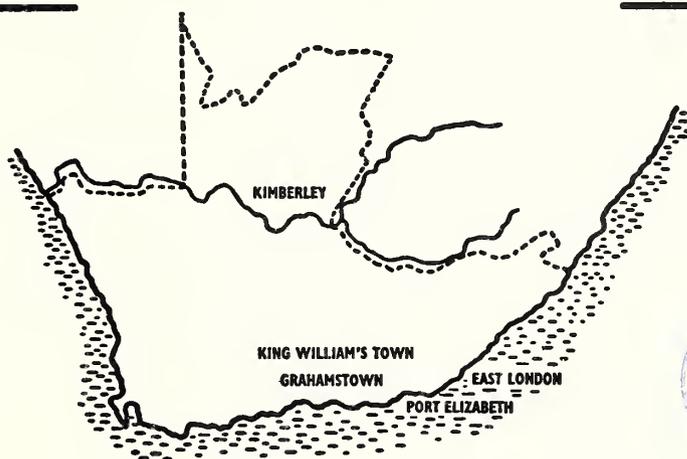
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On the taxonomic status of *Heleophryne regis* Hewitt, 1909 (Anura: Leptodactylidae)

RICHARD BOYCOTT

Cape Department of Nature and Environmental Conservation, Jonkershoek Nature Conservation Station, Stellenbosch, Cape Province, South Africa

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ABSTRACT

Heleophryne regis, which has for some time been regarded as the eastern subspecies of the *H. purcelli* complex in the Cape Folded Mountain Belt, has a mating call distinct from typical *H. purcelli* and is therefore reinstated to specific rank. It is geographically isolated from other species in the southern Cape Province. An account of the species' past taxonomic history is presented. Certain morphological characters hitherto employed to distinguish *H. regis* from its congeners do not withstand critical scrutiny.

INTRODUCTION

The genus *Heleophryne*, endemic to southern Africa, was described by Sclater in 1899. The description of the type-species, *H. purcelli*, was based on a single adult specimen. *H. regis*

was also described from one adult specimen by Hewitt in 1909. During the next seventeen years three further species were described by the same author, viz. *H. natalensis*, *H. rosei* and *H. sylvestris* (Hewitt, 1913, 1925, 1926). Du Toit (1934) in his revision of the genus recognized four species *H. purcelli*, *H. rosei*, *H. regis* and *H. natalensis*; the last species incorporated Hewitt's *H. sylvestris*. Poynton (1964) suggested that *H. regis* could be merely the eastern subspecies of a *purcelli* gradient extending from the south-western Cape eastwards along the Cape Folded Mountain Belt to the vicinity of Humansdorp. Van Dijk (1966) pointed out that a number of *H. p. regis* tadpoles in the Transvaal Museum collection differed from more typical *purcelli* from the species' western range and suggested that the relationships of *purcelli* and *regis* warranted re-examination.

In 1972 the Cape Department of Nature and Environmental Conservation initiated a project to establish the conservation status of Cape Province anurans. One member of the genus *Heleophryne*, *H. rosei*, was considered as a candidate for critical examination but its relationship to other members of the genus had first to be determined. This investigation led to the findings reported in the present publication.

VOCALISATION

Unequivocal species of frogs are generally recognized by distinctive adult external morphology and unique male mating call, however, morphological distinctness is not an essential requisite and many anuran species are so similar in appearance that initial recognition was based solely on the mating call (Littlejohn, 1971). It is now accepted that mating calls in amphibians are species-specific and that the voice is the most diagnostic feature of any frog species (Blair, 1958; Pengilley, 1971; Passmore and Carruthers, 1975; Passmore and Carruthers, 1979). Often it is the only character that can be safely used to distinguish between cryptic species.

Rose (1926) stated for *H. rosei* that ". . . on one occasion a *H. rosei* was heard to give a chirp, but no other vocal sound has been heard . . .". FitzSimons (1946) described the call of *H. p. orientalis* as ". . . a somewhat high-pitched, short, clinking whistle (not unlike that of an Anvil Bat when heard at a distance) . . .". The call of *H. natalensis* has been described as ". . . a soft melodious, high-pitched, bell-like 'ting', repeated slowly about ten times, and sometimes prefaced by a 'currick' . . ." (Wager, 1965). That of *H. p. purcelli* has been described as ". . . a clear, high-pitched ringing note, produced at regular intervals of one per second . . ." (Passmore and Carruthers, 1979). It is this last call with which the present author is most familiar. It is heard from September to January in typical habitat of *H. p. purcelli*. During 1978 very different "creaking calls" were heard in typical habitat of *H. p. regis* in the southern Cape Province. In December 1979 the same calls were heard in the Kareedouw Mountains where they were emitted by breeding males. Typical calls of *H. p. purcelli* were not heard on these occasions. Because of the striking call difference between *H. p. regis* and *H. p. purcelli* the calls were recorded for analysis and a series of specimens of both "subspecies" were collected to investigate possible morphological differences between them.

The recordings were made in the field on a Philips Automatic N2203 portable cassette recorder. The recorded calls were analysed on a sound spectograph (KAY 7029A spectrum analyser) within the frequency range 80–8000 Hz using a wide-band (300 Hz) filter.

Heleophryne purcelli regis (*sensu* Poynton) produces a harsh, low-pitched, creaking (almost rasping) call that differs markedly from the distinctive high-pitched ringing note of *Heleophryne purcelli purcelli* of the south-western Cape.

The sonograms of the calls of *H. p. purcelli* and *H. p. regis* (Figs 1 to 4) show clearly that the call of the former species is distributed over a relatively narrow range of frequencies (2–2.5 kHz) whereas that of the latter species is distributed over a wider range (1–2.5 kHz). The

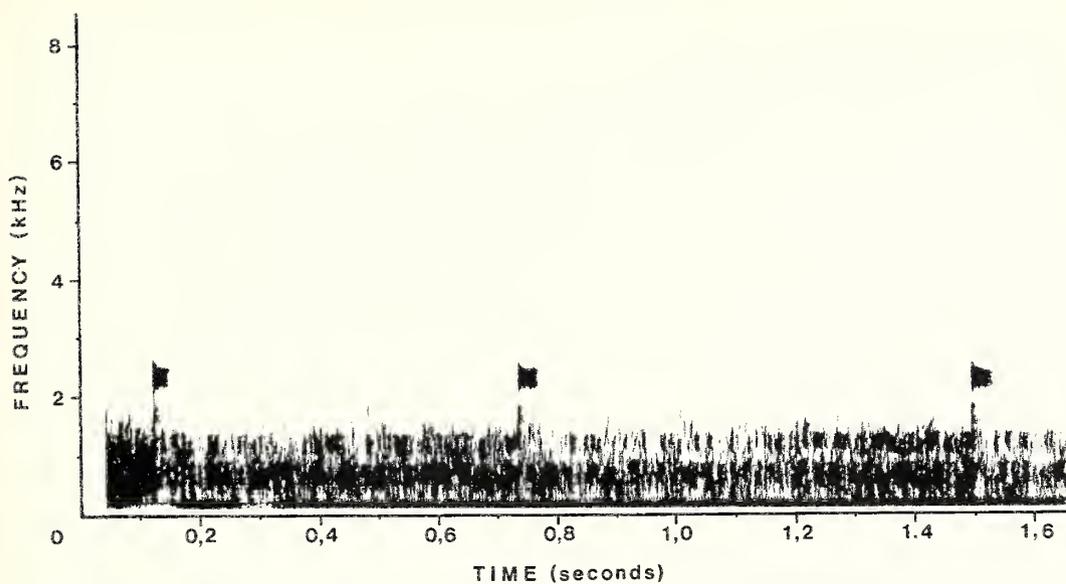


Fig. 1. *Heleophryne purcelli*—sonogram of 3 successive calls using wideband (300 Hz) filter. (Locality: Donkerkloof, Klein Drakenstein Mountains).

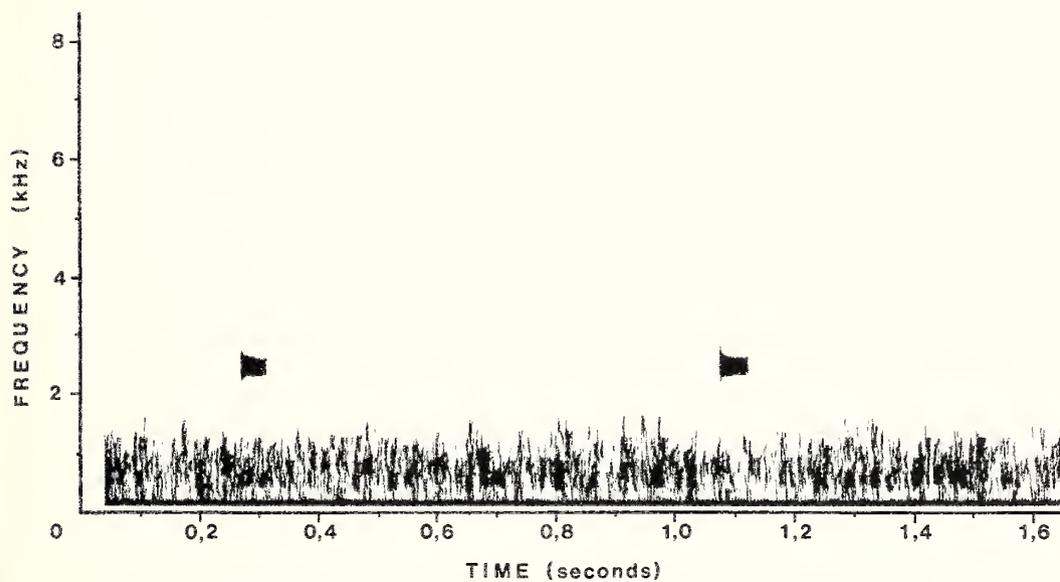


Fig. 2. *Heleophryne purcelli*—sonogram of 2 successive calls using wideband (300 Hz) filter. (Locality: Uitkyk River, Cedarberg Mountains).

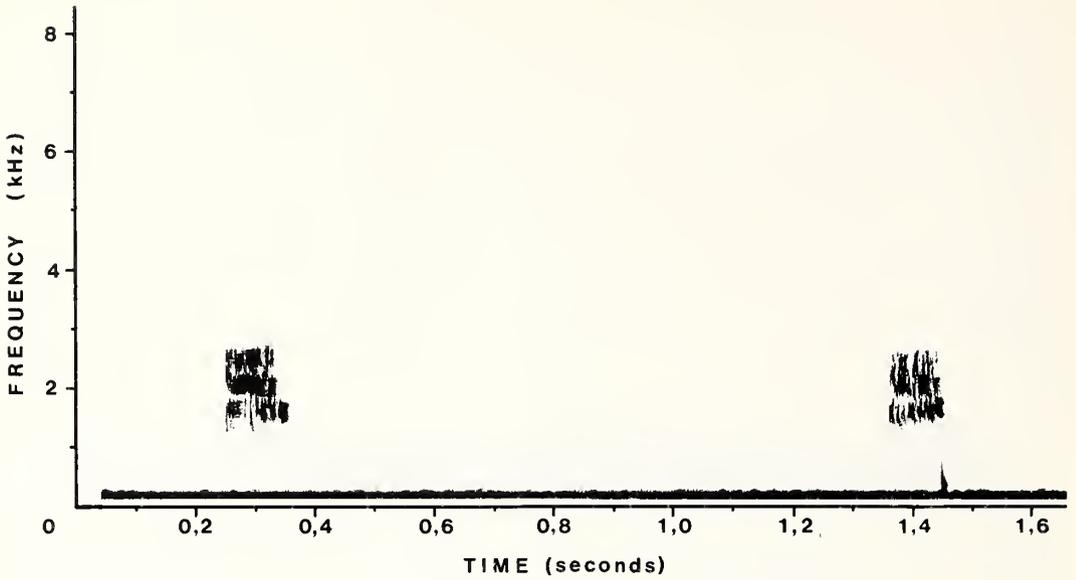


Fig. 3. *Heleophryne regis*—sonogram of 2 successive calls using wideband (300 Hz) filter. (Locality: Near Wolfkop, Kareedouw Mountains).

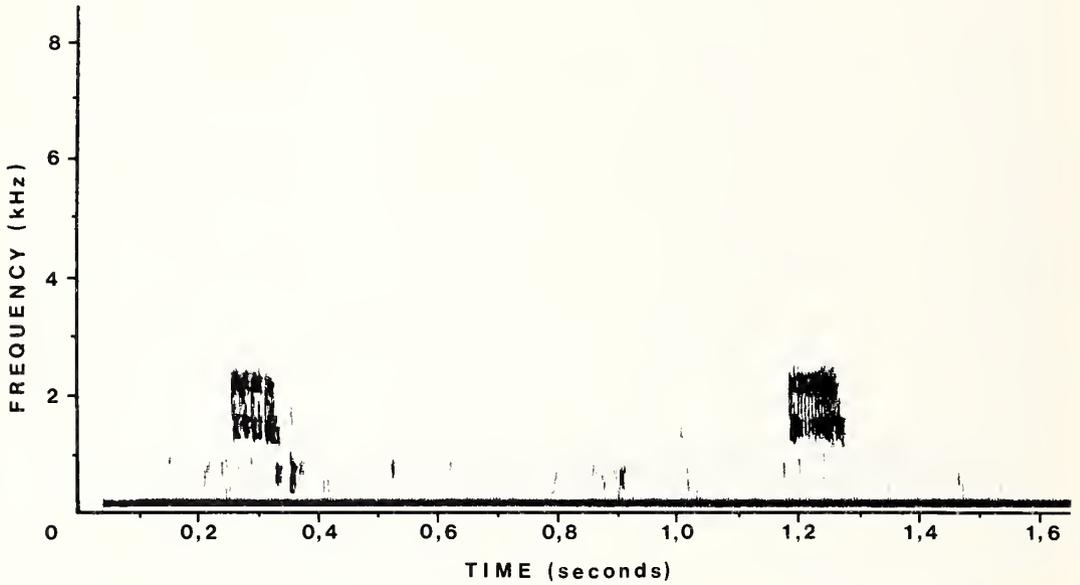


Fig. 4. *Heleophryne regis*—sonogram of 2 successive calls using wideband (300 Hz) filter. (Locality: Noghorakloof, Tsitsikamma Mountains).

background noise of rushing water has been left intact in Figs 1 and 2. There is no extensive background noise in the *H. p. regis* recordings presented here (Figs 3 and 4).

The call of *H. p. purcelli* is of short duration. The resulting high-pitched bell-like call stands out clearly against the background noise of rushing water. In *H. p. regis* the call is of longer duration and has a wider frequency range. The call duration varies from 0,03 to 0,05 seconds in *H. p. purcelli* and from 0,08 to 0,11 seconds in *H. p. regis*. The interval between successive calls varies from 0,61 to 0,88 seconds in the former and from 0,93 to 1,10 seconds in the latter. *H. p. purcelli* calls are non-pulsatile whereas the calls of *H. p. regis* are divided into a series of pulses. In summary, the call of *H. p. regis* differs substantially from that of *H. p. purcelli* in duration, frequency structure and in being pulsatile. It appears therefore that *H. p. regis* must be reinstated to specific rank as *Heleophryne regis* Hewitt, 1909.

The *Heleophryne purcelli* calls were recorded at Donkerkloof in the Klein Drakenstein Mountains (3319CC Franschhoek) on 21 October 1977 and at the Uitkyk River in the Cedarberg Mountains (3219AC Wuppertal) on 2 November 1978 (Figs 1 and 2). The *Heleophryne regis* calls were recorded near Wolfkop in the Kareedouw Mountains (3424AB Clarkson) on 1 December 1979 and at Noghorakloof in the Tsitsikamma Mountains (3324CC Witelsbos) on 14 December 1979 (Figs 3 and 4). On 15 January 1982 a typical call of *H. p. regis* was recorded at the Perdeberg River in the Outeniqua Mountains (3322CC Jonkersberg) and was found to be no different from the calls recorded above. During an earlier fieldtrip on 30 October 1981 *H. p. purcelli*-like calls were heard (but not recorded) at Garcia Pass in the Langeberg Mountains (3321CC Muiskraal). Although slight differences between the calls of *H.p. purcelli* and *H.p. orientalis* may be detected by detailed analysis, differences between the calls of *H.p. orientalis* and *H. p. regis* are readily detected as they are vast.

PAST TAXONOMIC HISTORY OF *HELEOPHRYNE REGIS*

The original diagnoses of *H. purcelli* (Sclater, 1899) and *H. regis* (Hewitt, 1909) have been condensed and presented in Table 1. In many of the characters used the two species are similar and it is therefore difficult to distinguish them on morphological grounds. Only three of the characters appear to distinguish the species from one another. These are italicized in Table 1. Of these, the webbing has received the most attention and was Hewitt's chief diagnostic character separating the two species (Hewitt, 1909, 1911, 1913, 1926).

Du Toit (1934) who had more *Heleophryne* material at his disposal than did previous workers carried out the first revision of the genus. He clarified certain aspects but at the same time confused others. In his key to the genus, *H. purcelli* and *H. regis* show few differentiating characters. This is perhaps not surprising as more than half of du Toit's *regis* material (excluding tadpoles) is referable, in the present author's opinion, to *H. purcelli*. Only one of du Toit's *H. regis* localities, "Knysna", falls into the range of *H. regis* as proposed in the present paper (15 of his 34 specimens came from this locality). No clear-cut morphological distinction between the two forms is therefore likely to result from using du Toit's key.

Poynton (1964), who carried out the second revision of the genus, suggested that *H. regis* be considered the eastern subspecies of a *H. purcelli* cline consisting of, from west to east, *H.p. purcelli*, *H.p. depressa* FitzSimons, *H.p. orientalis* FitzSimons and *H.p. regis*. He concluded that ". . . The forms of *Heleophryne* occurring in the Cape Folded Range are very similar to one another, and further collecting in intermediate areas may well make it impossible to distinguish between these forms . . .". Poynton's diagnoses of *H.p. purcelli* and *H.p. regis* are presented in Table 2.

REVIEW OF TAXONOMIC CHARACTERS

A series (n = 25) of adult specimens of *H.p. purcelli* was compared with a series (n = 25) of adult specimens of *H.p. regis* (*sensu* Poynton) in terms of characters held by Hewitt (1909),

TABLE 1.

A comparison of diagnoses for *Heleophryne purcelli* Sclater and *Heleophryne regis* Hewitt from the original descriptions. (The italicized characters are those which appear to hold most promise for distinguishing the one form from the other).

HELEOPHRYNE PURCELLI Based on SAM 1313 from Jonkershoek	HELEOPHRYNE REGIS Based on TM 10093 from Knysna
Snout obtuse	Snout rounded
Vomerine teeth in two linear groups	Vomerine teeth in two transverse groups
Interorbital space a little broader than upper eyelid	Interorbital space a trifle narrower than upper eyelid
Tympanum not visible	Tympanum indistinct
Fingers free - ending in broad, flat, somewhat truncate triangular expansions or discs	Fingers free - ending in triangular discs
<i>Toes completely webbed</i>	<i>Toes half-webbed</i>
Terminal discs on toes well developed but not as large or triangular as those on fingers	Terminal discs not as large as those on fingers
Subarticular tubercles oval and fairly large	Subarticular tubercles oval and well-developed
<i>Inner metatarsal tubercle oval and well developed</i>	<i>Inner metatarsal tubercle elliptic and of moderate size</i>
Outer metatarsal tubercle absent	Outer metatarsal tubercle absent
Tibio-tarsal joint reaches the end of snout	Tibio-tarsal joint reaches the end of snout
Skin smooth above and granular below	Skin smooth above and granular below
Colour purplish with darker round, faintly white edged spots of the same colour	Colour purplish above with irregular dark spots
<i>Hindlimbs cross-banded with darker purple bands</i>	<i>Limbs with indistinct dark cross-bands</i>
Yellowish white below	Yellowish white below

du Toit (1934) and Poynton (1964) to be diagnostic of the two forms. The *purcelli* series originated from: Bain's Kloof (Limietberge); Donkerkloof (Klein Drakenstein Mountains); Meerluskloof (Riviersonderend Mountains).

Mus. cat. nos.: SAM 1313 (Holotype); AM A Nos. 469, 470, 480-483, 502, 505-509, 511, 513, 569-573, 584-588, 664.

The *regis* series originated from: Perdeberg River, Deepwalls (Outeniqua Mountains); Lottering River, Heuningkloof, Sanddrif River, Witelsbos (Tsitsikamma Mountains); near Wolfkop (Kareedouw Mountains).

Mus. cat. nos.: TM 10093 (Holotype); PEM A Nos. 455, 456; AM A Nos. 516, 517, 521-523, 602, 604-606, 608, 612, 616, 618, 619, 623, 627, 632-635, 652, 653, 700.

Webbing

In the *purcelli* series males ($n = 15$) had 2 to $2\frac{1}{2}$ (3 in subadults) phalanges of the fourth toe free of webbing and all females ($n = 10$) had 2 to 3 phalanges of the fourth toe free of

webbing. In adult males the webbing extends to the tip of the fifth toe or to a point within 1 phalanx of the tip (1 to 1½ in subadults). The females usually have 1 to 2 phalanges of the fifth toe free of webbing although in exceptional cases webbing may extend to within ½ a phalanx of the tip. It appears as if juvenile and subadult males have less webbing than adults.

In the *regis* series all males (n = 15) had 2 to 3 phalanges (exceptionally 3½) of the fourth toe free of webbing and females (n = 10) had 3 to 3½ phalanges of the fourth toe free of webbing. In males the webbing extends to the tip of the fifth toe or to a point within ½, 1 or 1½ phalanges of the tip (a variable character in this species). The females had 1 to 2 phalanges of the fifth toe free of webbing.

In both species the extent of webbing is greater in males than in females (although there is some overlap between the sexes). Although it is also true that the extent of webbing in *H. purcelli* tends to be greater than that in *H. regis*, it is necessary to point out that the holotypes of *H. purcelli* and *H. regis* are respectively an adult male and an adult female. This could explain why the extent of the webbing was Hewitt's chief diagnostic character separating the two species. However, the overlap between the sexes and between the species renders the extent of webbing unreliable as a diagnostic character.

Inner metatarsal tubercle

Hewitt (1909) stated that the inner metatarsal tubercle was "oval and well-developed" in *H. purcelli* but "elliptical and of moderate size" in *H. regis*. Poynton (1964) considered the tubercle to be narrowly elliptical in both forms (Table 2) and made no mention of relative size. In the fifty specimens examined in the present study no difference in shape was found. The tubercle of *H. regis* is slightly smaller than that of *H. purcelli*, however, it is only a proportionate size difference as *H. regis* is smaller than *H. purcelli*. A subadult *H. purcelli* of the same size as an adult *H. regis* does not have a significantly larger inner metatarsal tubercle. The shape and size of this tubercle is not a clear-cut distinguishing character.

TABLE 2.

A comparison of Poynton's (1964) diagnoses for *Heleophryne purcelli purcelli* Sclater and *Heleophryne purcelli regis* Hewitt. (Apparently significant distinguishing characters are emphasized by italics).

HELEOPHRYNE PURCELLI PURCELLI Based on specimens from: Stellenbosh, Franschoek Pass, Bain's Kloof, Riviersonderend.	HELEOPHRYNE PURCELLI REGIS Based on specimens from: Knysna, Deepwells, Jonkersberg, Humansdorp district.
Tibio-tarsal articulation <i>not or only slightly extending beyond eye</i>	Tibio-tarsal articulation <i>reaching from eye to beyond nostril</i>
Outer metacarpal tubercle elliptical, long axis approximately continuous with axis of first finger	Outer and inner metacarpal tubercle elliptical, long axis approximately continuous with axis of first finger
Inner metatarsal tubercle narrowly elliptical 2 phalanges of 4th toe free of web Web reaching almost to tip of 5th toe	Inner metatarsal tubercle narrowly elliptical 2½ to 3 phalanges of fourth toe free of web Last phalanx of 5th toe free to nearly free of web

Banding on the hindlimbs

Slater (1899) describes the hindlimbs of *H. purcelli* as "cross-banded with darker purple bands". In all but one of the *H. purcelli* specimens examined in the present study the cross-banding of the hindlimbs was distinct (Fig. 5). Hewitt (1909) states that the bands on the hindlimbs of *H. regis* are "indistinct" and FitzSimons (1946) describes the hindlimbs as "more



Fig. 5. *Heleophryne purcelli* Slater—adult male specimen (AM A 513) from Donkerkloof, Klein Drakenstein Mountains (3319CC Franschoek).

or less banded". Poynton's (1964) photograph of *H.p. regis* shows clearly defined transverse bands, contrasting sharply with Hewitt's observation. In two of the *H. regis* specimens from the series of 25 banding was absent, in 10 it was reduced to blotches (Figs 6 and 8) and in the remaining 13 it was present (being noticeably more distinct in some than in others). Fig. 7 shows the rare, scarcely-banded pattern variant of *H. purcelli* and Fig. 8 shows a similarly unbanded *H. regis*. It is clear that the banding of the hindlimbs cannot be considered to be a reliable distinguishing character.

Relative body length

Two methods have been used to determine the ratio of body length to hindlimb length in *Heleophryne*. The first and more satisfactory method is to measure body length (snout/vent) and hindlimb length (vent/tibio-tarsal joint) independently. The second is to bend the hindlimb



Fig. 6. *Heleophryne regis* Hewitt—adult male specimen (AM A 632) from near Wolfkop, Kareedouw Mountains (3424AB Clarkson).

round until the tibio-tarsal joint is adpressed to the head region and to relate its position to the tympanum, eye, nostril or snout. Adpression of the hindlimb (“tibio-tarsal articulation” method) is the less accurate method since dislocation or breakage of the femur or tibia is not infrequent and different workers apply differing degrees of pressure. Furthermore, the distances between tympanum, eye, nostril and snout are often very small.

Sclater (1899), Hewitt (1909) and Poynton (1964) used the tibio-tarsal articulation method. Their data are therefore not directly comparable with those of du Toit (1934) and FitzSimons (1946) who used independent measurements of body and hindlimb length.

(a) *Tibio-tarsal articulation*

Both Sclater (1899) for *H. purcelli* and Hewitt (1909) for *H. regis* state that the tibio-tarsal joint of the adpressed hindlimb “reaches the end of the snout” (Table 1). For the 15 *H. p. purcelli* specimens examined by Poynton (1964) the tibio-tarsal joint is given as “not or only slightly extending beyond the eye” whereas for his 78 *H. p. regis* specimens it “reaches from the eye to beyond the nostril” (Table 2).

The tibio-tarsal articulation of the adpressed hindlimb does not extend beyond the tip of the snout in any of the 25 *H. purcelli* and 25 *H. regis* specimens examined for this paper. In both species, irrespective of sex, the tibio-tarsal articulation may extend to the eye, to a point between the eye and the nostril, or to a point between the nostril and the tip of the snout.



Fig. 7. *Heleophryne purcelli* Sclater—adult female specimen (AM A 546) from Donkerkloof, Klein Drakenstein Mountains. Note the absence of dorsal patches and limb-banding; this pattern morph is of rare occurrence in this species.

(b) *Body length/hindlimb length ratio*

Du Toit (1934) stated that *H. purcelli* has a proportionately greater snout/vent length than has *H. regis*. The present study contradicts his findings, however, it must be remembered that more than 50% of his “*regis*” material is in fact referable to *H. purcelli*. In the females of both species the body length was greater than, or equal to, the hindlimb length (SV/HL ratio 1,01–1,11 in *purcelli*; 1,00–1,16 in *regis*). In the males of both species, the body length was usually less than, or equal to, the hindlimb length (SV/HL ratio 0,93–1,05 in *purcelli*; 0,95–1,03 in *regis*). There was no difference between the two species. However, there is obviously considerable variation in this character particularly in immature specimens.

The possibility that there is a clear-cut sexually dimorphic distinction is discussed in the section on size and sexual dimorphism below.

Interorbital space

Sclater (1899) states for *H. purcelli* that the interorbital space is “a little broader than” (presumably the breadth of) the upper eyelid. Hewitt (1909), in his description of *H. regis*, considers it to be “a trifle narrower than” the upper eyelid, whereas FitzSimons (1946) states that in *H. regis* the interorbital space is “broad, equal to or greater than breadth of upper



Fig. 8. *Heleophryne regis* Hewitt—adult female specimen (AM A 700) from Noghorakloof, Tsitsikamma Mountains. Note the absence of dorsal patches and limb-banding; this pattern morph appears to be more common in *H. regis* than in *H. purcelli*.

eyelid". For *H. p. depressa* FitzSimons gives the interorbital space as "narrow, less than breadth of upper eyelid" and for *H. p. orientalis* "a little narrower than upper eyelid".

Slater, Hewitt and FitzSimons did not describe the method employed to obtain these measurements. The interorbital distance (= space) could have been measured at the narrowest point between the orbits or alternatively at the anterior or posterior corners. The *breadth of the upper eyelid* has not been accurately defined. It is often difficult to determine exactly where the orbit merges into the dorsal surface of the head, especially in poorly preserved specimens such as the holotypes of *H. purcelli* and *H. regis*.

In view of these problems the ratio of interorbital distance to eyelid breadth is of doubtful value as a diagnostic character.

SIZE AND SEXUAL DIMORPHISM

Poynton (1964) gives the maximum snout/vent length for *H. p. purcelli* as 53 mm and for *H. p. regis* as 47,5 mm. The largest specimens (both females) of *H. purcelli* and *H. regis* examined during the present study were 56,3 mm and 49,1 mm respectively. The largest male *purcelli* measured 47,3 mm and the largest male *regis* 42,6 mm. Females of both species attain a larger size than males (Table 3).

TABLE 3.

Comparison of the total length (snout to vent) and hindlimb length (vent to tibio-tarsal joint) measurements (mm) in *Heleophryne purcelli* Sclater and *Heleophryne regis* Hewitt.

Species	Sex	N	Total length			Hindlimb length		
			Range	Mean	S.D.	Range	Mean	S.D.
<i>H. purcelli</i>	♂♂	15	36,6–47,3	42,60	3,72	35,0–46,4	42,27	3,82
	♀♀	10	40,6–56,3	47,50	5,33	39,0–53,0	45,26	4,50
<i>H. regis</i>	♂♂	15	36,2–42,6	38,40	1,93	36,2–43,0	39,22	1,95
	♀♀	10	43,2–49,1	46,72	1,83	40,2–49,2	44,82	2,95

The hindlimb length was expressed as a percentage of the snout/vent length and subjected to the t-test procedure for a comparison of two sample means (Steel and Torrie 1960). In both *H. purcelli* ($P < 0,01$) and *H. regis* ($P < 0,001$) females had proportionately shorter hindlimbs than males (respective values for both species: $t = 3,03$ and $4,62$; $df = 23$ and 23).

Although there is some overlap between the sexes it appears that the webbing between the toes of the hindfeet is more extensive in males than in females (see review of taxonomic characters). The males of *H. purcelli* and *H. regis* can be distinguished from the females by the presence of a fleshy "anal flap". The cloacal orifice is ventrally directed in males and posteriorly directed in females.

During the breeding season both sexes develop secondary sexual characters which are more pronounced in males than in females. In males the forearms become thicker and swollen and bear elongated nuptial pads, dorsal skin folds develop and numerous asperities or spines appear on the surface of the skin. In some specimens asperities cover the entire dorsal surface. Asperities may develop on the skin in females but never to the same extent as in males. The number and stage of development of asperities varies considerably amongst individuals of the same population and is probably determined by the sexual maturity of each individual. At the termination of the breeding season a recession of the secondary sexual characters occurs.

The distribution and concentration of asperities in breeding males may be of some use as a taxonomic character in distinguishing those species which differ markedly from one another (*viz.* *H. rosei*; *H. natalensis*; *H. purcelli*/*H. regis*). In *H. natalensis* for example the spines are concentrated on the fingers and in the axilla (Passmore and Carruthers, 1979) whereas in *H. purcelli* and *H. regis* the asperities are more widely distributed and are concentrated along the margin of the lower jaw, on the inside surface of the forearms and on the central portion of the chest. *H. purcelli* and *H. regis* individuals at an advanced stage of development of secondary sexual characters possess concentrations of asperities around the vent and along the outer edges of the ventral surface between the fore- and hindlimbs. There is no difference in the distribution and concentration of asperities between *H. purcelli* and *H. regis*.

In *H. rosei* the asperities are concentrated on the outside surfaces of the forearms, on the back and sides and on the dorsal surfaces of the hindlimbs. A few scattered asperities are situated along the supratympanic fold. A clearly defined dorsal patch, in which asperities are absent, extends posteriorly from the nasal region to the sacral region. In *H. rosei* the asperities on the outer edges of the upper and lower jaws are, when compared with those of *H. purcelli*, poorly developed and are most distinctive in the region between the eye, the angle of the jaw

and the edge of the upper jaw. These observations have been made on a limited number of individuals and further collections of adults in breeding condition will have to be made for confirmation.

HABITAT AND DISTRIBUTION

The Cape species of *Heleophryne* are restricted to mountainous terrain with high rainfall (600 to 3 000 mm p.a.) and clear, swift-flowing, perennial mountain streams. The length of the larval phase has never been determined for any species of *Heleophryne*. However, it has been suggested that it lasts up to two years (Wager, 1965) and from personal observations is certainly in excess of 12 months. The genus is therefore prevented from colonizing non-perennial streams.

The rainfall patterns in the south-western and southern parts of the Cape Province differ considerably from west to east. The western species, *H. purcelli*, occurs in a predominantly winter rainfall region. In the southern Cape, *H. regis* habitats receive rain throughout the year. The range of *H. purcelli* (west of the 20° E line of longitude) has a rainfall peak in winter (June, July and August). The summers in this region are markedly dry. However, from Swellendam eastwards to the eastern limit of the Langeberg range, which corresponds approximately with the range of *H. p. orientalis*, rain falls throughout the year with peaks in spring and autumn. The range of *H. regis* is likewise subjected to year round rainfall with peaks in March/April/May and August/September/October.

The breeding seasons of *H. purcelli* and *H. regis* appear to be influenced by these rainfall peaks. Although *H. purcelli* normally breeds from October to January, a few individuals were heard calling at Dassieshoek (3319DB Koo) on 19 September 1980, which suggests that breeding may commence earlier. The southern Cape species, *H. regis*, usually breeds from December to February. The breeding season of this species may also start earlier as a single individual was heard calling in Noghorakloof (3324CC Witelsbos) on 3 November 1980. *H. regis* breeds when southern Cape streams are almost at their lowest level. This ensures survival of larvae as any stream that has water at this time will certainly be perennial. Furthermore the survival of eggs and young tadpoles would be greater when river flow is reduced.

In the south-western and southern Cape Province the genus *Heleophryne* is confined to the Macchia, False Macchia and Knysna Forest veld types (Acocks, 1975). The distribution range of *H. purcelli* is included in the Macchia and False Macchia veld types. Although *H. regis* may occur marginally in False Macchia the river courses throughout its range are essentially densely forested. There may be a greater tendency towards forest-dwelling in *H. regis* than in *H. purcelli*, however, *H. p. orientalis* does occur in heavily forested gorges and ravines on the southern slopes of the Langeberg range (e.g. at Swellendam and Grootvadersbosch). All *H. regis* material collected to date (from 21 localities) has originated from forested areas. Typical habitat of *H. regis* is shown in Fig. 9.

Poynton (1964) lists five localities for *H. p. regis*. One of these is based on a C.N.D. (Cape Nature Conservation Department) specimen from "Humansdorp district" and Poynton places this in the locus 3424BB Humansdorp. The only suitable habitat in the Humansdorp district for *Heleophryne* is in the Kromrivier Forest Reserve in the Kareedouw Mountains (3424AB Clarkson) approximately 45 km west of the town. It can therefore be assumed that the C.N.D. specimen, in fact, originated from the Kromrivier Forest Reserve. This specimen was never lodged in a museum and has since been lost (Poynton *in litt.*). Nevertheless, the presence of *Heleophryne* in the Kromrivier Forest Reserve has been confirmed by the recent collection of material from three localities in the Kareedouw Mountains (Table 4). The Kareedouw Mountains appear to be the eastern limit of *H. regis* (Fig. 10). The other four localities recorded by Poynton (Knysna, Deepwalls, Jonkersberg, Montagu Pass) are all acceptable for *Heleophryne regis* as understood in the present paper.



Fig. 9. Habitat of *Heleophryne regis*—Noghorakloof, Tsitsikamma Mountains (3325CC Witelsbos).

The western limit of *H. p. regis* is Jonkersberg (Poynton, 1964). This material is clearly assignable to *H. regis* as is material collected during the present study from the Perdeberg River (3322CC Jonkersberg) near the top of the Robinson Pass, approximately 20 km west of Jonkersberg (Table 4).

The area between Robinson Pass and the Gourits River was surveyed during March 1980 and November and December 1981. Many of the localities visited appeared unsuitable for *Heleophryne* with the exception of the Huis River (3322CC Jonkersberg), Attakwaskloof River, the upper reaches of the Meul River, the Goliats River (3321DD Attakwaskloof), the Jakkals River and the Dwars River (3321DC Langeberg). Of these six localities all but the first provide suitable habitat along only certain stretches. The Huis River is situated approximately 2,5 km south-west of Ruitersbos Forest Station, the Attakwaskloof River on the northern side of the Attaqua Mountains, the Meul and Goliats Rivers respectively south and south-west of the Attaqua Mountains and the Jakkals and Dwars Rivers at the eastern extremity of the Langeberg Mountains. There is in this region a marked difference between the types of habitat available for *Heleophryne*. The streams in this region, excluding the Huis River, are not forested and appear more suitable for *H. purcelli* than for *H. regis*, if it is assumed that the latter is more of a forest-dwelling species than *H. purcelli*. The area between the Gourits River and the Attaqua Mountains has lower rainfall (500–700 mm p.a.) than the areas to the east and west which have rainfall figures in excess of 700 mm (800–1 000 mm p.a.). This could account

TABLE 4.
Distribution records for *Heleophryne regis* Hewitt

Locality	Locus	Mus. cat. No.	Notes
Knysna, Outeniqua Mountains.	3423AA KNYSNA	TM 10093	Type-locality Recorded by Poynton (1964)
Forested stream north of George, Outeniqua Mountains.	3322CD GEORGE	AM A 720	Collected 30/vii/1972 Poynton (1964) records specimens from this locus.
Forested stream near Jonkersberg Forest Station, Outeniqua Mountains.	3322CD GEORGE	AM A 436	Collected J. C. Greig 31/xii/1973 Poynton (1964) records specimens from this locus.
Perdeberg River near Robinson Pass, Outeniqua Mountains.	3322CC JONKERSBERG	AM A 516-525 AM A 703-709 AM A 727-730	Collected 3/i/1977 Collected 14, 15/xii/1981 Collected 15/i/1982 Poynton (1964) records specimens from this locus.
Outeniqua Pass, Outeniqua Mountains.	3322CD GEORGE	AM A 595	D.O.R. collected 7/viii/1979 Poynton (1964) records specimens from this locus.
Montagu Pass, Outeniqua Mountains.	3322CD GEORGE	AM A 596 AM A 712-715	Collected 7/viii/1979 Collected 18, 19/xii/1981 Poynton (1964) records specimens from this locus.
Near Wolfkop, Kareedouw Mountains.	3424AB CLARKSON	AM A 597 AM A 632-635	Collected 28/viii/1979 Collected 1/xii/1979 New distribution record The recording illustrated in Fig. 3 was obtained here.
Tributaries of the Groot River, Tsitsikamma Mountains.	3324CC WITELSBOS	AM A 601-607	Collected 5, 6/x/1979 New distribution record
Noghorakloof west of Witelskop, Tsitsikamma Mountains.	3324CC WITELSBOS	PEM A 455, 456 AM A 608-613 AM A 647-650 AM A 700, 701	Collected 6/x/1979 Collected 6/x/1979 Collected 14/xii/1979 Collected 3/xi/1980 The recording illustrated in Fig. 4 was obtained here.
Sanddrif River, Tsitsikamma Mountains.	3323DD JOUBERTINA	AM A 615-620	Collected 13/x/1979 New distribution record
Lottering River, Tsitsikamma Mountains.	3323DC NATURE'S VALLEY	AM A 623	Collected 26/x/1979 New distribution record

Locality	Locus	Mus. cat. No.	Notes
Heuningkloof, Tsitsikamma Mountains.	3323DD JOUBERTINA	AM A 624-627	Collected 27/x/1979
Jack-se-bos, Kareedouw Mountains.	3424AB CLARKSON	AM A 631	Collected 30/xi/1979
Forested stream north of Clarkson, Kareedouw Mountains.	3324CD KAREEDOUW	AM A 636-646	Collected 2/xii/1979 New distribution record
Tierkloof, Outeniqua Mountains.	3322CD GEORGE	SZC 311	Collected P. W. de Kock 27/xi/1979 Poynton (1964) records specimens from this locus.
Plaat River near Karatara, Outeniqua Mountains.	3322DD KARATARA	SZC 312, 313	Collected P. W. de Kock 5/xii/1979 New distribution record
Groenkop near Saasveld, Outeniqua Mountains.	3322DC WILDERNESS	SZC 36	Collected J. C. van Dalen 26/viii/1977 New distribution record
Diepwal-se-Loop near Deepwells Forest Station, Outeniqua Mountains.	3323CC KRUISVALLEI	AM A 652, 653 AM A 716-718, 721-724 SAM 45192 SAM 45193	Collected N. I. Passmore 4/i/1980 Collected 19/xii/1981 Collected 12/i/1982 Poynton (1964) records specimens from this locus.
Swart River near Saasveld, Outeniqua Mountains.	3322DC WILDERNESS	AM A 702	Collected P. J. Louwrens 24/viii/1981 Poynton (1964) records specimens from this locus.
Huis River near Robinson Pass, Outeniqua Mountains.	3322CC JONKERSBERG	AM A 710, 711	Collected 16/xii/1981 Poynton (1964) records specimens from this locus.
Klein-Witelskloof near Keurbooms River Forest Station, Outeniqua Mountains.	3323CD THE CRAGS	AM A 725	Collected 11/i/1982 New distribution record
Watervalkloof near Jonkersberg Forest Station, Outeniqua Mountains.	3322CC JONKERSBERG	AM A 726	Collected 13/i/1982 Poynton (1964) records specimens from this locus.

for the absence of forested habitat. *H. regis* has only been found in forested areas that receive 900–1 200 mm of rain per annum.

Tadpoles and newly metamorphosed froglets from the Goliats and Jakkals Rivers and three adults from the Dwars River were collected in March 1980. In November 1981 three more adult females were collected from the Dwars River and one subadult from the Jakkals River. During December 1981 an adult female was collected from the Attakwaskloof River and a series of 10 tadpoles was collected from the Meul River. During the same fieldtrip tadpoles and newly metamorphosed froglets and a juvenile frog were collected from the Huis River. The eight adult specimens from the Dwars, Jakkals and Attakwaskloof Rivers have been tentatively identified as *H. p. orientalis* and the juvenile from the Huis River as *H. regis*. No adults have been collected from the Goliats River but it is likely that once they have been discovered they too will prove to be *H. p. orientalis*. Newly metamorphosed froglets of *H. purcelli* are usually found moving out of rivers and streams during March and April. *H. regis* froglets, on the other hand, have only been found leaving the river in November, December and January. If this behaviour pattern is characteristic of the two species, the finding of froglets in the Goliats and Jakkals Rivers would substantiate the assumption that these localities support *H. p. orientalis* populations. However, the final proof rests with the acquisition of tape-recordings of calls from these localities. Until then, the eastern limit of *H. p. orientalis* and the western limit of *H. regis* will remain speculative. At present *H. regis* calls have been acquired as far west as the Perdeberg River.

H. regis is endemic to the southern Cape Province. Its known distribution range extends from the Huis and Perdeberg Rivers near Robinson Pass in west, eastwards along the Outeniqua and Tsitsikamma mountain ranges to the Kareedouw Mountains in the east (Fig. 10). A list of collecting localities for *H. regis* is provided in Table 4.

CONCLUSION

The genus *Heleophryne* Sclater is confined to the mountain ranges of South Africa from the Cape Peninsula to the eastern Transvaal. One species, *H. natalensis*, occurs in the mountain streams of the Drakensberg and the plateau slopes in Natal and the Transvaal. In the Cape Province the isolated nature of the folded mountain belt on which the genus occurs has given rise to considerable taxonomic complexity (Poynton and Broadley, 1978). Considering topography, rainfall and other environmental factors it becomes apparent that ghost frogs are restricted to a specific type of habitat. As these mountains are not continuous, speciation in allopatry has occurred, giving rise to the four species recognized in the present paper. A new species is currently being described from the isolated Elandsberg range north-west of Port Elizabeth (Boycott, in prep.) and an isolated and possibly distinct form has recently been discovered in the Kammanassie Mountains. The morphological differences between the species are not conspicuous and the composition of the Cape species can be regarded as a complex of sibling species.

On the various forms occurring in South Africa, *H. rosei* and *H. natalensis* are the most distinctive and are well separated geographically and morphologically from the *H. purcelli*/*H. regis* complex. *H. rosei* is separated from *H. purcelli* by the Cape Flats and *H. natalensis* is separated from the species in the southern Cape mountains by a swathe of unsuitable habitat in the eastern Cape Province. Although differences between the tadpoles of *H. purcelli* and *H. regis* have been suspected (van Dijk, 1966), definitive morphological and behavioural differences between the two forms have yet to be detected.

The disjunct distribution of ghost frogs in South Africa is probably a reflection of their specialised habitat requirements. The question posed by Watson, Loftus-Hills and Littlejohn (1971) as to whether disjunct allopatric forms would remain distinct, if their ranges came into contact, is also appropriate in this case. Telford and Passmore (1981) have demonstrated the

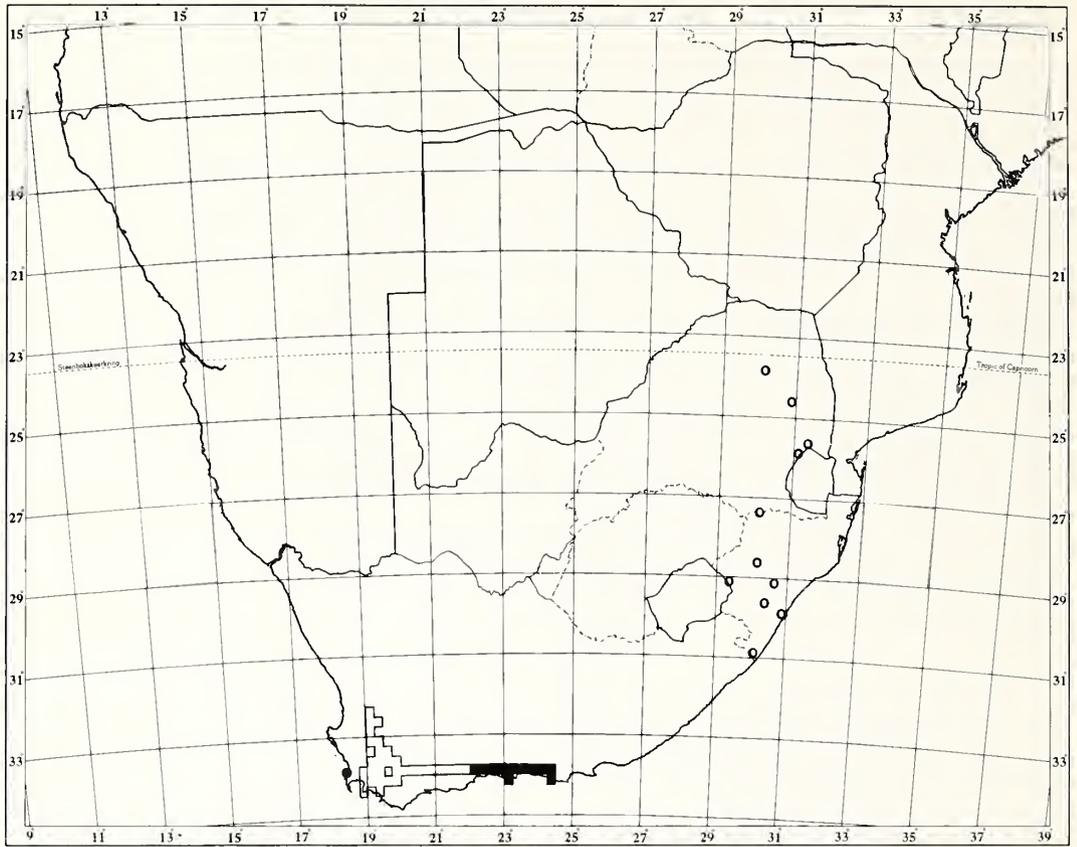


Fig. 10. The distribution of *Heleophryne* Sclater in South Africa.
 ● *Heleophryne rosei* Hewitt, □ *Heleophryne purcelli* Sclater,
 ■ *Heleophryne regis* Hewitt, ○ *Heleophryne natalensis* Hewitt.
 The distribution records for *H. natalensis* have been taken from Poynton (1964).

importance of the male mating call as the basis for conspecific recognition. Because of their role in maintaining species distinctness, pre-mating isolating mechanisms are the most important taxonomic characters that a species possesses (Littlejohn, 1968). In *H. purcelli* and *H. regis* no substantial morphological differences are apparent. Littlejohn (1968) goes on to say, however, that this does not necessarily mean that they are not both good biological species since the distinction depends on their basic genetic differences and their failure to interbreed in nature. Morphological differences, unless associated with ethological isolation, are of secondary taxonomic importance at the species level (Littlejohn, 1968). The fact that *H. purcelli* and *H. regis* have little or no apparent morphological differences suggests that they be classified as sibling species. The call difference described in the present paper is at this stage the only reliable character separating them unequivocally from one another.

MUSEUM ABBREVIATIONS

- AM Albany Museum, Grahamstown, South Africa.
 PEM Port Elizabeth Museum, Port Elizabeth, South Africa.
 SAM South African Museum, Cape Town, South Africa.
 SZC Saasveld Zoological Collection, Saasveld Forest Research Station, George, South Africa.
 TM Transvaal Museum, Pretoria, South Africa.

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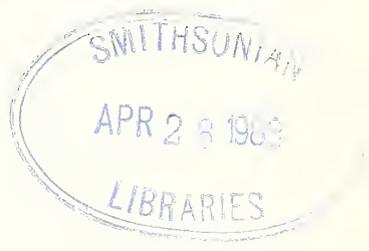
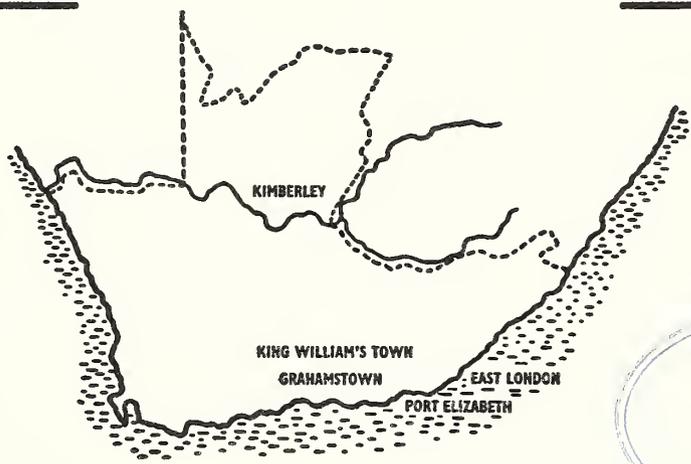
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Three new species and a new genus of tripterygiid fishes (Blennioidei) from the Indo-West Pacific Ocean

by

WOUTER HOLLEMAN

Albany Museum, Grahamstown, South Africa

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ABSTRACT

A new species of *Helcogramma*, *H. fuscopinna*, which ranges across the Indo-West Pacific (excluding the Red Sea) from as far south as Durban to southern Japan, is described. Two new species of *Enneapterygius*, *E. clarkae* from the western Indian Ocean including the Red Sea, and *E. ventermaculus* from Zululand, Aden and Pakistan, are described. The possibility that *Enneapterygius* may not be monophyletic is discussed. *Gillias capensis* (Gilchrist & Thompson) is assigned to a new genus, *Cremnochorites*, and the species is redescribed. Reference is made to certain osteological features of the family, particularly the presence of a free pterygiophore between the second and third dorsal fins and the occurrence of a septal bone in certain tripterygiid genera.

INTRODUCTION

Recent collecting of inshore fishes from the Zululand coast revealed the presence of several undescribed species in the family Tripterygiidae. These collections formed the basis for a revision of the South African species by Holleman (1978).

With the exception of Clark's (1979) revision of the Red Sea species and Holleman's (1978) unpublished dissertation of the South African taxa, little is known of the taxonomy of the family. Confusion abounds, particularly in the assignation of nominal Indo-Pacific species and genera.

Pending revisions of the two largest genera, *Helcogramma* and *Enneapterygius* which are currently in progress (by Hanson and Holleman respectively), the new species are here de-

scribed without providing keys to the species of each genus. Diagnoses are provided for the genera, and the species are distinguished from apparently closely related species. Comments are also made on the status of *Enneapterygius* since an investigation of the osteology of this genus (Holleman, 1978) casts some doubt on its monophyly.

Gillias capensis (Gilchrist & Thompson) was placed in *Gillias* Everman & Marsh, 1899 by Barnard (1927). Rosenblatt (1960) synonymised *Gillias* with *Enneanectes* but did not refer any of the South African or Australian species ascribed to *Gillias* to other genera. *Gillias capensis* is not referable to *Enneanectes*. The latter genus is reputedly endemic to the eastern Pacific Ocean and Caribbean (Rosenblatt, 1960). *Enneanectes* lacks the characteristic scalation of *G. capensis*. Clark (1979) suggests that *G. capensis* may be referable to *Norfolkia* Fowler. This is not the case, however, as the two genera differ considerably in osteology and scalation. A new genus, *Cremnochorites*, is thus proposed for *G. capensis*. *Cremnochorites* appears to be monotypic and endemic to the southern coast of South Africa.

METHODS

The methods of taking measurements follow those outlined by Hubbs & Lagler (1958). All fin elements were counted following Rosenblatt (1960) and Springer (1968). The last dorsal and anal fin rays are almost without exception divided to the base and are counted as a single element. The caudal fin of tripterygiids, with the exception of the highly specialized *Notoclinus* which has ten principal rays, invariably has seven dorsal and six ventral segmented principal rays, with the upper- and lowermost rays unbranched and the remainder bifurcate. There is also a variable number of dorsal and ventral unsegmented procurrent rays.

All species here considered have two undivided segmented rays and one short hidden spine in each pelvic fin. The rays are united by a membrane for part of their length. The inner ray is always the longest.

The following measurements and counts are given in Tables 1-3: standard length (SL); head length; horizontal eye diameter; snout length; upper jaw length; snout angle (measured as shown in Fig. 1—the “angle of head profile” of Zander & Heymer (1979)); counts for all fins except pelvic fins; number of caudal and precaudal vertebrae; lateral line counts; transverse scales, and total lateral scales.

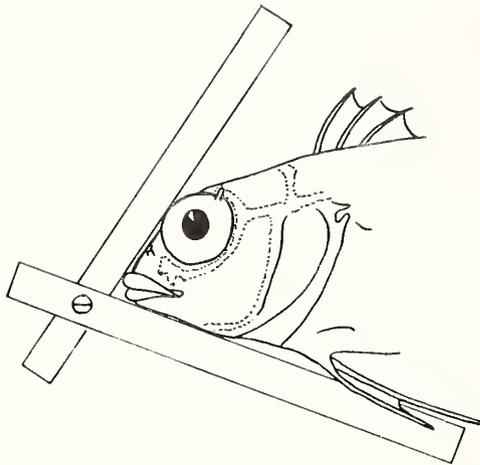


FIG. 1. Diagram to show how “snout angle” is measured.

The numbers of caudal and precaudal vertebrae were determined from cleared and stained specimens and from radiographs. The choice as to which vertebra to count as the first caudal vertebra poses a problem. Springer (1968) considered the first vertebra bearing a well-developed haemal spine as the first caudal vertebra for Blenniidae, where the first proximal anal pterygiophore is associated with the first haemal spine. Certain authors consider the first vertebra with closed haemal arch as the first caudal vertebra. The first "well-developed" haemal spine of most tripterygiids is distally forked (Fig. 2) and the subsequent centrum has a conventional haemal spine (Fig. 2). The first two proximal anal pterygiophores fall between the forked haemal spine and the first proper haemal spine and the third pterygiophore is associated with the latter. The first closed haemal arch is usually coincident with the forked haemal spine but closure may occur in one or two preceding vertebrae. As closure of the haemal arch is extremely difficult to determine from radiographs, it is expedient to consider the centrum with the forked haemal spine as the first caudal vertebra. This is most easily determined as the vertebra with a haemal spine immediately anterior to or in contact with the first anal pterygiophore. This criterion for the first caudal vertebra is thus adopted here.

Clark (1979) does not state which vertebra she considers the first caudal vertebra. Vertebral counts given by Clark and herein are therefore not necessarily comparable.

Where the lateral line is divided into two portions, one of pored and one of notched scales, these are referred to as "anterior" and "posterior series". Counts of total lateral scales were made from the first scale in the pectoral fin axil to the last scale on the caudal peduncle, not counting scales on the caudal fin. Transverse scale counts were taken along a diagonal from the first spine of the second dorsal fin to the base of the anal fin and the count is given as x/y where x is the number of scales above the lateral line and y the number of scales below the lateral line.

Osteological observations were made on specimens cleared and stained by the trypsin-alizarin technique of Taylor (1967).

Abbreviations— BMNH = British Museum of Natural History; BPBM = Bernice P. Bishop Museum; LACM = Los Angeles County Museum of Natural History; RUSI = J. L. B. Smith Institute of Ichthyology; SAM = South African Museum; USNM = United States National Museum of Natural History.

TABLE 1
Frequency distribution of number of vertebrae.

Species	Precaudal			Caudal vertebrae						
	9	10	11	22	23	24	25	26	27	28
<i>Helcogramma fuscopinna</i>		12						3	8	1
<i>Enneapterygius clarkae</i>		10		2	8					
<i>E. ventemaculus</i>		12				1	3	8		
<i>Cremnochorites capense</i>		23							13	10

TABLE 2
Frequency distribution of meristic data.

	First Dorsal			Second Dorsal					Third Dorsal					Anal									
	III	IV		XI	XII	XIII	XIV	XV	8	9	10	11	I	II	15	16	17	18	19	20	21	22	
<i>Helcogramma fuscopinna</i>	75					4	68	3			14	61	74										
<i>Enneapterygius clarkae</i>	22	11	11						3	18	1	22			19	3							
<i>E. venternaculus</i>	60	4	48	8					1	13	44	2	60				1	15	42	2	21	4	
<i>Cremnochorites capense</i>		26					23	3			2	24		25									

—Posterior Series

Lateral line—Anterior Series

	Lateral line—Anterior Series											—Posterior Series														
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
<i>Helcogramma fuscopinna</i>																										
<i>Enneapterygius clarkae</i>	6	12	1								4	7	17	17	7	2	1									
<i>E. venternaculus</i>			3	13	27	8					5	5	9	3							1	5	2	2	2	1
<i>Cremnochorites capense</i>																										

TABLE 3
Summary of Morphometric Data. (Mean values given in parenthesis.)

	<i>Helcogramma fuscopinna</i>	<i>Enneapterygius clarkae</i>	<i>E. venternaculus</i>	<i>Cremnochorites capense</i>
Head in SL	75 specimens 19.6–42.3 mm SL	24 specimens 15.5–25.2 mm SL	56 specimens 17.8–31.8 mm SL	26 specimens 18.5–80.8 mm SL
Eye in Head	3.2–3.7(3.4)	3.3–3.9(3.5)	3.5–4.0(3.7)	3.2–3.7(3.5)
Upper Jaw in Head	2.6–3.1(2.9)	2.8–3.6(3.1)	3.0–3.7(3.3)	3.0–3.6(3.3)
Snout in Head	2.0–2.4(2.1)	2.5–4.0(2.8)	2.8–3.3(3.1)	2.0–2.4(2.3)
Snout Angle	2.9–4.2(3.5)	3.7–4.9(4.2)	3.0–3.4(3.5)	3.6–4.2(4.0)
	68°–73°(70°)	71°–76°(73°)	76°–78°(78°)	71°–75°(74°)

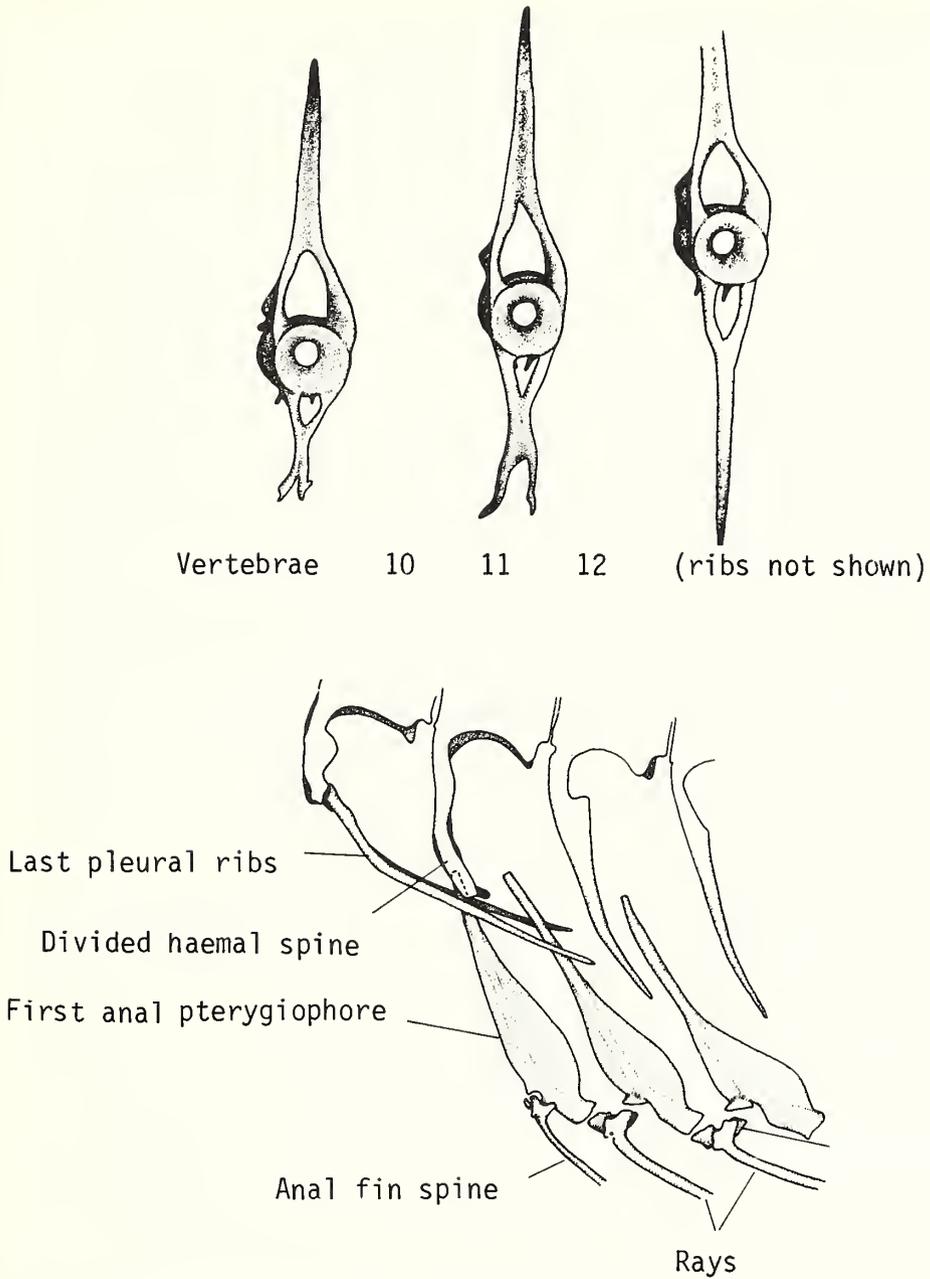


FIG. 2. Last precaudal and first two caudal vertebrae of *Enneapterygius clarkae* with associated anal pterygiophores.

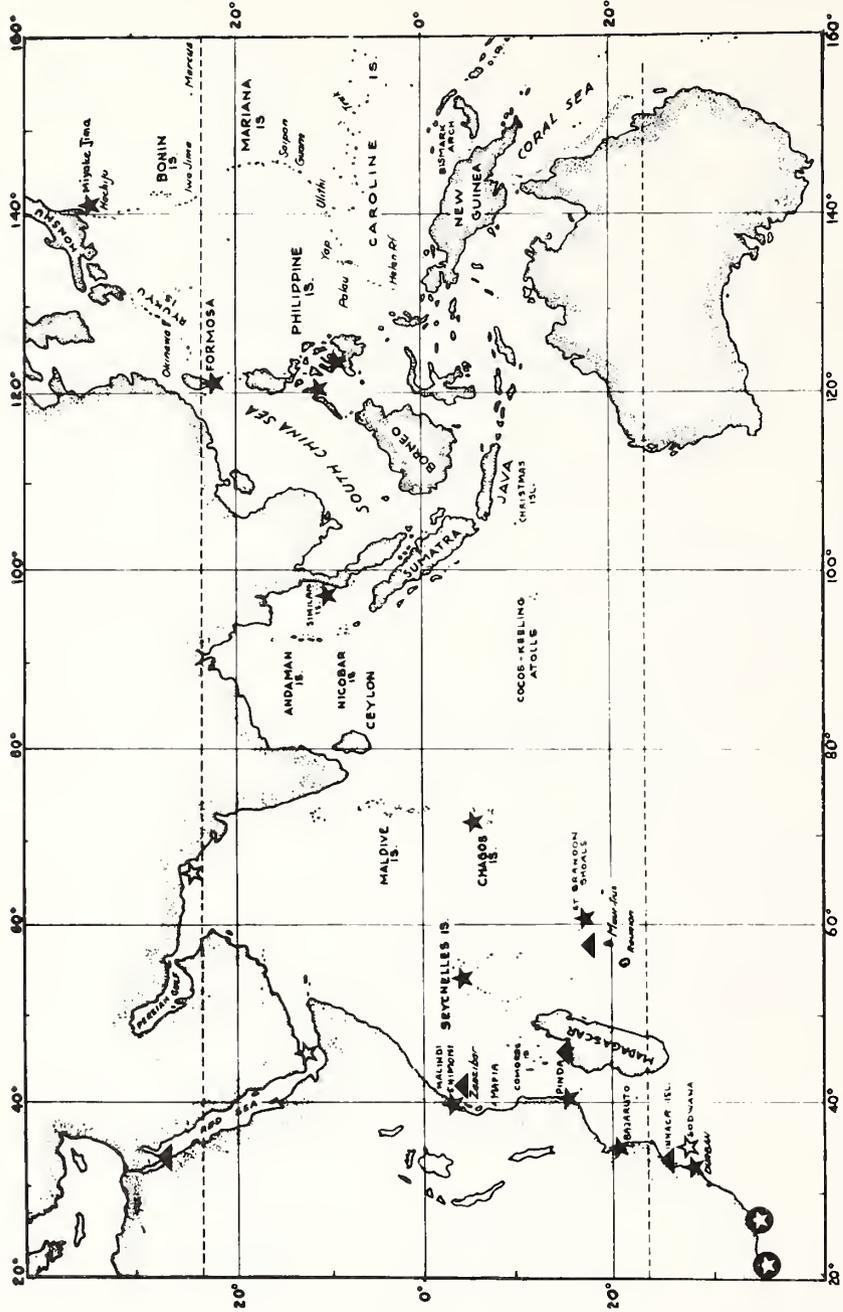


FIG. 3. Distribution of tripterygiid fishes based on examined material. ★ *Helcogramma fuscopinna*; ☆ *Enneapterygius venternacutus*; ▲ *E. clarkae*; ⊙ *Crennochorites capensis*

DESCRIPTION OF SPECIES

Genus *Helcogramma* McCulloch & Waite

Helcogramma McCulloch & Waite 1918: 51 (Type-species, *Helcogramma decurrens* McCulloch & Waite, 1918, by original designation).

Diagnosis

First dorsal fin with three spines; anal fin with one spine. Lateral-line a continuous series of pored scales curving down behind pectoral fin base and continuing midlaterally to below second or third dorsal fin or onto caudal peduncle. Head naked, nape of some species scaled; body, except abdomen and pectoral fin bases, with ctenoid scales. Scalation at base of first and second dorsal fins reduced in some species. Two or three rows of conical teeth on vomer and anterior ends of palatines.

Description (Characters in diagnosis not repeated)

Dorsal fins III+X-XVI+6-12. Anal fin I+14-21. Pectoral fin rays 15-17, lowermost 6-7 simple and thickened, uppermost 1-5 simple, remainder bifurcate. Caudal fin 8-10 dorsal, 7-10 ventral procurrent rays. Small, simple orbital and anterior nasal tentacles usually present. Mandibular sensory canals confluent, opening as single or double pore just posterior to lower jaw symphysis. Lateral-line a continuous series of 17-37 pored scales. Jaws with slightly recurved, fixed teeth in bands in front, decreasing posteriorly to a single row; teeth in outer rows enlarged; 2-3 rows of conical teeth on vomer and anterior ends of palatines. Septal bone (see under General Discussion) present; cephalic lateralis canals not covered by bone; hypural 5 small and unossified, one or two epurals.

Discussion

Helcogramma is confined to the Indo-Pacific Oceans as far east as Hawaii. There appear to be in excess of 17 species which can be ascribed to the genus. Clark (1979) states that about 10 species are known from the Indo-Pacific and Red Sea. Most of Fowler's (1964; 1958) species, which he placed first in *Enneapterygius* and then *Tripterygion*, appear to belong in *Helcogramma*.

Helcogramma fuscopinna. sp. nov. Fig. 4.

Diagnosis

Second dorsal fin usually with 14 rays; anal fin usually with 21 rays. First two dorsal fins and anal fin conspicuously dark to black; a distinct blue-white line finely stippled with melanophores extends from upper lip, below eye, to posterior margin of preopercle.

Description (characters for holotype in parenthesis).

Dorsal fins III+XIII-XV+10-11 (III+XIV+11), usually III+XIV+11. First dorsal fin slightly lower than, or equal to, second dorsal, slightly higher in males than in females; anal fin I+19-21(1+21), usually 21; pectoral fin 16-17 upper 3-4 simple, lowermost 7 simple and thickened, remainder bifurcate; caudal fin 9-10,7+6,9-10; pelvic fin rays united by membrane for half to third of their length. Lateral-line 22-33 (25), usually 24-25, pored scales ending below front of third dorsal fin; transverse scales 6/8; lateral scales 38-41 (40), usually 39. Precaudal vertebrae 10; caudal 26-28, usually 27. Head 3,2-3,7 in SL; eye 2,6-3,4, upper jaw 2,0-2,4, snout 2,9-4,2 in head. Snout angle 68°-73°. Body scales do not extend to bases of first and second dorsal fins.

Colour

Freshly caught adult males with orange-pink body and conspicuously dusky anal and first two dorsal fins. Scales generally with row of small melanophores along posterior margin. Small

dusky rosettes scattered over body, generally more densely below midline. Darkly pigmented specimens have a row of five or six grey-white blotches stippled with small melanophores above and below midline. These may produce faint vertical banding. There may also be two pairs of white blotches on either side of dorsum at posterior ends of second and third dorsal fins. Distinct blue-white line stippled with very fine melanophores extends from upper lip, below eye to posterior edge of preopercle. This line may be continued as two or three spots on opercle and upper pectoral fin base. Head below blue-white line, throat and chest heavily stippled with dusky to black spots and rosettes; head above line pale. Orbital tentacle black; nasal tentacle unpigmented. Nape and interorbital area pinkish. First two dorsal fins heavily stippled; stippling on third dorsal lighter, occurring mainly on the fin margin. Anal fin darkly pigmented; caudal fin slightly darker than third dorsal but not as dark as second. Melanophores decrease in size from fin base to margin and grade from dark brown at base to black at margin. Lower half of pectoral fins darker than upper, with oblique white blotch on middle of base; melanophores on lower part of base tend to form a large dark blotch. Pelvic fins finely stippled, darker basally than distally.

Juveniles and small females are virtually immaculate; larger females have lower half of body lightly dusted with small melanophores, dusky margins to anal and first two dorsal fins and stippling on lower part of pectoral fin base, mid-opercle, cheek, snout and nape. Orbital tentacle dark. Sometimes white blotches at posterior ends of second and third dorsal fins.

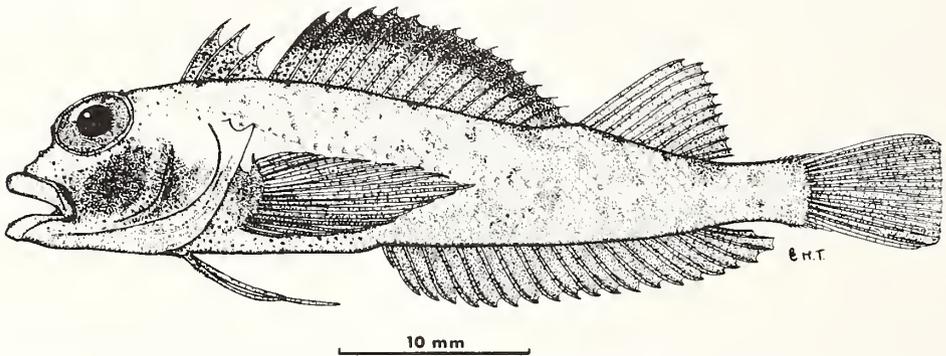


FIG. 4. *Helcogramma fuscopinna* sp.n. RUSI 954. Holotype, male 37,6 mm SL.

Material examined

Holotype—RUSI 954 (out of former RUSI 77–18) male, 37,6 mm SL; reef offshore Sodwana Bay (27° 31'S, 32° 41'E), Zululand, South Africa; depth 10 m; June, 1977; M. S. Christensen, W. Holleman, W. Devos; field number MSC 77–18.

Paratypes—RUSI 955 (2, 36,5 & 40,0 mm SL), taken with holotype. RUSI 956 (6, 32,0–41,7 mm SL), Bazaruto Isl., Mozambique; Sept., 1954; J. L. B. & M. M. Smith.

RUSI 489 (15, 26,0–36,9 mm SL), gully with vertical sides offshore Sodwana Bay; depth 10 m; 28 July, 1976; R. Winterbottom, M. S. Christensen, A. E. Louw (field number RW 76–21).

RUSI 190 (28, 22,0–43,0 mm SL), as preceding—remainder of former RUSI 76–8.

BPBM 21164 (5, 31,5–41,3 mm SL), reef 1 km off north of Sodwana Bay; depth 10–12 m; 21 June, 1977; J. E. Randall, M. S. Christensen.

BMNH 1978.5.30. 1-2 (2, 31,4 & 40,5 mm SL) patch reef, 1 km offshore Sodwana Bay; depth 10 m; July, 1976; R. Winterbottom, M. S. Christensen; A. E. Louw (both out of former RUSI 76-8).

USNM 227738 (4, 28,5-39,9 mm SL); southwest shore just off Ch'uan-fan-shih, Taiwan (21° 55' 48"N, 120° 48' 48"E); depth 8-9 m; 3 May, 1968; V. G. Springer *et al.*; field number VGS 68-14.

USNM 227740 (33, 28,9-39,1 mm SL); rocky reef with some live coral, coarse sand bottom off northern tip of St Brandon's Shoals (16° 25'S, 59° 36'E); depth 6-11 m; 6 April, 1976; V. G. Springer *et al.*; field number VGS 76-10.

USNM 227741 (33, 13,7-36,3 mm SL); dead coral channels, about half mile SW of tip of North Island, St Brandon's Shoals (10° 9'S, 56° 35'E); depth 0-8 m; 17 April, 1976; V. G. Springer *et al.*; field number VGS 76-24.

USNM 227742 (3, 35,0-36,4 mm SL); west side Apo Island about 1/3 km north of South end, Philippine Islands (09° 04' 25"N, 123° 16' 05"E); depth 0-6 m; 6 June, 1978; V. G. Springer *et al.*; field number SP-78-34.

USNM 227743 (3, 33,2-40,3 mm SL); blind surge channel with many small caves, 100 yards off west side of Raphael, St Brandon's Shoals (16° 26'S, 59° 36'E); depth 0-8 m, 2 April, 1976; V. G. Springer *et al.*; field number VGS 76-6.

USNM 227744 (2, 31,7 & 39,3 mm SL); northwest side (Cuyo Island) Putic Island, Palawan, Philippine Islands (10° 55' 05"N, 121° 02' 03"E); depth 0-4,6 m; 22 May, 1978; V. G. Springer *et al.*; field number SP-78-18.

USNM 227746 (19, 14,4-30,7 mm SL); about 1 km south of west of north end of North Island, Agalega Island, St Brandon's Shoals; depth 6-8 m; 19 April, 1976; V. G. Springer *et al.*; field number VGS 76-29.

ROM 38782 (4, 27,3-32,8 mm SL), patch reef, inshore off Isle Fouguet, Peros Banhos, Chagos Archipelago (05° 26' 40"S, 71° 41' 02"E); depth 0,5-4 m; 21 February, 1979; R. Winterbottom *et al.*; field number WE 79-33.

ROM 38783 (1, 21,2 mm SL), steep drop off with mixed coral and sand, on lagoon side of Isle Mapua, Peros Banhos, Chagos Archipelago (05° 26' 44"S, 71° 47' 42"E); depth 3-7 m; 6 March, 1979; R. Winterbottom *et al.*; field number WE 79-55.

ROM 38784 (2, 30,9 & 23,6 mm SL), reef off Isle Anglaise, Peros Banhos, Chagos Archipelago (05° 24' 40"S, 71° 46' 12"E); depth 5-7 m; 8 February, 1979; R. Winterbottom & A. Emery; field number WE 79-10.

ROM 38785 (1, 26,8 mm SL), spur and groove formation, reef top on ocean side of SW tip of Isle Boddam, Salomons, Chagos Archipelago (05° 21' 05"S, 72° 12' 12"E); depth 0-3 m; 18 March, 1979; A. Emery *et al.*; field number WE 79-78.

WAM P26507-016 (2, 32 & 35 mm SL), Ko Similan, Similan Islands (8° 40'N, 97° 38'E); depth 3 m; 13 February, 1979; G. Allen and R. C. Steene.

USNM 227747 (91, 24, 4-38, 4 mm SL), face of channels of reef along SE side of Grande Passe, St Brandon's Shoals (16° 28' S, 59° 40'E); depth 0-3 m; 5 April, 1976; V. G. Springer *et al.*; field number VGS 76-9.

USNM 227739 (1, 43,0 mm SL), bay with rock and coral, SE of K'enting, SE Taiwan; depth 0-3 m; 22 April, 1968; V. G. Springer *et al.*; field number VGS 68-1.

USNM 227745 (9, 29,8-40,8 mm SL), SW shore just off Ch'uan-fan-shih, Taiwan; depth 5-7 m; 28 April, 1968; V. G. Springer *et al.*; field number VGS 68-9.

Comparisons

There are six other species of *Helcogramma* described from the Red Sea, Indonesia and the Indian Ocean: *H. ellioti* (Herre, 1944), *H. indicus* Talwar & Sen (1971), *H. obtusirostre* (Klunzinger, 1871), *H. shinglensis* Lal Mohan (1971), *H. steinitzi* Clark (1979), *H. trigloides*

(Bleeker, 1858). Salient comparative features of these six species and *H. fuscopinna* are given in Table 4.

Herre (1944) provided a detailed description of the colour of *H. ellioti*. In males the head and trunk are brilliant blue ventrally (other species except *H. trigloides*, are dark brown to black); anal fin brilliant blue, caudal and dorsal fins lighter blue, and pectoral fin base with a bright blue ocellus outlined in golden red. This essentially agrees with the colour pattern of *H. trigloides* as described by Day (1876) from illustrations by Elliot. Bleeker (1858) gives an anal fin count of 10 (rays?) for *trigloides* whereas Day recorded 18–20 and de Beaufort & Chapman (1951) 19 rays. Talwar & Sen (1971) intimate that the species described by Day as *trigloides* was *indicus*. These authors do not give a source for their data for *trigloides*. The distinctive colour pattern of *trigloides* and *elliotti* does, however, distinguish them from other species.

H. fuscopinna is the only species with a norm of 14 spines in the second dorsal fin. It appears to be similar in colour pattern to *H. steinitzi* but lacks the scaled nape. It can also be clearly distinguished from *H. obtusirostre* by colouration (particularly the distinctive stipple line below the eye), relative eye size (the eye of *H. fuscopinna* is relatively larger than that of *H. obtusirostre*—Fig. 5) and snout angle (Table 1). There appears to be little to distinguish *H. shinglensis* from *H. obtusirostre*. Lal Mohan's (1971) description of *H. shinglensis* is based on only three specimens. This species is very similar in meristic data and colour pattern to South African *H. obtusirostre* and it is possible that *H. shinglensis* is referable to *H. obtusirostre*. Pending revision of the genus no further comments can be made on the status of the other species.

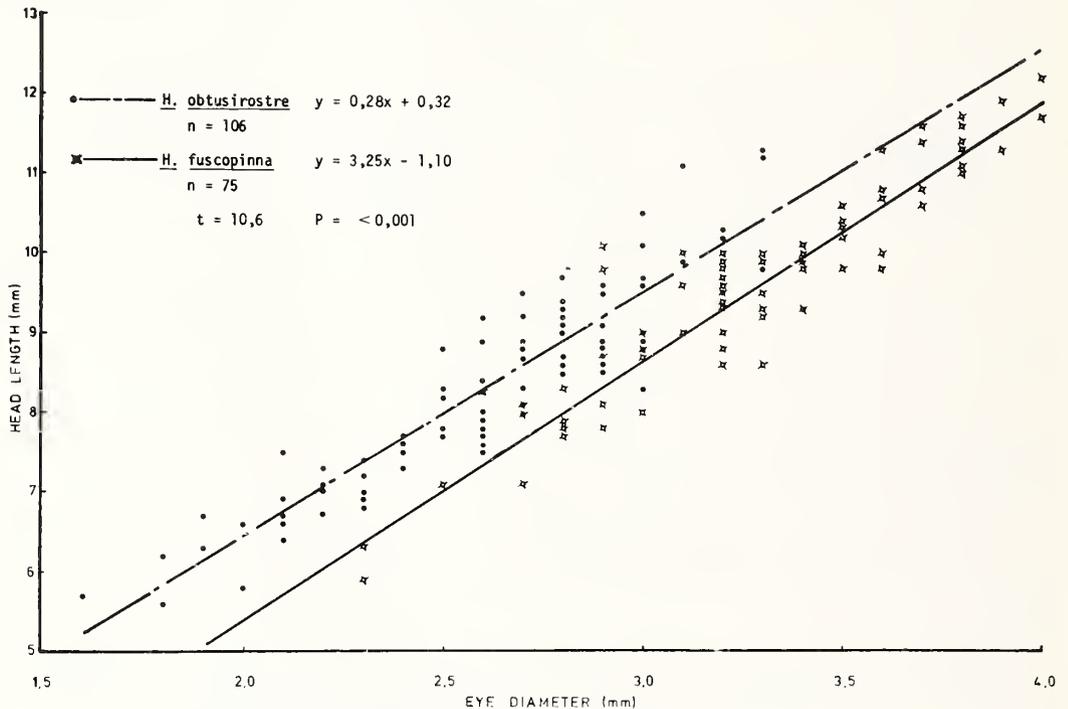


FIG. 5. Comparison of relative eye diameter of *H. obtusirostre* and *H. fuscopinna*.

TABLE 4.
Comparative features of seven species of *Helcogramma* from the western and central Indian Ocean.

	<i>H. ellioti</i>	<i>H. fuscipinna</i> 73 specimens	<i>H. indicus</i> 4 specimens	<i>H. obtusirostre</i> 106 specimens	<i>H. steinitzi</i> 88 specimens	<i>H. shinglensis</i> 4 specimens	<i>H. trigloides</i> (from de Beaufort & Chapman)
Second dorsal fin spines (usual number)	13	13-15 (14)	13	12-14 (13)	12-14 (13)	12,13	13
Third dorsal fin rays (usual number)	8-10*	10-11 (11)	9-10	9-11 (10)	10-12 (11)	9	10
Anal fin rays (usual number)	16-19* (18)	19-21 (20-21)	17	17-20 (18-19)	29-21 (20)	20	10
Lateral line scales (usual number)	34-35	22-23 (23)	33-34 (34)	19-29 (22-24)	21-27 (25)	20-22	50?
Head in SL (mean)	2,9-3,2	3,2-3,7 (3,4)	3,0-3,3 (3,3)	3,2-4,1 (3,6)	3,1-3,5	3,0-3,8	4
Eye in head (mean)	3,3-3,4	2,6-3,1 (2,9)	3,2-3,4 (3,3)	2,8-3,6 (3,2)		2,7-3,0	2,5
Snout angle (mean)	"nearly* vertical"	68-73° (70°)	naked	70-80° (77°)	naked	naked	naked
Scalation: (a) nape (b) base of D ₁ & D ₂	naked	naked	naked	naked	scaled	naked naked?	naked

Data for *H. ellioti* from Herre (1944) and Lal Mohan (1971). (The figures with an asterisk taken from Herre, remainder from Lal Mohan. Lal Mohan gives dorsal fins III+XIII+II, anal fin I,20 in his key which disagrees with the original description).
Data for *H. steinitzi* from Clark (1979), for *H. indicus* from Talwar & Sen (1971), and for *H. trigloides* from Bleeker (1858) and de Beaufort & Chapman (1951).

Etymology

The name is derived from the combination of the Latin *fuscus*, dark coloured, and *pinna*, fin, referring to the dark dorsal and anal fins. It is to be treated as a noun in apposition.

Distribution and variation

Helcogramma fuscopinna appears to be a remarkably widely distributed species (Fig. 3). The only other tripterygiid which is apparently as nearly widely distributed is *H. obtusirostre* which has been recorded along the east coast of Africa from the Red Sea to the Transkei (Klunzinger, 1871; Clark *et al.*, 1968; collected by J. L. B. & M. M. Smith in East Africa during the 1950's; collected by the author in Zululand and on Natal Coast in 1976, 1977; collected by R. Winterbottom in Transkei in 1975). *H. fuscopinna* is not represented in recent collections from Christmas Island (collection of G. R. Allen and R. G. Steene, 1978) and the Cocos-Keeling Islands (collection of W. Smith-Vaniz *et al.*, 1974). It is also not one of the many tripterygiids described by Fowler (1946) from the Ryu Kyu Islands. A few large specimens were, however, collected by Hanson in southern Japan in 1978.

The specimens from Taiwan and Japan are considerably more heavily pigmented than those from the Indian Ocean. Five male specimens collected by Springer in the Philippine Islands also differ from the Indian Ocean specimens. Three of these (from Apo Islands) are very darkly pigmented, like those from Taiwan and Japan, and two (from Putic Island, Palawan Province) are considerably lighter. The three from Apo Island also have an unusually long first dorsal fin spine—in two specimens it is twice the length of the first spine of the second dorsal fin. Usually the difference in length is only about one third. The same three specimens also have a sharper snout (58°–64° versus 68°–73°). All five specimens have lower lateral-line counts, namely 20–23 (usually 24–25 in *H. fuscopinna*). In contrast the specimens from Taiwan have higher lateral-line counts, namely 26–33, except one with a count of 23. Comparable data are not available for the specimens from Japan. In all other respects the specimens from the Philippines conform to the description of the species and, until further material is available, are referred to *H. fuscopinna*.

Genus *Enneapterygius* Rüppell

Enneapterygius Rüppell 1835: 2 (Type species *Enneapterygius pusillus* Rüppell, 1835, by original designation).

Diagnosis

First dorsal fin with three spines; anal fin with one spine. Lateral-line divided into an anterior series of pored scales which ends below the second dorsal fin and a posterior series of notched scales from $\frac{1}{2}$ to 2 scales below end of anterior series to base of caudal fin. Small, simple orbital and anterior nasal tentacles present. Head and nape naked; body with ctenoid scales, except abdomen and pectoral fin bases which are usually naked but with cycloid scales in some species. Vomer with 1–3 rows of conical teeth, palatines edentate.

Description (Characters in diagnosis not repeated).

Dorsal fins III+XI–XIV+8–11. Anal fin I+17–22. Pectoral fin 13–16, lowermost 6–7 simple and thickened, uppermost 1–4 undivided, remainder bifurcate. Caudal fin with 7–8 dorsal, 6–7 ventral procurent rays. Lateral-line anterior series of 9–15 pored scales ending below second dorsal fin, posterior series of 21–28 notched scales from $\frac{1}{2}$ to 2 scale rows below end of anterior series to base of caudal fin. Mandibular sensory canals confluent, opening as single pore just posterior to lower jaw symphysis. Supratemporal sensory canal "U"-shaped, curving around base of dorsal fin, or crescentic (Fig. 13). Jaws with slightly recurved conical teeth in

bands in front, decreasing to single rows at sides of jaws; teeth in outer rows enlarged; septal bone present; cephalic lateralis canals not covered by bone; ascending and articular processes of premaxilla partly or completely fused; hypural 5 present or absent; single epural; free pterygiophore between second and third dorsal fins ossified or unossified (see General Discussion).

Remarks

The monophyly of the genus as described above is in doubt. The disparity in the form of the supratemporal sensory canal and associated structures, the ossification or non-ossification of a free pterygiophore between the second and third dorsal fins, the degree of fusion between the articular and ascending processes of the premaxilla and the presence or absence of hypural 5 suggests that the genus might potentially be divided into two. Pending a revision of the genus currently in progress, all the species below are referred to *Enneapterygius*.

Enneapterygius clarkae sp. nov. Fig. 6

Enneapterygius n. sp. 2 Clark, 1979: 104.

Diagnosis

Abdomen scaled; single row of thin cycloid scales on pectoral fin base parallel to margin of branchiostegal membrane. Body with four conspicuous vertical dark bars which divide ventrally and continue onto anal fin. Two less conspicuous bars under pectoral fin.

Description

(Except for colour pattern, characters in diagnosis not repeated).

Dorsal fins III+XI–XII+8–10, usually III+XII+9; anal fin I+16–17, usually 16; pectoral fin 14–15, usually 15, with uppermost 1–3 undivided, lowermost 7 undivided and thickened, remainder bifurcate; caudal fin 6–8, 7+6, 5–6. Pelvic fin rays united by membrane for less than quarter of their length. Lateral-line anterior series 11–12, usually 12, pored scales, posterior series 20–22, usually 22, notched scales from one scale below end of anterior series, overlapping by 2–3 scales, to base of caudal fin; transverse scales 3/6; longitudinal scales 29–30. Vertebrae, 10 precaudal and 22–23 caudal. Head 3,3–3,6 in SL; eye 3,0–3,3, upper jaw 2,5–4,0, snout 3,8–4,8 in head; snout angle 71°–73°. Supratemporal canal crescent shaped, free pterygiophore between second and third dorsal fins present. Orbital tentacle of same length as nasal tentacle, about three times as wide, with serrated margin. Longest pectoral fin ray reaches first ray of third dorsal fin.

Colour

No live or freshly dead specimens have been seen. Side of body marked with four conspicuous vertical dark bands, usually divided ventrally and continuing on to anal fin as 5–7 oblique bars. First band on body from middle of second dorsal fin, second from junction of second and third dorsal fins, third from posterior half of third dorsal fin and fourth on caudal peduncle. Last bar may be considerably darker than the others, particularly ventrally. Also one or two less distinct dusky vertical bands on body under pectoral fin. Black pre-anal mark present. Anterior half to two thirds of body and head dusted with melanophores. Abdomen unpigmented in females. Lower portion of the head and base of the pectoral fin with irregular bars. Pelvic fins unpigmented. First dorsal fin dusky, darker in males than females, with partial black margin in males. Faint, irregular dusky bars on third dorsal fin, lower half of pectoral fins and base of caudal fin.

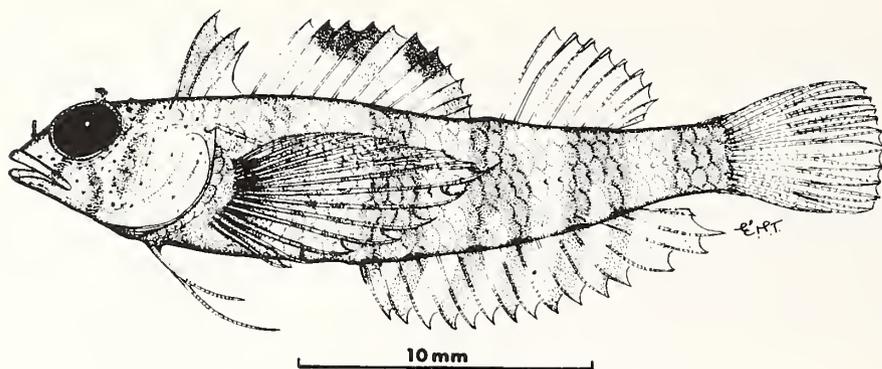


FIG. 6. *Enneapterygius clarkae* sp.n. RUSI 14175. Holotype, male, 23,5 mm SL.

Material examined

Holotype—RUSI 14175, male, 23,6 mm SL; coral reef off Barreira Vermelha, Inhaca Island, Mozambique; 5 December, 1970; T. H. Fraser; field number THF-SA-14.

Paratypes—RUSI 14174 (4, 18,9–24,0 mm SL); taken with holotype.

RUSI 14176 (1, 21,9 mm SL); reef with coral, Sodwana Bay, Zululand, South Africa; depth 15 m; 25 July, 1976; R. Winterbottom *et al.*; field number RW 76-15.

RUSI 7939 (2, 18,5 & 21,6 mm SL); Shimoni, Kenya; November, 1952; J. L. B. & M. M. Smith.

RUSI 14177 (3, 11,3–24,9 mm SL); rock arch with coral and sponges over sand, Sodwana Bay, Zululand, South Africa; depth 13 m; 24 July, 1976; R. Winterbottom *et al.*, field number RW 76-14.

RUSI 7938 (1, 20,5 mm SL); reef with coral, sponges, Sodwana Bay, Zululand; depth 14–17 m; 18 June, 1977; M. S. Christensen *et al.*, field number MSC 77-20.

RUSI 9842 (2, 17,9 & 23,4 mm SL); reef with coral and sponges, Sodwana Bay, Zululand; depth 8–10 m; 19 May, 1979; P. C. Heemstra *et al.*, field number PCH 79-23.

RUSI 14629 (4, 17,4–25,2 mm SL); Malindi Marine Reserve, Malindi, Kenya; April, 1978; P. Wirtz.

LACM 31617-27 (1, 24,5 mm SL); Manda Island, Kenya; 27 November, 1970; P. Saw.

USNM 231380 (1, 20,4 mm SL); reef station, Chesterfield Island (16° 21'S, 43° 59'E); depth 5 m; 16 October, 1964; Anton Bruun Cruise No. 8, Station 408F, International Indian Ocean Expedition; field number LK 64-66.

USNM 231378 (1, 23,1 mm SL); fossil coral rock patch with young corals, blind surge channel about 100 yards off Raphael on West side, St Brandon's Shoals (16° 26'S, 59° 36'E); depth 0–8 m; 2 April, 1976; V. G. Springer *et al.*; field number VGS 76-6.

USNM 231381 (1, 17,0 mm SL); coral reef off northwest shore, Albatross Island, St Brandon's Shoals (ca 16° 15'S, 59° 35'E); depth 0–18 m; 14 April 1976; V. G. Springer *et al.*; field number VGS 76-22.

USNM 231379 (1, 23,4 mm SL); Red Sea (27° 16' 46"N, 33° 46' 25"E); depth 0–3 m; International Indian Ocean Expedition; 1 January 1965; L. Kornicker & H. A. Feldmann; field number HA 29.

USNM 231382 (3, 13,5–21,7 mm SL); rock reef with live coral, channels, coarse sand bot-

tom, off northern tip of St Brandon's Shoals (16° 25'S, 59° 36'E); depth 6–10 m; 6 April 1976; V. G. Springer *et al.*; field number VGS 76–10.

The larger two specimens of RUSI 14177 were cleared and stained.

Discussion and comparisons

Clark (1979) described five specimens of a species from the Red Sea which most probably is *E. clarkae*. The specimens were lost prior to the publication of the description and the species was consequently not named.

Clark was unsure whether these five specimens, described by her as *Enneapterygius* n.sp.2, represented a new species or were merely large adults of *E. destai* Clark, 1979. The South African specimens essentially agree with the description of Clark's n.sp.2 and not with that of *destai*. The only meristic difference between the two species is the number of pored scales in the anterior lateral-line series (Table 5). However, Clark does not describe the scalation of either her n.sp.2 or *destai*. The abdomen of *clarkae* is entirely covered with ctenoid scales and there is a single row of cycloid scales on the pectoral fin base. Both these features are absent in *destai* (Springer, pers. comm.). The two species also differ in colour pattern. The body bars of *clarkae* and Clark's n.sp.2 are vertical and very distinct, whereas those of *destai*, except the bar on the caudal peduncle, are faint and oblique. The peduncular bar of *destai* is dark and constricted in the centre giving the impression of an hour-glass. Another species with a very distinctive hour-glass-like peduncular is *E. elegans* (Peters, 1876). However, *elegans* has a scaled abdomen, 17 anal fin rays and 17+17 lateral line scales. Finally, this series of *clarkae* includes specimens smaller than the largest specimens of *destai*. The two species are thus clearly distinct.

Etymology

Eugenie Clark was aware of the South African specimens of her *Enneapterygius* n.sp.2 prior to publication of the Red Sea revision. She, however, very kindly consented that I name and describe the species. Eugenie Clark also provided me with a draft manuscript of her Red Sea revision in 1976. This was of invaluable assistance in a revision of the South African tripterygiids which formed the basis of my Masters dissertation. It is thus fitting—and it gives me great pleasure—to name the species for her.

Distribution

The distribution of *E. clarkae* is shown in Fig. 3.

Enneapterygius ventermaculus sp.nov. Fig. 7

Diagnosis

Third dorsal fin usually with 10 rays; anal fin usually with 19 rays. Supratemporal sensory canal "U"-shaped. Row of 5–6 conspicuous black spots at base of anal fin and one anterior to vent.

Description

(Characters in diagnosis not repeated; characters for holotype in parenthesis).

Dorsal fins III+XI–XIII+9 – 10 (III+XII+9), usually III+XII+10; first dorsal fin height equal to second dorsal fin in females, slightly higher than second in males; anal fin I+17–20 (I+18), usually 19 rays; pectoral fin rays 14, upper 1–3 undivided, lower 7 thickened and undivided, remainder bifurcate; caudal fin 7–8 7+6, 6–7 pelvic fin rays united by membrane for about half their length. Lateral-line anterior series 13–16 (13), usually 15 pored scales ending under last third of second dorsal fin; posterior series 21–25 (22), usually 23 notched scales from

two scale rows below end of anterior series, overlapping by 1–3 scales and continuing to base of caudal fin; transverse scales 2/6; lateral scales 32–34, usually 33. Precaudal vertebrae 10, caudal 24–26. Head 3.4–4.0 in SL; eye 3.0–3.7, upper jaw 2.8–3.3, snout 3.0–3.4 in head; snout angle 76° – 78° . Head and pectoral fin bases naked; body except abdomen from line between upper angle of pectoral fin base to origin of anal fin with ctenoid scales. Free pterygiophore between second and third dorsal fin cartilaginous; hypural 5 absent.

Colour (in preservative)

No live or freshly dead specimens have been seen. The body is irregularly pigmented with dark brown to black melanophores, the pigment normally occurring on the posterior margins of the scales. There is a row of irregular blotches along the lateral midline, the darkest forming a bar at the base of the caudal fin. This bar may be divided ventrally to form an inverted "Y". The head is lightly spotted with small clusters of melanophores on the cheeks. The lower half of the pectoral fin bases have clusters of melanophores forming narrow bars. There is a dark blotch on either side of the midline on the throat and near the base of the brachioistegals. The abdomen is unpigmented except for a conspicuous black mark, frequently triangular in shape with apex anterior, which lies just anterior to the anus (Fig. 7b). This mark may also be roundish or crescentic. The caudal and pectoral fins each have 4–5 irregular, faint dusky bars, with the pigmentation on the rays only, giving the fins a spotted appearance. There are 5–6 irregularly spaced dark spots at the anal fin base. These are continued as "bars" across the fin. Pigmentation occurs only on the rays so that when the fin is extended these spots form a dotted line running obliquely forward from the basal spot. The first dorsal fin is irregularly dusky whereas the second may have four broad, irregular bars, and the third three broad irregular bars. There is considerable variation in the intensity of pigmentation in different individuals. However, all specimens have a spotted appearance with the distinct preanal mark. No sexual dichromatism is evident.

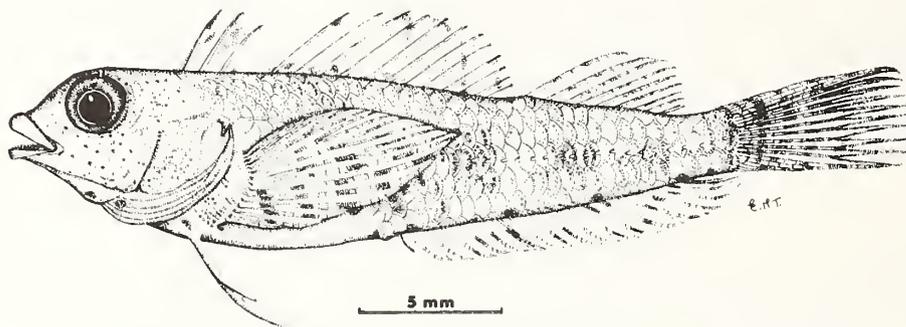


FIG. 7. *Enneapterygius ventermaculus* sp.n., RUSI 7943, Holotype, female, 24.8 mm SL.

Material examined

Holotype—RUSI 7943, female (24.8 mm SL); rock pool about 10 km south of Sodwana Bay ($27^{\circ} 37' 30''$, $33^{\circ} 40' 50''$ E), Zululand, South Africa; depth 0–3 m; July, 1976; R. Winterbottom *et al.*; field number RW-76-8.

Paratypes—RUSI 7947 (1, 24.7 mm SL); from same collection as holotype.

RUSI 7944 (4, 17.8 & 25.7 mm SL); rock pool at six mile reef, Zululand; depth 0–2 m; July 1976; R. Winterbottom *et al.*; field number RW-76-9.

RUSI 7945 (1, 23,5 mm SL); reef with corals about $\frac{1}{2}$ km offshore Sodwana Bay, Zululand; depth 8 m; June, 1877; M. S. Christensen *et al.*; field number MSC-77-18.

RUSI 7946 (1, 27,1 mm SL); reef with corals and sponges about $\frac{3}{4}$ km offshore Sodwana Bay, Zululand; depth 11-13 m; June, 1977; M. S. Christensen *et al.*; field number MSC-77-17.

LACM 38309-5 (6, 25,6-27,7 mm SL); tide pool with rock and algae, Beluji Point, Sind, Pakistan; depth 20-60 cm; 27 January, 1979; C. C. Swift *et al.*; field number CCS 79-20.

LACM 38310-10 (43, 20,2-31,8 mm SL); tide pool with sand, rocky rubble and algae. Beluji Point, Sind, Pakistan; depth 20-60 cm; 27 January, 1979; C. C. Swift *et al.*; field number CCS 79-21.

LACM 38320-9 (2, 27,2 & 31,8 mm SL); small cove with boulders and algae, 4,8 km west of nuclear power plant, Karachi, Pakistan; depth 0-5 m; 13 February, 1979; C. C. Swift *et al.*; field number CCS 79-34.

BMNH 1954.4.26.209-214 (6, 19,5-21,9 mm SL); rock pools, Aden; 1954; A. Fraser-Brunner.

BMNH 1954.4.26.191-196 (6, 17,2-23,6 mm SL); rock pools, Mukalla, Aden; 1954; A. Fraser-Brunner.

BMNH 1954.4.26.197-208 (12, 17,0-24,0 mm SL); tide pools, Alayu, Aden; 1954; A. Fraser-Brunner.

Etymology

The name is a combination of the Latin *venter*, meaning "belly" and *maculus*, a spot or a mark, and is given for the distinct black preanal mark. It is to be treated as a noun in apposition.

Distribution

On the east coast of Africa this species has only been taken in Zululand but may also occur further north. The species appears to be fairly common in Pakistan and there are a few specimens known from Aden.

Comparisons

The only species which approaches *E. ventermaculus* in overall appearance is *E. clarkae*. In the latter species the bars on the body are much more distinct; it has fewer scales in the anterior lateral line series (11-12 vs. 13-16), fewer anal fin rays (16-17 vs. 18-19), a crescent-shaped supraoccipital sensory canal, and a scaled abdomen and pectoral fin base. The salient features of six Indian Ocean species of *Enneapterygius* are compared in Table 5.

Genus Cremnochorites gen. nov.

Type-species *Tripterygium capense* Gilchrist & Thompson, 1908

Diagnosis

First dorsal fin with four spines; anal fin with two spines. Lateral line divided. Body heavily scaled with ctenoid scales; head with denticle like scales; row of "ctenii" around perimeter of eye. Orbital tentacle large and multifid, nasal tentacle similar but smaller. Single row of conical teeth on vomer and palatines.

Description

Dorsal fins IV+XIV-XV+10-11; some rays may be bifurcate and the last is usually divided to its base; first dorsal fin lower than second. Anal fin II+21-22, the last ray usually divided to its base. Pectoral fins with 16 rays, upper 8 bifurcate, lower 8 simple and thickened.

TABLE 5
Comparison of selected characters of five species of *Enneapterygius*

	<i>E. venter-maculatus</i> (58 specimens)	<i>E. destai</i> (Red Sea- 87 specimens)	<i>E. n. sp. 1</i> (Red Sea- 5 specimens)	<i>E. clarkae</i> (11 specimens)	<i>E. elegans</i> (30 specimens)
Second dorsal fin spines (Usual number)	11-13 (12)	11-13 (12)	12-14 (12)	11-12 (12)	11-13 (12)
Third dorsal fin rays (Usual number)	9-10 (10)	8-9 (9)	8-9 (9)	8-10 (9)	8-10 (9)
Pectoral fin rays (Usual number)	14 (14)	14-15 (15)	14-15 (15)	14-15 (15)	16 (16)
Anal fin rays (Usual number)	18-19 (19)	15-17 (16)	15-17 (16)	16-17 (16)	16-17 (17)
Lateral line:					
Anterior series (Usual number)	13-16 (15)	8-12 (10-11)	12-13	11-12 (12)	16-18 (17)
Posterior series (Usual number)	21-25 (22)	19-23 (21-22)	22	20-22 (22)	16-18 (17)
Vertebrae: precaudal (Usual number)	10 (10)	10-11 (11)		10 (10)	10 (10)
Caudal (Usual number)	25-26 (26)	20-22 (21)		22-23 (23)	23
Scalation: abdomen	naked	naked	?	scaled	scaled
Pectoral fin base	naked	naked	?	single row scales	naked
Supratemporal sensory canal	"U"	crested	crested	crested	crested
Colour in preservative	spotted with distinct preanal mark.	Faint oblique bars, prominent hour-glass-like peduncular mark; preanal mark.	conspicuous vertical bars, distinct preanal mark.	conspicuous vertical bars, distinct preanal mark.	Irregular faint bars; prominent hour-glass-like peduncular mark; no preanal mark.

The data for Red Sea species were taken from Clark (1979). Vertebral counts of Red Sea specimens are not comparable with counts given for South African specimens. (See methods).

Caudal fin 6 dorsal, 5 ventral procurent rays. Lateral-line anterior series of 21–24 pored scales running to below anterior of third dorsal fin; posterior series of 17–20 notched scales extending from below end of anterior series onto caudal peduncle. Body heavily scaled, all scales with relatively large, irregular cteni (Fig. 8 A–D); scales on abdomen with few cteni. A few cycloid scales occur around vent and at base of pelvic fins. Scale rows somewhat irregular. Head and pectoral fin bases covered with ctenoid scales; those on posterior edge of opercle about half size of body scales, decreasing in size anteriorly to small denticle-like scales with few, large cteni below eye and on cheeks (Fig. 9A). Scales on head and particularly on cheeks appear to be situated on small pedestals, creating appearance of shark denticles. Small denticle-like spines on nape and interorbital area, apparently ankylosed to cranial bones. Perimeter of eye with ring of “cteni” (Fig. 9B); similar “cteni” on posterior end of maxilla. Skin of isthmus papillose with single “cteni” or spines embedded in papillae (Fig. 9C).

Posterodorsal margin of post-temporal serrated; interorbital concave, with ridge over each orbit; transverse depression behind orbits. Head broad with rounded profile. Large multifid orbital tentacle present; similar, small tentacles on posterior margin of anterior nostrils. Mandibular sensory canals confluent, opening as single pore posterior to lower jaw symphysis. Both jaws with slightly recurved conical teeth, a patch in front grading to a single row at back of jaw. Teeth unequal in size on lower jaw; upper jaw with outer row of large teeth and inner band of small teeth. Vomer with single row of slightly recurved conical teeth which continues into palatines. Septal bone present; cephalic lateralis canals covered by bone. Caudal skeleton with large hypural 5 and two free epurals.

DISCUSSION

Cremnochorites capense was originally placed in *Tripterygium* (= *Tripterygion*) by Gilchrist & Thompson (1908). It was later transferred to *Gillias* Evermann & Marsh, 1899 by Barnard (1927) and retained there by Smith (1949). Rosenblatt (1960) placed *Gillias* in synonymy with *Enneanectes* Jordan & Evermann, 1895 (a genus restricted to the eastern tropical Pacific and the western tropical Atlantic). Rosenblatt (1960: 3) did not refer Indo-Pacific species in *Gillias* to any other genus but merely stated that “none of the Australian or South African species referred to *Gillias* has anything to do with that genus”. Clark (1979) suggested that *G. capense* be referred to *Norfolkia* Fowler, 1953 for these taxa share four first dorsal fin spines, two anal fin spines and a scaled head. However, *Cremnochorites* differs from *Norfolkia* in a number of characters: palatine teeth are present in *Cremnochorites* and absent in *Norfolkia*; lateral-line counts are reversed, 21–22 pored, 15–16 notched scales for the former compared with 13–17 pored, 21–23 notched scales for *Norfolkia*. The head scales of *Cremnochorites* are quite unlike those of any other tripterygiid examined (see Description).

Body scales of the species in the two genera are also very different. Those of *Cremnochorites* (Fig. 8) are heavily ctenoid and the cteni are generally unequal in size. Pored lateral-line scales frequently have 2–3 rows of cteni in the centre of the row. Scale foci are close to the posterior edge of the scale and the radii are thus comparatively long. (Radii occur only in the anterior field). In *Norfolkia* (Fig. 10) cteni are smaller, more or less equal in size and always in a single row. Scale foci are further away from the posterior margin of the scale and the radii are consequently relatively shorter.

Cremnochorites also possesses a septal bone (*sensu* Springer & Freyhofer, 1976; Fig. 16) which is absent in *Norfolkia*. Furthermore, the sensory canals in the infraorbitals and nasals of *Cremnochorites* are complete, as are those portions of the preopercle, posttemporal and pterotic which carry sensory canals. In *Norfolkia* these canals are open laterally, except the nasals which may be narrowly bridged.

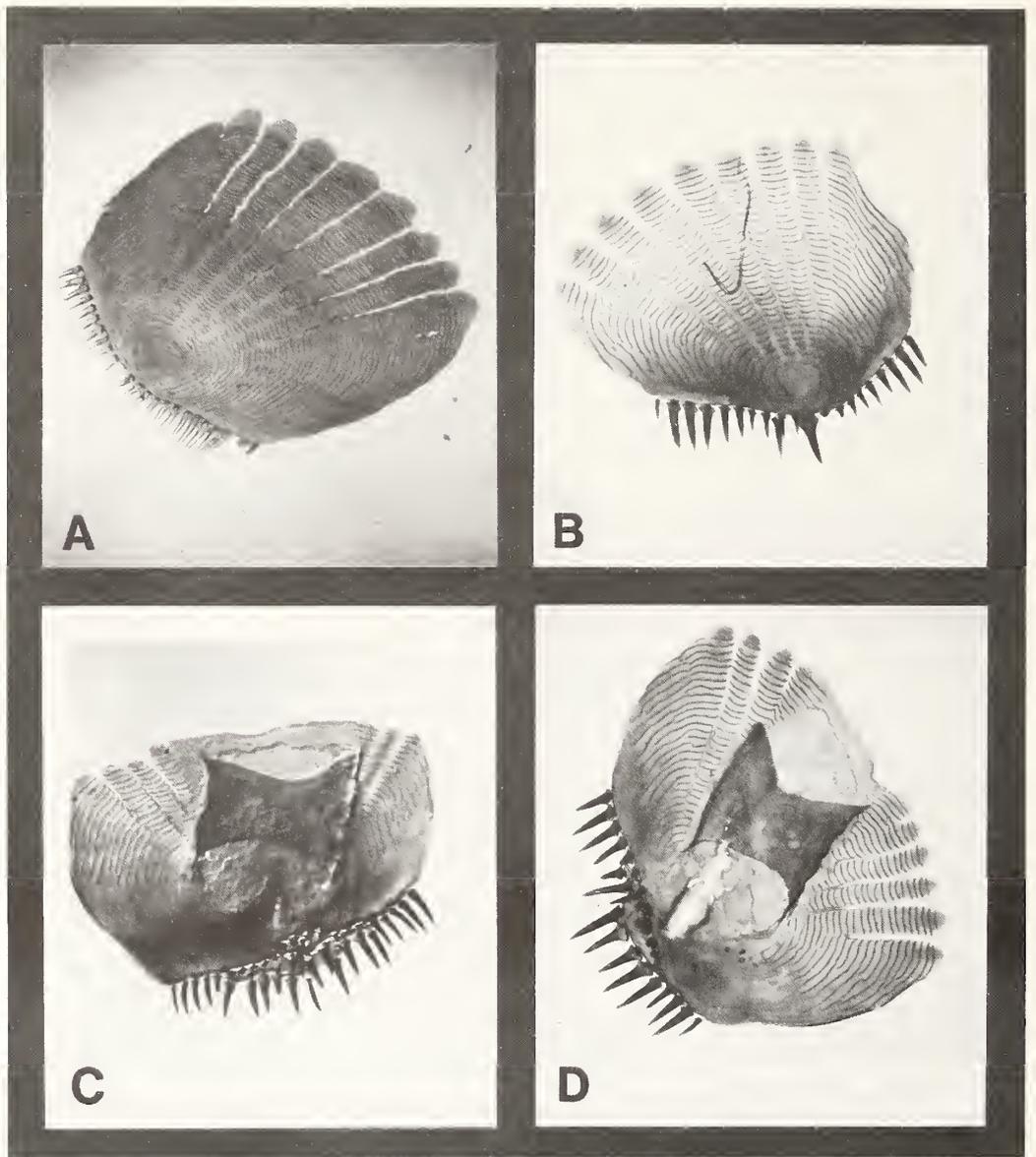


FIG. 8. Examples of body scales (A, B) and pored lateral-line scales (C, D) of *Cremnochorites capensis*.

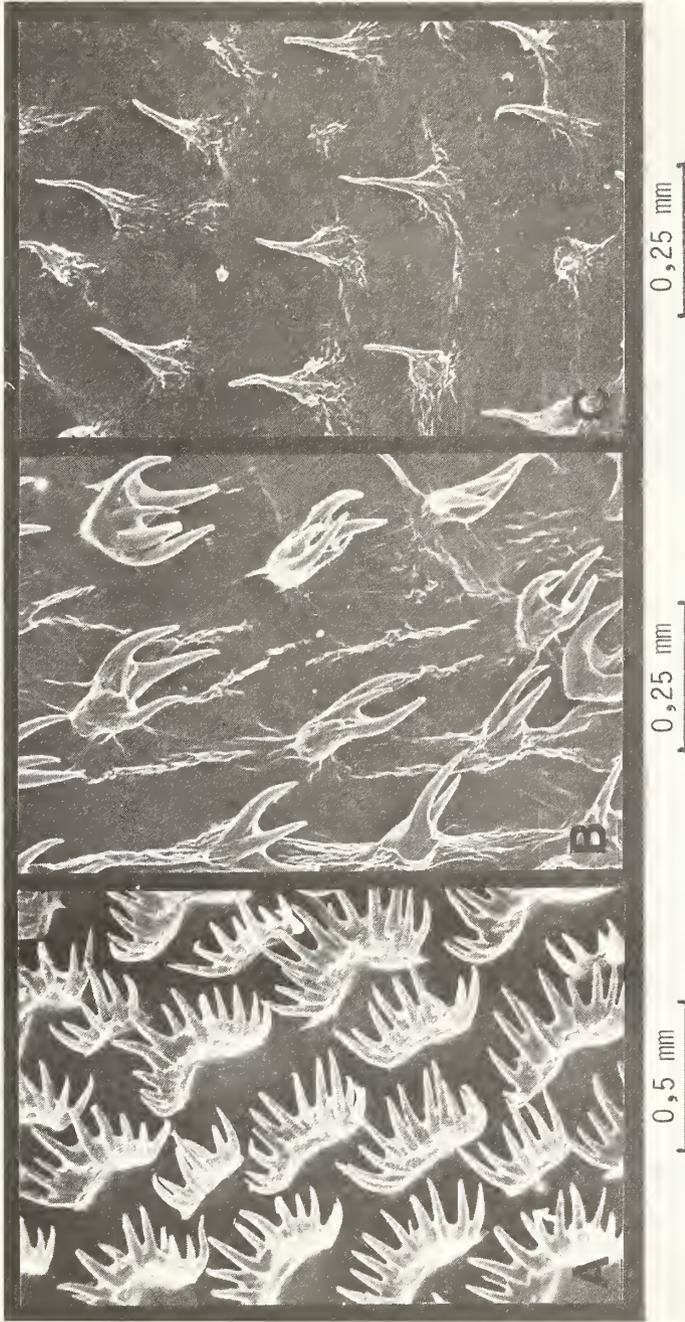


FIG. 9. Stereoscan photographs of the head scales of *Crennochorites capense*. All examples from a 70 mm SL specimen. (A) Cheek scales (40 \times). (B) Portion of skin from perimeter of eye (80 \times). (C) Portion of skin from throat (papillae shrivel with vacuum coating) (80 \times).

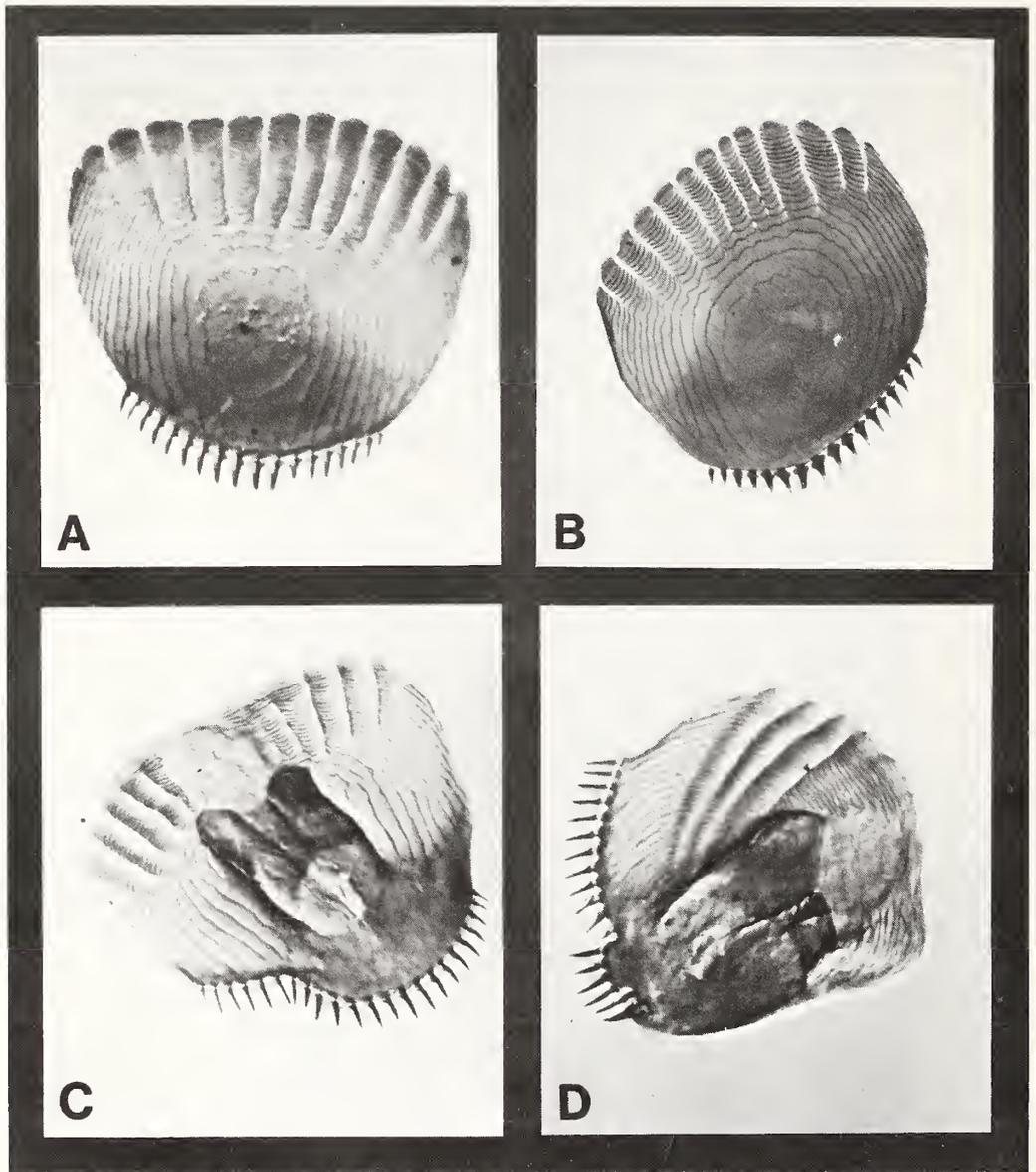


FIG. 10. Examples of body scales (A, B) and pored lateral line scales (C, D) of *Norfolkia springeri*.

Specimens of all nominal species of *Norfolkia* have been seen. The species appear to form a coherent group with little interspecific variation. There are no species which share the curious head scalation with *Cremnochorites* or have palatine teeth. The loss of palatine teeth and the possible secondary loss of the septal bone in *Norfolkia* may represent synapomorphies for the genus. However, pending revision of *Norfolkia* and an assessment of the septal in Tripterygiidae, no further comments can be made about *Norfolkia*.

The species *capensis* can patently not be referred to *Norfolkia*. The septal and highly derived head scalation is considered sufficient to warrant the placing of this species in a new genus.

Cremnochorites capense is the only species thus far examined which can be ascribed to this genus. It has been taken in False Bay, western Cape, at Skoenmakerskop (near Port Elizabeth) and at Port Alfred (gully at 15 m), eastern Cape, South Africa. Specimens have also been taken at the Storms River mouth and in the mouth of the Knysna estuary. The four type specimens were taken in shrimp trawls, two at 5 fms (10 m) and two at 14 fms (28 m). The other specimens were taken at 1–20 m depth. With the exception of the types, for which there are no other collection data, all other specimens were taken from relatively sheltered, vertical, seaweed and *Pyura* covered rock faces.

Etymology

Cremnochorites is derived from the Greek *kremnos*, a cliff, and *chorites*, native or country man. It is thus named because it has only been found associated with vertical rock faces. The gender is masculine.

Cremnochorites capense (Gilchrist & Thompson) **comb. nov.** Fig. 11

Tripterygium capense Gilchrist & Thompson, 1908: 140 (Type locality False Bay, Cape, South Africa); Thompson, 1918: 151; *Gillias capensis* Barnard, 1927: 827; Smith, 1949: 359.

Diagnosis

As for the genus.

Description

Dorsal fins IV+XIV–XV+10–11, usually IV+XIV+11, first dorsal fin lower than second, rays except first branched once; anal fin II+21–22, usually 21 rays; pectoral fin rays 16, lower 8 thickened and undivided, uppermost sometimes undivided, remainder divided once; caudal fin 6,6+7,5. Lateral-line anterior series 21–24 pored scales to end of second or beginning at third dorsal fin, posterior series 17–20, usually 19, notched scales from two scales below anterior series and frequently overlapping by 4 or more scales, to base of caudal fin; transverse scales 5/11; longitudinal scales 36–37. Precaudal vertebrae 10, caudal 27–28. Head, 3,3–3,7 in SL; eye 3,0–3,6, upper jaw 2,0–2,4, snout 3,6–4,4 in head. Snout angle 71°–76°. Balance of description is as given for the genus. The only sexual dimorphism noted consists of a single, conical papilla at the posterior of the vent in males and a “rosette” around the vent of females. This “rosette” may or may not protrude a short distance. Although these features appear to be common to many tripterygiids, they cannot always be distinguished.

Colour

In preservative, these fishes are generally grey with a pale belly. There are six, irregular, vertical dark bars on the body above the lateral midline. These may divide into eight or more bars below the midline. The lower body bars may alternate with the upper bars. In juveniles the bars are continuous across the body and are more distinct. The penultimate bar is across the peduncle and the last bar lies at the base of the caudal fin. A dark bar extends across the

nape and continues on to the opercles. Another bar runs from below the midline of the eye to the corner of the mouth. There is an irregular dark blotch on the lower portion of the opercle. The orbital tentacles are dusky. The anal and caudal fins have irregular small dark blotches. The first dorsal fin is dark whereas the second and third have dusky margins. Neither the pelvic nor pectoral fins are pigmented although there are two short dark bars on each pectoral fin base. Males have dusky brachioistegal membranes and a more darkly pigmented head than females. Freshly caught fishes are rust-coloured and the irregular blotching renders them cryptic in brown and purple algae. One live specimen was seen in the mouth of the Knysna estuary. It may have been a male in breeding dress as it had a bright yellow head and first dorsal fin.

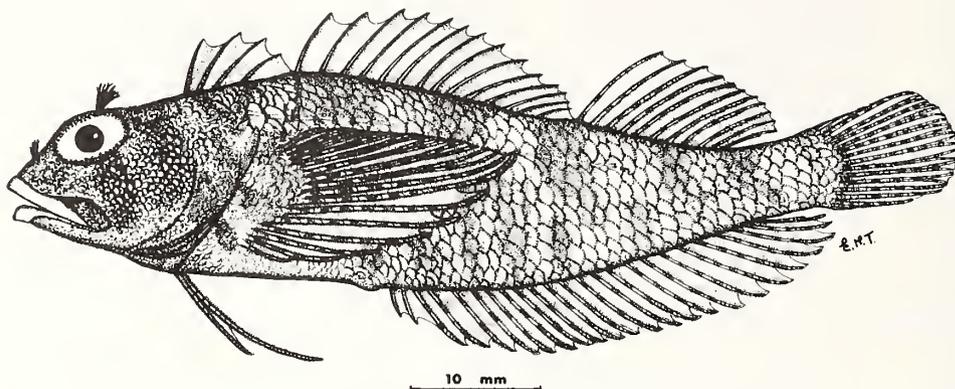


FIG. 11. *Crennochorites capense*. RUSI 75-21. male, 80 mm SL.

material examined

3 *Syntypes*, SAM 9900, females (46-53 mm SL), 10-28 m depth, False Bay, Cape, South Africa, collected in a shrimp trawl; 1 *Syntype*, SAM 9901, male (54,7 mm SL), collected with SAM 9900.

RUSI 7384 (49,3 mm SL), False Bay, Cape, South Africa, no date.

RUSI 75-22 (8, 46,9-61 mm SL), cliff with *Pyura* sp., False Bay, Cape, South Africa; depth 6-8 m; 1 November, 1975; R. Winterbottom *et al.*; field number RW-75-22.

RUSI 75-21 (1, 80 mm SL), sheltered bay with vertical rock walls; Platboom, Cape, South Africa; depth 2-3 m; 1 November, 1975; R. Winterbottom *et al.*; field number RW-75-20.

RUSI 76-7 (12, 26,9-55,6 mm SL) from vertical rock wall with algae; Skoenmakerskop, Eastern Cape, South Africa; depth 4 m; 19 January, 1976; R. Winterbottom *et al.*; field number RW 76-1.

RUSI 77-7 (2, 18,5 & 41,7 mm SL) same site as above; depth 5 m; 1 February, 1977; M. Christensen *et al.*; field number MSC 77-4.

GENERAL DISCUSSION

Only one major revision of the family Tripterygiidae has ever been undertaken; that by Rosenblatt (1959) as a Ph.D. dissertation. To date the major portion of this revision is unpublished.

The concepts of systematics have undergone radical changes in the past 20 years. With the introduction of the Hennigian approach to systematics it has become accepted to consider as valid only those taxa that comprise entities that share one or more derived characters—synapomorphies. Only by identifying synapomorphic characters can taxa be properly defined and the interrelationships of taxa assessed. No such study has been undertaken for the Tripterygiidae and as such the family, as well as the genera within it, remain undefined.

Springer (pers. comm.) informs me that the one osteological character that serves to define the family and delimit it from all other blennioid fishes is the derived loss of at least the posteriormost spine of the second dorsal fin (Fig. 12C). All other blennioids have a spine immediately anterior to the first ray (Fig. 12A) although it may be greatly reduced, as in *Entomacrodus nigricans* Gill (Fig. 12B). In many tripterygiid genera the first ray of the third dorsal fin is also lost, leaving a free pterygiophore which supports nothing in the “gap” between the second and third dorsal fins (Fig. 12D). This pterygiophore frequently becomes considerably reduced (Fig. 12E) and in some specimens of *E. pusillus* and *E. ventermaculus* a spine and two rays have been lost, and the free pterygiophores are unossified (Fig. 12F). It is as yet not known how consistent the degree of loss is within a genus. The minimal loss of the posteriormost spine is found in representatives of 12 genera inspected and is synapomorphic for the family.

The species *E. pusillus* and *E. ventermaculus* which have at least one unossified pterygiophore also have a “U”-shaped supratemporal sensory canal (Fig. 13A) whereas the species of *Enneapterygius* which have an ossified free pterygiophore (*E. abeli*, *E. clarkae*, *E. elegans*) have a crescentic supratemporal sensory canal (Fig. 13B). Furthermore, in those species which possess a “U”-shaped supratemporal sensory canal, it would appear that the extreme curvature of the canal around the first dorsal fin has been brought about by the forward movement of the dorsal fins. This has resulted in a compression of the pterygiophores of the first dorsal fin as they have moved forward over the back of the neurocranium (Fig. 14) and a concomitant depression of the supraoccipital giving rise to a concave supraoccipital bone.

If these two states (the non-ossification of the free pterygiophore plus “U”-shaped supraoccipital sensory canal and associated features as opposed to an ossified free pterygiophore plus crescentic supratemporal sensory canal) are found to be consistent for all species ascribed to *Enneapterygius* there may be sufficient reason to divide the genus into two separate taxa.

Springer & Freihofner (1976) described a *de novo* autogenous ossification in the interorbital septum of *Pholidichthys leucotaenia* and named the bone the septal. Ruck (1977) found the same bone in the tripterygiid *Forsterygion varium*; Springer (pers. comm.) found it present in *Gilloblennius*, another tripterygiid, and Holleman (1978) found a septal in species of a number of other tripterygiid genera viz. *Cremnochorites*, *Enneapterygius*, (Fig. 15) *Helcogramma*, *Notoclinops*, *Tripterygion* and *Vauchusella*. It is absent in *Brachynectes*, *Lepidoblennius*, *Norfolkia* and *Notoclinus*. Whether the septal was originally developed in those last four genera and secondarily lost, or not developed at all has still to be determined.

The presence of a septal in certain tripterygiid genera suggests some relationship between the Tripterygiidae and Pholidichthyidae. Freihofner (pers. comm.) informs me that there are considerable similarities between the trunk lateral line nerve patterns of *Pholidichthys* and *Forsterygion* which is again suggestive of relationship between the two families. Springer & Freihofner (1976) only considered *Pholidichthys* to show possible relationship with the tropical blennioid fishes (superfamily Blennioidea) considered by George & Springer (1980) to include the Clinidae, Blenniidae, Dactyloscopidae, Tripterygiidae, Labrisomidae and Chaenopsidae.

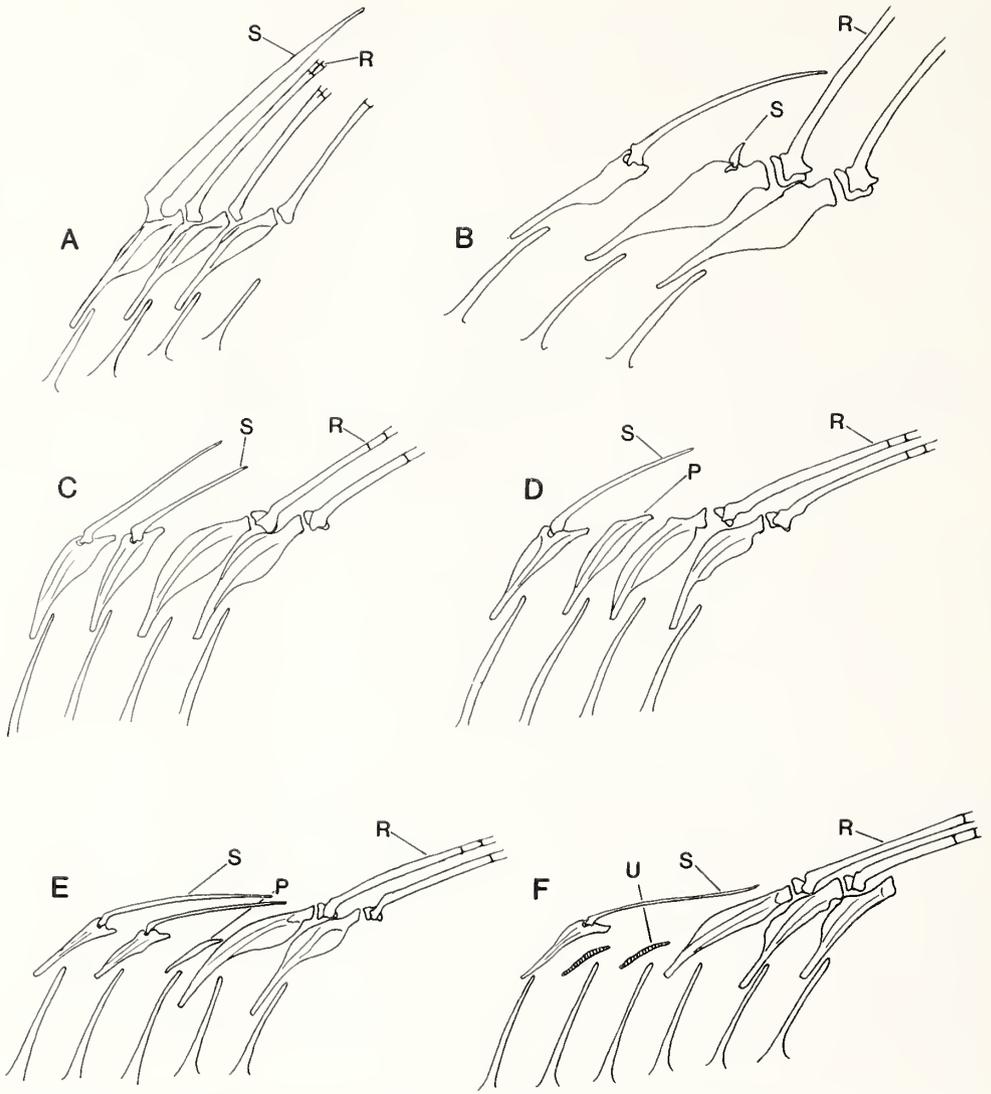


FIG. 12. Junction of spinous and rayed dorsal fins of: A—*Pavoclinus laurentii* (Clinidae); B—*Entomacrodus nigricans* (Blenniidae); C—*Norfolkia squamiceps* (Tripterygiidae), D—*Cremnochorites capensis* (Tripterygiidae); E—*Enneapterygius elegans* (Tripterygiidae), and F—*Enneapterygius pusillus*. S—last spine, R—first ray, P—free pterygiophore, U—unossified free pterygiophore. (B—portion of Figure 10, Springer 1968).

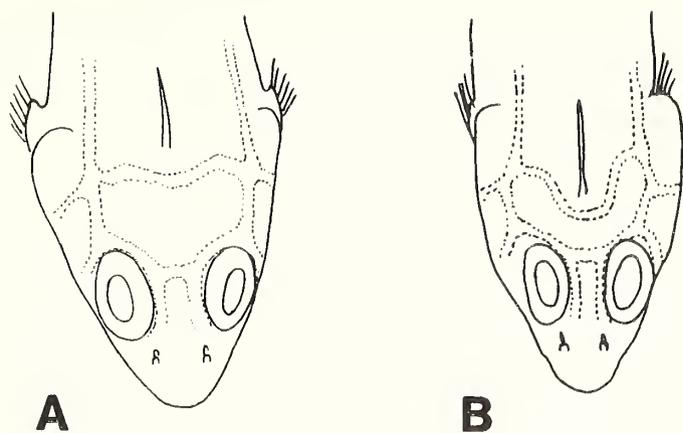


FIG. 13. Diagram of crescentic (A) and "U"-shaped (B) supratemporal sensory canals in *Enneapterygius* spp.

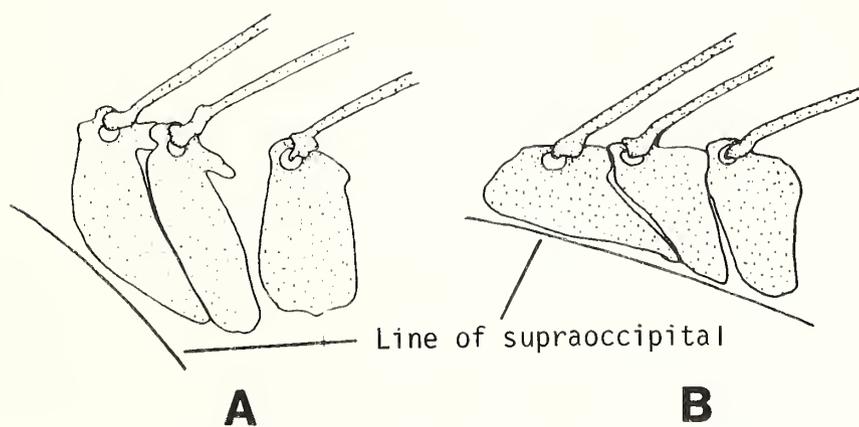


FIG. 14. First dorsal fin spines and pterygiophores of *Enneapterygius* spp. with (A) crescentic and (B) "U"-shaped supra-temporal sensory canals.

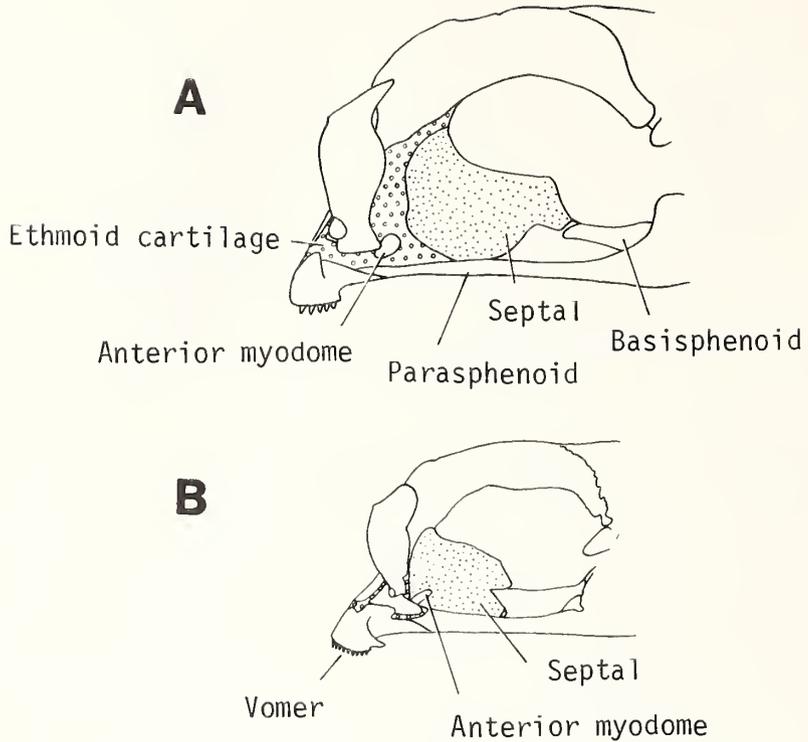


FIG. 15. Septal of (A) *Cremnochorites capensis* and (B) *Enneapterygius clarkae*.

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HOLLEMAN: THREE NEW SPECIES AND NEW GENUS OF TRIPTERYGIID FISHES (BLENNIOIDEI)

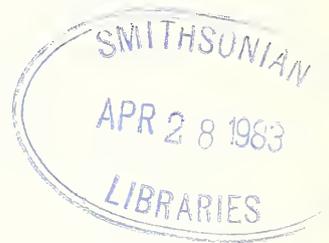
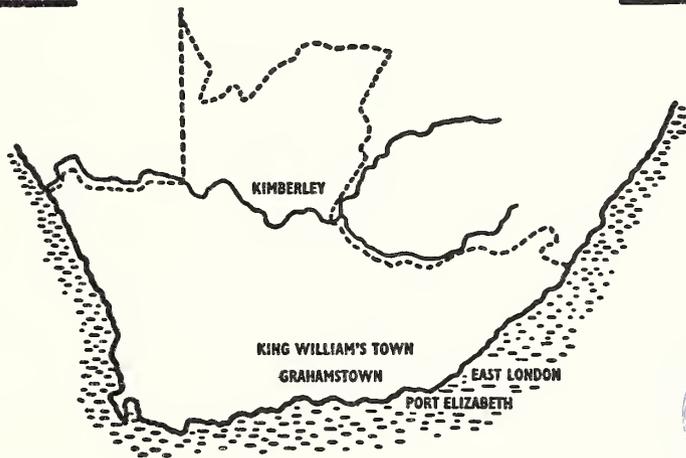
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Some aspects of the ethology of *Chalybion (Hemichalybion) spinolae* (Lepeletier) (Hymenoptera: Sphecidae: Sphecinae) in the Eastern Cape Province of South Africa

by

F. W. GESS, S. K. GESS and A. J. S. WEAVING

(Albany Museum, Grahamstown)

ABSTRACT

Some aspects of the ethology of *Chalybion (Hemichalybion) spinolae* (Lepeletier) are described, particular attention being paid to the situation and nature of the nest, the mode of its construction, provisioning and sealing. Published accounts concerning the nesting of species of *Hemichalybion* are briefly reviewed. Data attributed to certain species, including *H. spinolae*, are shown to be misleading due to the confusion by some authors of species of *Hemichalybion* with those of *Sceliphron*. The nesting of *Hemichalybion* (as exemplified by that of *H. spinolae* here described) is discussed with reference to that of the Sceliphronini as a whole. Possible specific interactions between three spider-hunting Sceliphronini nesting at Hilton are touched upon as is resource partitioning with respect to their prey.

INTRODUCTION

That some confusion exists in the literature concerning the nesting of species of the subgenus *Hemichalybion* Kohl, 1918, has been clear to two of the authors (F. W. G. and S. K. G.) for some years. Consequently it was with considerable interest that during the autumn of 1978 they twice witnessed part of the process of nest construction by *C. (H.) spinolae* (Lepeletier). Unfortunately, both nests were abandoned by their builders prior to their being provisioned and, though the site was visited frequently during the succeeding months, no further nesting activity was observed. The consequent nesting data obtained were published in outline (Gess, 1981: 24).

Late in the summer of 1982 two females provisioning nests at a site a little removed from that of the previous observations were discovered by the third author (A. J. S. W.) who excavated the nests after their completion and thereby established the identity of the prey. Having been alerted to the nesting of *C. (H.) spinolae* at the new site, F. W. G. and S. K. G. during the week following closely observed a female constructing, provisioning and sealing a further three nests. In their turn these were excavated and examined. The present account is therefore based on a total of seven nests, five of which were completed.

The present paper is the twelfth of a series of publications dealing with the ethology of certain solitary wasps occurring at Hilton, a farm situated 18 kilometres WNW of Grahamstown (33° 19'S, 26° 32'E) in the Albany Division of the Eastern Cape Province of South Africa. A detailed account of various aspects of the ecology of Hilton has previously been given (Gess, 1981: 3-9).

THE NESTING OF CHALYBION (HEMICHALYBION) SPINOLAE (LEPELETIER)

Description of the nesting sites

Two nesting sites of *C. (H.) spinolae* were located at Hilton. Both are north-facing vertical banks. One is naturally occurring and is the bank of the New Year's River. It is composed of a mixture of sand and clay which, as a result of recent mineralization, has the character of a weak and crumbly sandstone-like material and is referred to as the "sandstone" bank (Gess, 1981: 58 and Fig. 8). The other is man-made and is a wall of a sandpit dug in the flood plain of the Iron Put River, a tributary of the New Year's River (Gess, 1981: 58 and Fig. 5). The bank (Fig. 1), created in 1981 by an enlargement of the sandpit in a direction away from the river, differs from the other banks of the sandpit in that it is cut in non-friable soil. Although it is composed largely of firmly compacted fine sand, it has a considerable content of colloidal material as was demonstrated at the time of study by the presence of the nest turrets of eumenids and, on small ledges, those of the pompilid *Dichragenia pulchricoma* (Arnold).

At both nesting sites *C. (H.) spinolae* favoured slightly protected situations such as beneath overhangs caused by uneven weathering of the banks or by man's undercutting of the same (Figs 2 and 3). All nest entrances were located above the base of the banks, at heights ranging from 16,5–70 cm.

Water, required by the wasp for nest construction, was available at the two sites as pools in the river beds. At the time of nesting there was in addition a temporary rain water pool on the floor of the sandpit.



FIG. 1. Hilton, vii. 1982. North-facing bank of sandpit, the location of Nests 3–7.

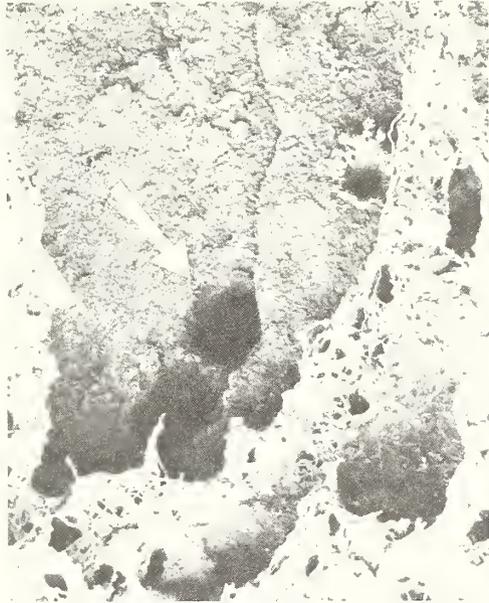


FIG. 3. Hilton, 6.iv.1978. Entrance of Nest 1 (arrowed) with flanking it quarry from which cell-lining material was obtained. Turret on lower left that of an unidentified eumenid. (x c.1.0)

Fig. 3 inverted

FIG. 2. Hilton, 6.iv.1978. Situation of Nest 1 in sheltered position on north-facing "sandstone" bank.

Flight season and daily flight period

The flight season of *C. (H.) spinolae* at Hilton starts in early November. Males have been collected through to early March and females to mid May. Nesting was observed from mid-March through to the first week of June.

Both males and females were observed and collected near the water puddles, while foraging and while flying about in front of the banks. Though suitable opportunities for mating occurred it was not, however, observed.

The day's nesting activities started at about 10 a.m. though, shortly before this, females were observed sunning themselves near nests started the previous day. If a nest is completed in the early afternoon a new nest may be initiated on the same day. Provisioning and sealing of nests in all cases took place during late morning and early to mid afternoon.

Female *C. (H.) spinolae* do not shelter or sleep in or near their nests and their sheltering places were not discovered.

Plants visited by adult wasps

Adult *C. (H.) spinolae* of both sexes have been observed visiting flowers for the purpose of imbibing nectar. The following associations between this wasp and forage flowers in the eastern Cape have been recorded: on *Maytenus linearis* (L.f.) Marais (Celastraceae) at Hilton, Grahamstown, 9–11.xii.1969, 8♀♀, 4♂♂ (F. W. Gess) and 6.xii.1972, ♂ (F. W. Gess); on *Foeniculum vulgare* Mill. (Umbelliferae) in Belmont Valley, Grahamstown, 20.i.1970, 6♀♀, 2♂♂, 22.i.1970, ♀, 23.i.1970, ♀, 24.i.1970, ♂, 5.ii.1970, 2♀♀, 28.iv.1970, ♂ (all F. W. Gess), 17–25.i.1970, 2♀♀ (J. G. H. Londt) and 24.i.1970, ♂ (C. F. Jacot-Guillarmod); on *Zizyphus mucronata* Willd. (Rhamnaceae) at the Koonap River, 17 miles from Adelaide on Grahams-town road, 20–22.xii.1972, ♀, ♂ (C. F. Jacot-Guillarmod); on *Acacia karroo* Hayne (Leguminosae) at Hilton, Grahamstown, 3.i.1977, ♂ (D. W. Gess); and on *Hedera helix* L. (Araliaceae) in a garden, Grahamstown, 27.xii.1981–4.i.1982, ♀, 2♂♂ (R. W. Gess).

In addition one male was collected on young foliage of *Acacia karroo* at Hilton on 6.xii.1977 (H. W. Gess).

Identification of the prey

Twenty-eight prey individuals were recovered from the five provisioned nests examined (Table 1). All were spiders of the genus *Latrodectus* (Theridiidae), 26 being *L. geometricus* Koch and the remaining two *L. mactans* (Fabr.). Four were adult females, two were subadult females and the remaining 22 were immatures, apparently all females.

Description of the nest

The nest of *C. (H.) spinolae* consists of a short, slightly upwardly inclined burrow terminating in a single ovate mud-lined cell and sealed at the entrance with a mud plug (Fig. 4). The average total length of the burrow is 36 mm (sample of 7), that of the entrance passage 15 mm (sample of 4) and that of the cell 23 mm (sample of 4). The average diameter of the entrance passage is 8 mm (sample of 7) and that of the cell at its widest point is 12 mm (sample of 5). The nest closure is concave towards the outside and is 2–3 mm thick at the centre and somewhat thicker around its perimeter. A sealed nest is characterized by the presence of two quarries of similar diameter to the nest closure and situated with their edges 4–20 mm from it.

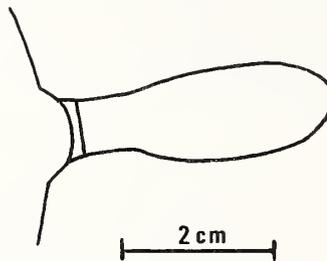


FIG. 4. Hilton, 25.iii.1982. Plan of Nest 7.

Method of nest construction, provisioning and oviposition

Nest construction follows three distinct phases: excavation of the burrow, lining of the cell, nest closure. Water is required for working the substrate during all three phases. This is collected from a nearby pool, the wasp, whilst filling her crop, standing on the earth at the water's edge.

TABLE 1.

Details of the prey recovered from five provisioned nests of *C. (H.) spinolae*.

Date	Nest no.	Prey (listed in decreasing order of weight)				
		No.	Identity: sp. of Latroectus	Developmental stage, sex, individual bearing wasp's egg.	Individual wt. (mg)	Total wt. (mg)
18.3.82	3	4	geometricus geometricus geometricus geometricus	ad. ♀ (one of these) subad. ♀ (two with egg) imm. ♀ imm. ♀	268 208 81 29	586
19.3.82	4	3	mactans geometricus geometricus	ad. ♀ ad. ♀ ad. ♀ (with egg)	318 300 240	858
20.3.82	5	7	geometricus geometricus geometricus geometricus mactans geometricus geometricus	imm. ♀ (with egg) imm. ♀ imm. ♀ imm. ♀ imm. ♀ imm. ♀ imm. ♀	194 168 136 91 54 41 39	723
23.3.82	6	3	geometricus geometricus geometricus	subad. ♀ (with egg) imm. ♀ imm. ♀	207 139 45	391
25.3.82	7	11	geometricus geometricus geometricus geometricus geometricus geometricus geometricus geometricus geometricus geometricus geometricus	imm. ♀ imm. ♀ imm. ♀ (with egg) imm. ♀ imm. ♀ imm. ♀ imm. ♀ imm. ♀ imm. ♀ imm. ♀ imm. ♀	143 98 81 81 70 55 53 43 43 32 15	714

Excavation of the burrow is by wetting the chosen nest site or the working face of the developing cavity with regurgitated water, by working this moisture into the substrate with the aid of the mandibles, and by forming the resultant mud into pellets. These are not carried away to be disposed of at a distance but are simply dropped at the mouth of the burrow and consequently collect at the foot of the bank immediately below the nest.

Burrow excavation having been completed, lining of the cell is commenced. For this purpose mud, mixed in a quarry close to the burrow entrance (Fig. 3) is introduced into the nest. At the quarry only a small quantity of water is regurgitated from the crop at any one time, just enough for the formation of a single pellet. Holding this in her mandibles, the wasp walks to the nest which she enters head first. Application of the introduced mud to the surface of the excavated cell is aided by vibrations produced by manipulation of the flight mechanisms and

transmitted through the mandibles. These vibrations are accompanied by a buzzing sound clearly audible from without the nest. The application of that pellet of mud having been completed the wasp backs out of the nest and on foot returns to the quarry to form another pellet. The sequence is repeated until all the water in the crop is used up. The number of pellets produced per water load will vary with the nature and moisture content of the substrate. However, at Hilton in the sand pit 5-8 pellets were formed per water load. It is possible that, due to the porous nature of the substrate, additional water may be regurgitated from the crop to aid in the application and smoothing of the cell lining. Indicative of this is that a greater number of pellets (14) was formed per water load during the construction of the nest closure which is in contact with the dry substrate only around its periphery. The water in the crop having been exhausted, the wasp walks along the bank for a distance of 25-50 cm before taking off and flying to the water source from which she returns rapidly, flying directly to the nest and alighting at the entrance. Several such cycles of water collection, quarrying and mud application/smoothing are required for the completion of the cell lining. Under the conditions at the Hilton sandpit during the period of observation water collection took two minutes and quarrying and cell lining five minutes in each cycle.

Cell lining having been completed the wasp flies off in search of prey. The length of time which elapses before the wasp returns with the first prey is presumably dependent upon the success of the hunt. During observations at Hilton it varied from 30 minutes to several hours. However, a source of prey spiders having been discovered further prey are brought in in quick succession. In one instance (Nest 7) eleven spiders were brought in within an hour, the first six in the amazingly short time of 14 minutes which would indicate that they must have been found all together in one place. The return with the seventh and eighth spiders took 13 and 16 minutes respectively and the remaining four 3-8 minutes each.

If the hunt is of considerable duration the wasp will return to inspect her nest at intervals of about 15 minutes. During these inspections she touches the bank around the nest entrance with her antennae. Furthermore, she appears to mark the nest for, before flying off again, she turns round and rubs the tip of her abdomen around the rim of the nest entrance.

When flying in with prey the wasp alights on the bank immediately below and facing the nest entrance and, walking, enters the nest rapidly. The prey spider is held beneath the wasp, orientated dorsum-up and facing the direction of travel. The mandibles grip the paralysed prey at its anterior end and the first pair of legs support it from below. After a very short time the wasp emerges rapidly from the nest, pauses to groom her face and antennae, walks along the bank as before and then flies off. Whereas during the construction of the nest the wasp takes little notice of the presence of other insects or of a human observer, during provisioning they were "buzzed" on her departure from the nest even if this meant changing her course of flight.

Within the nest the prey are positioned on their backs or sides, facing the inner end of the cell. Oviposition takes place on one of the spiders during its positioning within the cell for during provisioning the wasp enters the nest only when carrying prey. In the five provisioned cells examined (Table 1) the spider bearing the wasp's egg was mostly of large size though not necessarily the largest. Adult, subadult or very large immature spiders were therefore chosen though in Nest 7 oviposition was on a medium-sized immature. The order of prey introduction, as deduced from the position of the individual spiders within the cell, was recorded in full detail only for Nest 6. In that nest the first prey was the egg-bearing subadult ♀ of 207 gms, followed by the immatures of 45 gms and 139 gms. In Nests 3, 4 and 7 only the position of the egg-bearing spider was noted. This in each case was at the innermost end of the cell. Lack of such data for Nest 5 was due to the accidental disarrangement of the prey during cell opening. From the evidence it appears that in at least four of the five nests examined oviposition was on the first spider to be introduced into the cell. However, as it is likely that a spider has to be of a certain minimum size if it is to be suitable as the initial food source of the newly-hatched

wasp larva, it is probable that oviposition upon the first-introduced prey takes place only if it attains or exceeds this size. If smaller, it is likely that oviposition is delayed until a large prey individual is subsequently introduced.

The egg of *C. (H.) spinolae* is white, curved and measures $3,68 \times 1,01$ mm (average of 5). It is attached medially on one side or other of the anterior part of the spider's abdomen (Fig. 5).

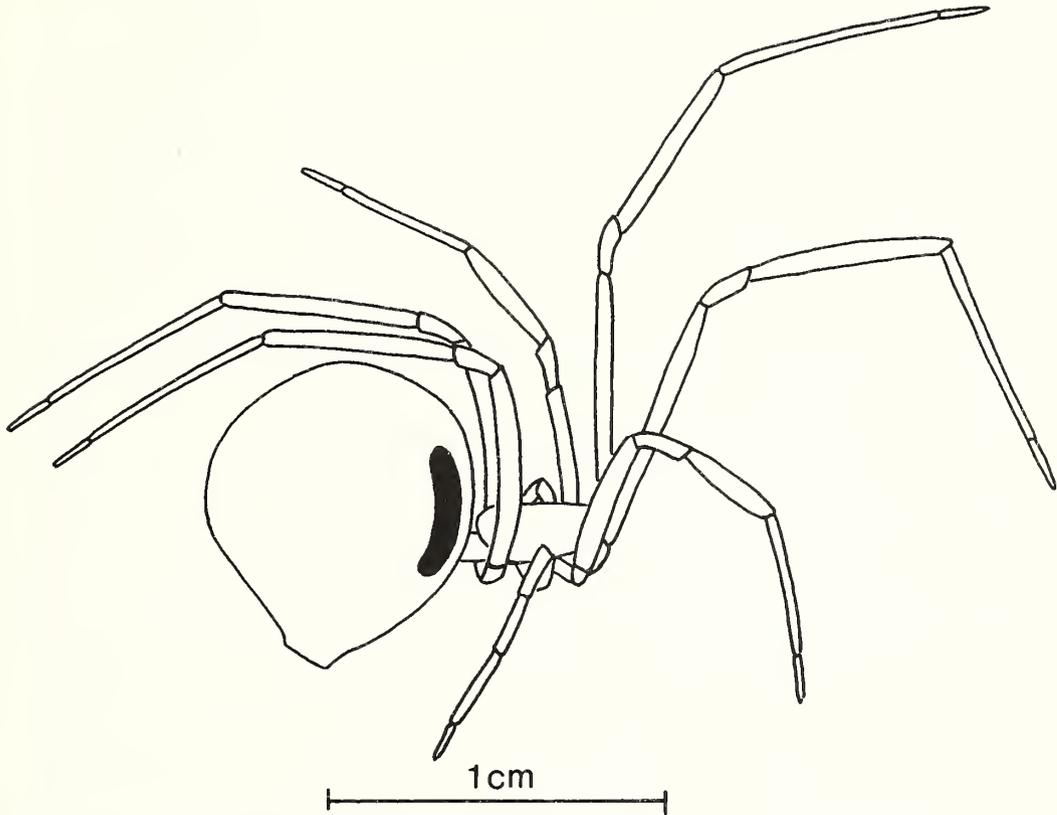


FIG. 5. Diagrammatic representation of immature ♀ *Latrodectus geometricus* showing position of attachment of egg of *C. (H.) spinolae*.

Provisioning of the cell having been completed, the wasp immediately flies off to collect water for the sealing of the nest. Mud for this purpose is mixed in a new quarry which like the first (formed by extraction of material for cell lining) is close to the nest entrance. Pellets for sealing the nest are laid down spirally. The nest opening having been closed, more pellets are added to thicken the plug which when complete is not flush with the surface of the bank but is somewhat concave. In an observed instance of nest sealing which took 11 minutes, the plug was formed of 28 mud pellets, 14 being produced and positioned for each of two water loads. Whereas the nest as a whole is sealed by the construction of the above-described mud plug, the cell itself is not sealed nor is the entrance passage filled. No temporary closures of the nest are made at any time during the provisioning of the cell.

A nest having been completed, the wasp begins another that may be closely associated with the first. Thus excavation of Nest 6 was initiated within the second quarry associated with the sealed Nest 5, the distance between the two nests being therefore less than 1 cm. The next nest excavated by the female, Nest 7, was in its turn initiated within the concavity represented by the remains of the exposed and longitudinally cut away cell of Nest 6 after its excavation by the authors. It is probable that under undisturbed conditions a female may construct a series of closely associated nests, each excavated within a quarry of the nest immediately preceding it.

Life history

After removal from the cells and subsequent examination the contents of Nests 5, 6 and 7 were placed in cotton wool stoppered glass vials of similar dimensions to the wasp cells and kept indoors at room temperature. Two eggs, those from Nests 5 and 6, were viable. Larval hatching occurred 5 and 7 days after oviposition and feeding took place on the first prey for a period of 8 days. A further 4 days were required to complete feeding and to reach larval maturity. In feeding the larvae first consumed the abdomens of all the spiders making up the provision, then turned to the cephalothoraxes and legs previously left intact. Eventually only a few leg fragments remained uneaten. Cocoon spinning commenced two or three days after the cessation of feeding. The winter months were spent in a state of pre-pupal diapause.

The cocoon of *C. (H.) spinolae* is pale brown and translucent, the insect within being clearly visible, and is attached to the walls surrounding it by sparse silken threads. It varies in length from 23–25 mm and in breadth at its midlength from 7–8 mm, widens slightly towards the rounded anterior end and narrows to 5,5–6,5 mm at the truncate posterior end at which the meconium is deposited.

An attempt was made to establish the number of generations which occur during a season by estimating the age of female specimens. As the number of specimens from Hilton was very small, material from other localities in the eastern Cape was included in the analysis. The mandibles of females vary considerably in length due to wear resulting from nest excavation. In order to eliminate errors due to variation in wasp size, the ratio of mandible length to face width was used as a measure of age. These parameters showed a linear relationship on unworn specimens ($r = 0,91$; $n = 22$). The resulting age distributions (Fig. 6) show that at the beginning of the season only young wasps are present. Adults do not therefore survive the winter. By January, the proportion of young wasps is much lower and in February very few freshly-emerged

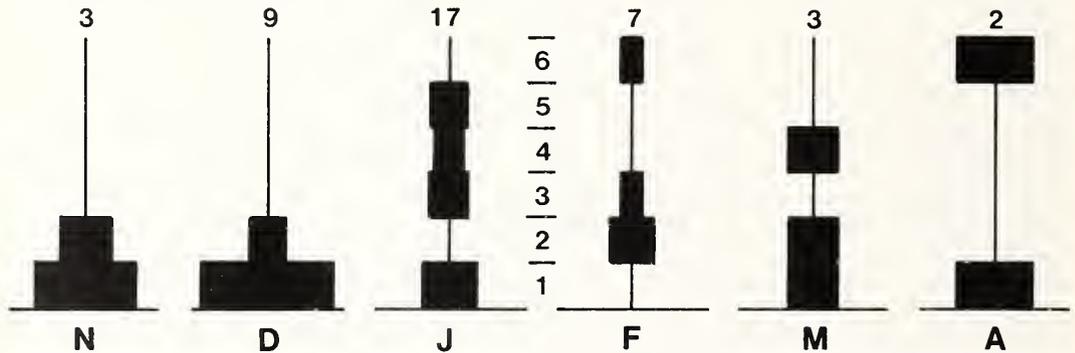


FIG. 6. Percent age distribution from November to April of female *C. (H.) spinolae* from the eastern Cape. The width of the base line of each histogram represents 100%. Sample size appears above each month. Classes 1 to 6 on the vertical scale represent increasing age, as indicated by mandibular wear (face width/mandibular length), and have the following intervals: 1(0,951–1,020), 2(1,021–1,090), 3(1,091–1,160), 4(1,161–1,230), 5(1,231–1,300), 6(1,301+).

wasps are found. There is an indication that a second generation of wasps may emerge during March. However, since the sample size is so small, much more data are required before this conclusion can be substantiated. In addition, ages of both male and female specimens were estimated according to four categories of wing tatter. Although sample size was still small ($\text{♀}n = 41$; $\text{♂}n = 26$), both sexes showed similar age distributions which were moreover in agreement with those obtained using mandibular wear in females.

DISCUSSION

The subgenus *Hemichalybion* Kohl, as presented by Bohart and Menke (1976: 103) is constituted of five Old World species: the African *clypeatum* (Fairmaire) and *spinolae* (Lepeletier) [= *eckloni* (Dahlbom)], the southern European and western Asian *femoratum* (Fabricius), and the Asian *fuscum* (Lepeletier) and *sumatranum* (Kohl).

Biological data attributed to three species of *Hemichalybion*, *clypeatum*, *femoratum* and *spinolae*, have been published by various authors. However, the similarity in general appearance and in colour pattern between *Hemichalybion clypeatum* and *H. spinolae*, and the widespread and common *Sceliphron spirifex* (L.) occurring sympatrically with them has, it would appear, been the cause of at least two authors being confused about the identity of the species upon which they were reporting.

According to van der Vecht (see Bohart and Menke, 1976: 102) the extensive papers by Verlaine (1924, 1926) on a species called *clypeatum* actually pertain to *S. spirifex*. In the light of the present account of the nesting of *H. spinolae* it is clear that a similar confusion of identity exists in the literature between this species and *S. spirifex*. Arnold (1928: 243) following his systematic account of *H. spinolae* stated that it is "a common insect, frequently seen in houses, with an inconvenient partiality for building its mud nests at the angles of walls, or on furniture, books and boxes". The above quoted statement characterizes the nesting behaviour of *S. spirifex* under synanthropic conditions and clearly does not pertain to *H. spinolae*. It is of interest that in the same paper Arnold gave no biological notes following his account of *S. spirifex*. Arnold's continued misconception concerning the nesting of *H. spinolae* is evident from a statement made by him in correspondence with van der Vecht (see van der Vecht, 1961: 256).

The nesting of *H. femoratum* has been the subject of two reports: Rudow (1912) recorded it using a *Eumenes* mud nest, and Bonelli (1969) recorded it from an old mud nest which Bohart and Menke (1976: 102) presumed was abandoned by a species of *Sceliphron*. A similar association with aerial mud nests is recorded by van der Vecht (1961: 256) with respect to *H. clypeatum* for, according to a note in the Paris Museum, this species is a "commensal des nids de la moyenne *Synagris*". The validity of these associations cannot either be proved or disproved at this stage. However, in view of the confusion of specific identity attending other accounts, there is a need for confirmation of the reported association of *Hemichalybion* species with the aerial mud nests of other aculeate wasps.

No doubt influenced by the reports of Rudow, Bonelli and van der Vecht, Bohart and Menke (1976: 102) expressed the view that "quite likely Arnold made the same mistake with *spinolae* that the Peckhams and Rau (early papers) made in their observations of *C. californicum* in not realizing that the wasp does not build its own mud nest, but takes empty *Sceliphron* nests for its own". This has now been shown to be incorrect.

Brauns (1911: 118) was nearer the truth when he wrote concerning *H. spinolae*: "In der Nistweise nähert sie sich den *Chalybion*-Arten, indem sie ihre Zellen ebenfalls in Höhlungen, innerhalb von Mauern, Erdwänden etc. verbirgt, welche dunkel sind und nur eine kleine Zugangsöffnung aufweisen". (In its manner of nesting it approaches the *Chalybion* species, in that it likewise conceals its cells in hollows within walls, earth banks etc., which (hollows) are dark and only exhibit a small entrance hole.) Though correct in saying that *H. spinolae* nests in cavities in earth banks Brauns was mistaken in believing that these cavities were pre-existing

ones and in classing the species with species of *Chalybion* (*sensu stricto*) which are gallery renters, not gallery excavators.

That *H. spinolae* nests in vertical banks where it excavates cavities itself, rather than utilizing pre-existing cavities, was indicated by Gess (1981: 24) on the basis of information then available and is confirmed in the present paper.

Both van der Vecht (1961) and Bohart and Menke (1963 and 1976) have attempted to elucidate the relationship between *Chalybion* (*sensu stricto*), *Hemichalybion* and *Sceliphron*. These attempts have, however, been largely thwarted by the overall dearth of information concerning the biology of *Hemichalybion* and by the misleading nature of at least some of the limited data attributed to individual species.

The present study has shown that *Hemichalybion* (as represented by *H. spinolae*) shares with *Chalybion* (*sensu stricto*) and *Sceliphron* the habit of constructing its nests in situations raised up above the ground. It has, however, shown also that *Hemichalybion* differs from both the other taxa in its behaviour with respect to nest construction. Thus whereas *Hemichalybion* excavates cells within vertically-presented earthen banks, *Chalybion* seeks and modifies pre-existing cavities and *Sceliphron* builds free aerial cells.

With respect to its nest building behaviour *Hemichalybion* may therefore be seen as the least specialized of the three taxa. This view accords well with the statement by van der Vecht (1961: 256) that morphologically *Hemichalybion* species are clearly very close to the hypothetical ancestor of the *Chalybion-Hemichalybion-Sceliphron* complex. There is moreover no difficulty in accommodating the suggested behavioural and morphological status of *Hemichalybion* within the dendrogram given by Bohart and Menke (1976: Fig. 83) to express their thoughts on the relationships of the genera in the tribe Sceliphronini.

Within the Sceliphronini there appear to have been strong pressures to abandon nesting in friable soil for it is only in the two most primitive genera, the mantid-hunting *Stangeella* and the cricket-hunting *Chlorion*, that the females possess foretarsal rakes and excavate their nests by digging. In all the other genera, divisible into two distinct lines—the predominantly cockroach-hunting *Penepodium*, *Dynatus*, *Podium* and *Trigonopsis* and the exclusively spider-hunting *Chalybion* (including *Hemichalybion*) and *Sceliphron*, the females lack foretarsal rakes but make use of mud in nest construction.

Behaviourally most primitive of these rake-less forms are probably those species of *Penepodium*, *P. luteipenne* (Fabricius) and *P. haematogastrum* (Spinola), the nesting of which was studied by Williams (1928: 118–126 and Figs 179, 180, 183, 185–189, 192 and 193) in British Guiana and in Brazil respectively. *P. luteipenne*, of which Williams gave the fuller account (as *Podium flavipenne* Latreille), was found to nest in bare, hard, solid ground, either level or sloping, in close proximity to water. Excavation of the simple, shallow, single-celled burrow was effected by the jaws, regurgitated water being used to soften the soil. The excavated material was deposited about the hole in the form of mud pellets. The nest was left open until fully provisioned when it was sealed with a plug of mud mixed with the aid of regurgitated water at a quarry site a few inches removed from the nest.

The nesting behaviour of *Hemichalybion spinolae* is in many respects very similar to that of *Penepodium luteipenne* but does represent an advance for instead of nesting in the ground, the surface presentation of which is horizontal or sloping, this species has left the ground and nests in earth banks, the surface presentation of which is vertical. Furthermore *H. spinolae* lines its burrow with a layer of mud, a habit not recorded for *P. luteipenne*.

Behaviourally more advanced are the species of *Chalybion* (*sensu stricto*) and their nest-form homologues of the cockroach-hunting line—*Penepodium goryanum* (Lepeletier) and species of the genus *Podium* and possibly *Dynatus*, the biologies of which have been reviewed by Bohart and Menke (1976). These forms do not themselves hollow out nesting cavities but seek and modify pre-existing ones in situations above the ground. Mud is used for cell parti-

tions and for nest closures. More advanced still are the species of *Sceliphron* and their nest-form homologues, species of *Trigonopsis*, all of which construct free aerial nests made of mud.

Three species of spider-hunting Sceliphronini have been found nesting at Hilton: *Chalybion (Hemichalybion) spinolae* (Lepeletier), *Chalybion (Chalybion) tibiale* (Fabr.) and *Sceliphron spirifex* (L.). Whereas *C. (H.) spinolae* is on account of the nature of its nest restricted to vertical earthen banks the other two species are not so limited but may nevertheless nest there also. Thus during the summer of 1982 *S. spirifex* constructed its aerial nests on the sand-pit bank not far from the excavated nests of *C. (H.) spinolae* and all three species were previously recorded (Gess, 1981: 24, 25 and 27) in association with the "sandstone" bank. Under such circumstances a certain degree of specific interaction may well occur. Though *C. (H.) spinolae* and *S. spirifex* construct very different nests, interspecific competition for nesting sites may arise when there is a scarcity of the overhangs and similar sheltered situations favoured by both. *C. (C.) tibiale* clearly would not enter into such competition for nesting sites but may yet be associated with them by virtue of the probable adoption and modification for its own use of the old abandoned nests of the other two species.

With respect to the prey utilized by the three species for cell provisioning a high degree of resource partitioning appears to pertain. As far as can be judged from the present paper *C. (H.) spinolae* appears to be restricted to species of *Latrodectus* (Theridiidae). *C. (C.) tibiale* nesting in trap-nests sited in riverine bush alongside the sandpit has previously been recorded (Gess and Gess, 1980: 13) as provisioning principally with Argiopidae and in addition with a small number of Theridiidae (*Rhomphaea* sp.) and Zodariidae. Most commonly represented among the Argiopidae were species of *Isoxya*, *Nephila* and *Cyclosa* whereas present only in small numbers were species of *Araneus*, *Argiope* and *Caerostris*. In contrast, *Sceliphron spirifex* at Hilton and elsewhere in the Grahamstown district has been found to provision exclusively with Argiopidae of the genus *Araneus*.

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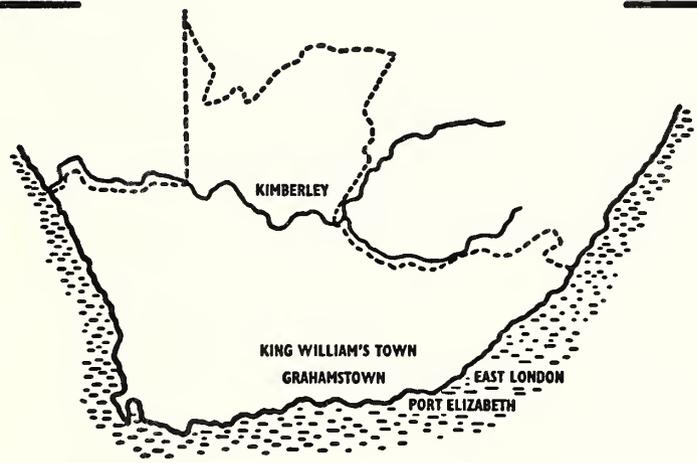
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Ethological studies of *Isodontia simoni* (du Buysson), *I. pelopoeiformis* (Dahlbom) and *I. stanleyi* (Kohl) (Hymenoptera: Sphecidae: Sphecinae) in the Eastern Cape Province of South Africa

by

F. W. GESS and S. K. GESS
(Albany Museum, Grahamstown)

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ABSTRACT

Some aspects of the ethology of three southern African species of *Isodontia*, *I. simoni* (du Buysson), *I. pelopoeiformis* (Dahlbom) and *I. stanleyi* (Kohl) are described. Particular attention is paid to: the situation and nature of the nest; the nature of the materials introduced into it and the manner of their arrangements; provisioning; oviposition. With respect to *I. pelopoeiformis*, the most common species, accounts are given also of the life history, sequence of sexes in the nests, cannibalism and parasites. Certain aspects of the nesting of a total of 14 *Isodontia* species are briefly reviewed. *I. simoni* is shown to differ from the other species in that the pre-existing cavity chosen for nesting is situated in horizontal ground and not in vertical banks, in plants, or in other situations above ground level. On the basis of the situation of its nest and the nature of the materials introduced into it, *I. simoni* is considered to be primitive, a conclusion which agrees with that reached by other authors from a consideration of structural characters.

INTRODUCTION

Fifty-four species of the genus *Isodontia* Patton (Sphecidae: Sphecinae) are listed by Bohart and Menke (1976). Of this total, five species occur in and are restricted to the Afro-tropical Region. *I. longiventris* (Saussure), *I. pelopoeiformis* (Dahlbom), *I. simoni* (du Buysson) and *I. stanleyi* (Kohl) are found on the African mainland and *I. leonina* (Saussure) on the island of Malagasy.

Biological data pertaining to fourteen species, including two from Africa, have been published. Smithers (1958) gave a detailed account of the nesting of *I. pelopoeiformis* in trap-nests in Zimbabwe (formerly Southern Rhodesia) and the same species in Angola was the subject of a note by Heinrich (1969). Gess (1981) gave brief accounts of the nesting in the Eastern Cape Province of South Africa of both *I. pelopoeiformis* and *I. stanleyi* and suggested that a third species, *I. simoni*, occurring sympatrically with the first two, nested in similar situations. The subsequent discovery and study of nests of *I. simoni* has shown the suggestion to have been incorrect and that this species nests in a situation fundamentally different from those recorded for all other *Isodontia* species.

The present paper, a comparative account of the nesting of the three species of *Isodontia* known to occur in Africa south of the Limpopo, is the thirteenth in a series of publications dealing with the ethology of certain solitary wasps occurring at Hilton, a farm situated 18 kilometres WNW of Grahamstown (33° 19'S, 26° 32'E) in the Albany Division of the Eastern Cape Province of South Africa. Nesting of *I. pelopoeiformis* and *I. stanleyi* is described from Hilton but that of *I. simoni* is described from a neighbouring farm Thursford as, although this species occurs at Hilton, its nesting site on this farm was not located.

A detailed account of various aspects of the ecology of Hilton has previously been given (Gess, 1981: 3–9).

DESCRIPTION OF THE NESTING SITES

Four nests of *I. simoni*, 85 nests of *I. pelopoeiformis* and 18 nests of *I. stanleyi* were studied.

The nests of *I. simoni* are constructed in pre-existing cavities in the ground. The nesting cavities investigated were subvertical burrows, 64–95 mm long and of average bore 12 mm. They did not appear to be the burrows of a hymenopteran as they showed no evidence of any previous cells. However, they agreed in appearance and dimensions with the burrows of the cockroach, *Pilema thoracica* (Walker), which are common in the nesting area of *I. simoni* (Fig. 1). The investigated nests were in an eroded area of clayey non-friable soil sparsely covered by dwarf karroid scrub (Fig. 2). The karroid scrub in the areas studied on both Thursford and Hilton is characterized by *Pentzia incana* (Compositae), however, that on Thursford includes many more succulent species than that on Hilton.

The nests of *I. pelopoeiformis* and of *I. stanleyi* are constructed in pre-existing cavities above the ground. All the nests of *I. pelopoeiformis* were in trap-nests having cavities of length 155 mm and bore either 9,5 mm or 12,7 mm. These trap-nests were suspended horizontally at heights of from 10–210 cm above the ground in shrubs and small trees of *Acacia karroo* (Leguminosae), *Maytenus linearis* (Celastraceae) and *Rhus lancea* (Anacardiaceae) in thorn scrub and riverine bush (Fig. 3). Eight nests of *I. stanleyi* were in trap-nests of the same dimensions as and similarly situated to those occupied by *I. pelopoeiformis*. The other ten nests of this species were in naturally occurring pre-existing cavities which were abandoned nesting galleries of carpenter bees (Anthophoridae: Xylocopinae), three of *Xylocopa sicheli* Vachal in dry inflorescences of *Aloe ferox* (Liliaceae) (Gess 1981: Fig. 38) and seven of *Xylocopa scioensis* Gribodo (as *X. caffrariae* Enderlein, a junior synonym of *X. scioensis*, in Gess, 1981) in dry culms of *Phragmites australis* (Gramineae).



Fig. 1. Burrow entrance of *Ptelema thoracica* in *I. simoni* nesting site on Thursford.

The favoured nesting sites of *I. pelopoeiformis* and *I. stanleyi* would appear from trap-nesting data to be within the riverine bush and thorn scrub. The nests of *I. stanleyi* in *Aloe ferox* and *Phragmites australis* are probably on the fringes of the main nesting areas as these plants occur respectively on the slopes above the riverine bush in proximity to thorn scrub and fringing a river bed and the associated riverine bush (Gess 1981: Figs 13–15). A search was made for nests in woody stems with little success. However, branches of *Acacia karroo* bored by the larvae of *Ceroplesis hottentota* (Fabricius) (Coleoptera: Cerambycidae) were found to contain nesting materials of the type used by *I. stanleyi*.

FLIGHT PERIOD

The three species of *Isodontia* are proterandrous. *I. simoni* has been collected at Hilton from the beginning of November to early December and at Thursford was nesting in January. *I. pelopoeiformis* and *I. stanleyi* at Hilton fly from December to late February and nest from late December and from mid December, respectively, to late February.

YOUNG GROWTH, FLOWERS AND DRY INFLORESCENCES VISITED

At Hilton a male of *I. simoni* was collected on flowers of *Lasiospermum bipinnatum* (Compositae) (3.xi.1977) and three females were recorded on the flowers of *Senecio pterophorus* (Compositae) (29.xi.1979, 1.xii.1979 and 5.xii.1979). Three males of *I. pelopoeiformis* were collected on *Acacia karroo*, two on young growth (6.xii.1972 and 5.xii.1973) and one on flowers (4.i.1978). Numerous females were observed visiting flowers of *Acacia karroo*. However, as there were trap-nests in the vicinity only one specimen was collected (3.i.1977) to confirm the identity. There are no records of *I. stanleyi* visiting flowers.



Fig. 2. A nesting site of *I. simoni*, an eroded area on Thursford.



Fig. 3. A nesting site of *I. pelopoeiformis* and *I. stanleyi*, riverine bush on Hilton. The figure indicates a bundle of trap-nests suspended in *Maytenus linearis*.

I. simoni and *I. pelopoeiformis* visit seeding plants to collect fluff for the construction of nest plugs. It is likely that any suitable fluff of this type will be taken. At Thursford *I. simoni* collected fluff derived from the fruit of plants of the family Asclepiadaceae which are common in its nesting area and to a lesser degree made use of fluff from flowers of Compositae. *I. pelopoeiformis* at Hilton used only fluff from flowers of Compositae and was observed collecting this from *Lasiospermum bipinnatum* and *Senecio* species. No fruiting plants of Asclepiadaceae were present in the vicinity of its nests.

I. stanleyi visits flowering grasses (Gramineae) including *Danthonia curva*, *Diplachne fusca*, *Eragrostis* sp. (probably *E. curvula*), *Melica racemosa* and *Sporobolus* sp. (probably *S. fimbriatus*) to collect materials, short lengths of leaf blades and longer lengths from inflorescences including stems and flowers, for the construction of nest plugs.

IDENTIFICATION OF THE PREY

The prey of all three species of *Isodontia* consists of various species of Tettigoniidae: Phaneropterinae (katydids). Nymphs of both sexes are most commonly taken but sometimes in the case of the smaller prey species also adults of both sexes.

Species represented amongst the prey examined included the following: *Terpnistria zebra* (Serville) which is easily recognized by the highly characteristic saddle-shaped pronotum (Fig. 4), *Eurycorypha prasinata* Stal and two species of *Phaneroptera*. One cell of *I. stanleyi* was found to contain in addition to several Phaneropterinae two specimens (an adult male and a nymphal female) of *Oecanthus capensis* Saussure (Gryllidae: Oecanthinae), a tree cricket.

Provisioning by *I. pelopoeiformis* appears to be effected by the wasp's hunting whatever species are common in the immediate vicinity of the nest. Marked differences are consequently found in the composition of the prey used by this species in provisioning nests located in different plant communities. Thus 372 of a total of 377 prey katydids in 83 cells constructed in trap-nests suspended from *Acacia karroo* in thorn scrub were nymphs of *Terpnistria zebra* whereas only two of a total of 179 prey katydids in 37 cells constructed in trap-nests suspended from *Maytenus linearis* and *Rhus lancea* in the riverine bush were of this species. In the riverine bush

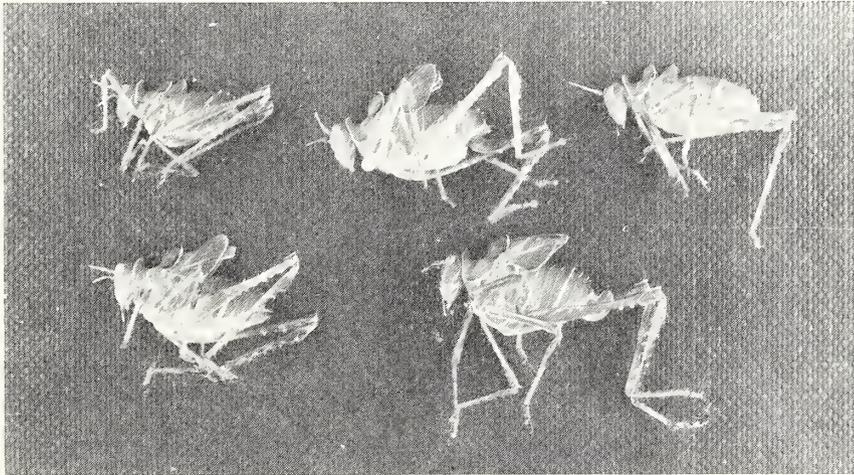


Fig. 4. Provision of a single cell of *I. pelopoeiformis*, 5 individuals of *Terpnistria zebra* all with antennae cut short. Middle prey of upper row bears the wasp's egg. ($\times 1,18$).

Eurycorypha prasinata (nymphs with one exception) and *Phaneroptera* species (nymphs and adults) constituted the prey commonly used for provisioning.

Provisioning by *I. stanleyi* in the riverine bush, where most of its nests were located, appeared to be with the same species as or similar species to those taken there by *I. pelopoeiformis*. However, *I. stanleyi* generally took smaller prey individuals than did *I. pelopoeiformis*.

Provisioning by *I. simoni* at Thursford was with small nymphs of *Phaneroptera* species.

DESCRIPTION OF THE NEST

The nests of *I. simoni*, *I. pelopoeiformis* and *I. stanleyi* consist of a number of serially arranged cells each sealed with a plug, the series frequently preceded by a preliminary plug and always succeeded by a closing plug which fills the space between the last cell and the nest entrance (Figs 5-8).

The materials from which the plugs are constructed are in each species of two types. In nests of *I. simoni* and *I. pelopoeiformis* the materials are "a", clods of earth with, in the case of *I. pelopoeiformis*, the addition of debris collected off the ground including pieces of stick, bark, vetch burs, insect remains and small mammal droppings, and "b", plant fluff. The preliminary plug in the nests of *I. simoni* is a thin layer of material "b" and where present in nests of *I. pelopoeiformis* is of either or both materials in distinct layers. The cell partitions in nests of *I. simoni* are constructed of materials "a" with an admixture of a little of material "b". However, those of *I. pelopoeiformis* are constructed almost exclusively from material "b". The closing plug in the single completed nest of *I. simoni* consisted of material "b" sealed at the ground surface with a thin layer of wet dung. The closing plugs of nests of *I. pelopoeiformis* are constructed in two distinct layers, the first of "a" and the second of "b". Exceptionally, when material "b" is in short supply lengths of very soft grass leaf blades are used as a substitute by *I. pelopoeiformis* in the construction of cell partitions. It may, however, be omitted from the nest closure.

The materials from which the plugs in nests of *I. stanleyi* are constructed are "c", short lengths of grass blades, and "d", longer lengths cut from grass inflorescences including lengths of unbranched culm and the branched portions including the flower heads. The cell partitions are constructed from material "c" transversely arranged, the preliminary plug and the inner part of the closing plug from material "d" transversely coiled and the outer part of the closing plug from material "d" arranged longitudinally, the stems lying parallel, and projecting from the nest entrance.

In order that the cells should be of adequate volume their lengths vary according to the diameter of the cavity used. The nests of *I. pelopoeiformis* and *I. stanleyi* in trap-nests were used for analysis. Due to there being a considerable variation in the lengths of the cell closures the lengths of the storage space of each cell was measured for comparison, not the length of the entire cell (Table 1). Cell length is dependent also upon the sex of the wasp that will develop within it. From Table 2 it can be seen that, in *I. pelopoeiformis* at least, cells which will cradle female wasps are larger than those which will cradle male wasps and that the diameter of the boring in the lower ranges becomes a limiting factor as only males are produced in 9.5 mm borings.

METHOD OF CONSTRUCTION OF THE NEST, PROVISIONING AND OVIPOSITION

Nesting activity is at its height at midday. Nest construction is initiated by the wasp's selecting a suitable pre-existing cavity and cleaning out any small pieces of debris. A preliminary plug may then be constructed at the inner end of the cavity, or in the case of the two trap-nesting species, some distance from it if some foreign object such as extensive spider-spinning obstructs the end. In a sample of 81 *I. pelopoeiformis* nests in trap-nests preliminary plugs were present in 60 and ranged in thickness from 1-36 mm and in a sample of eight *I. stanleyi* nests in

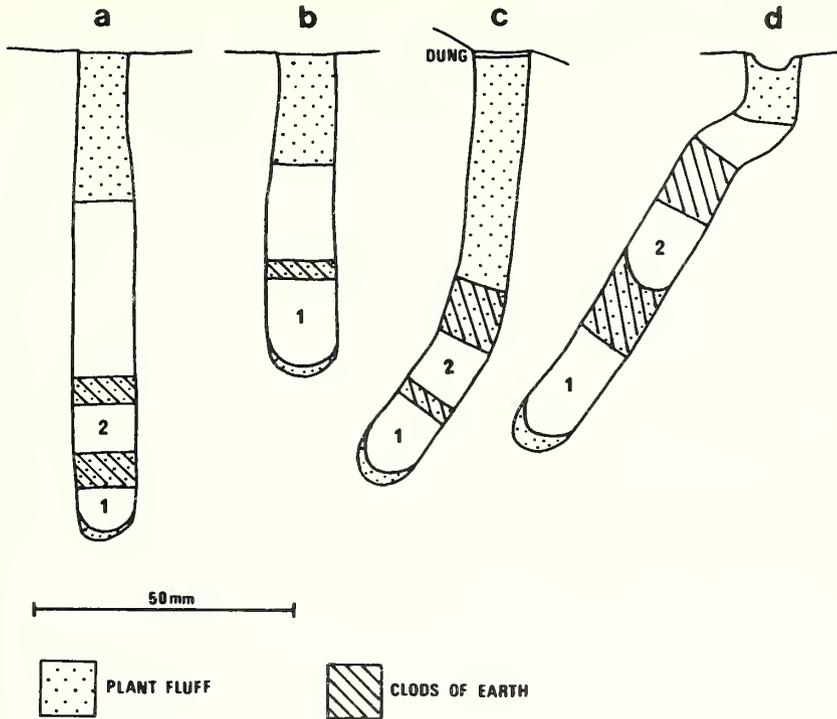
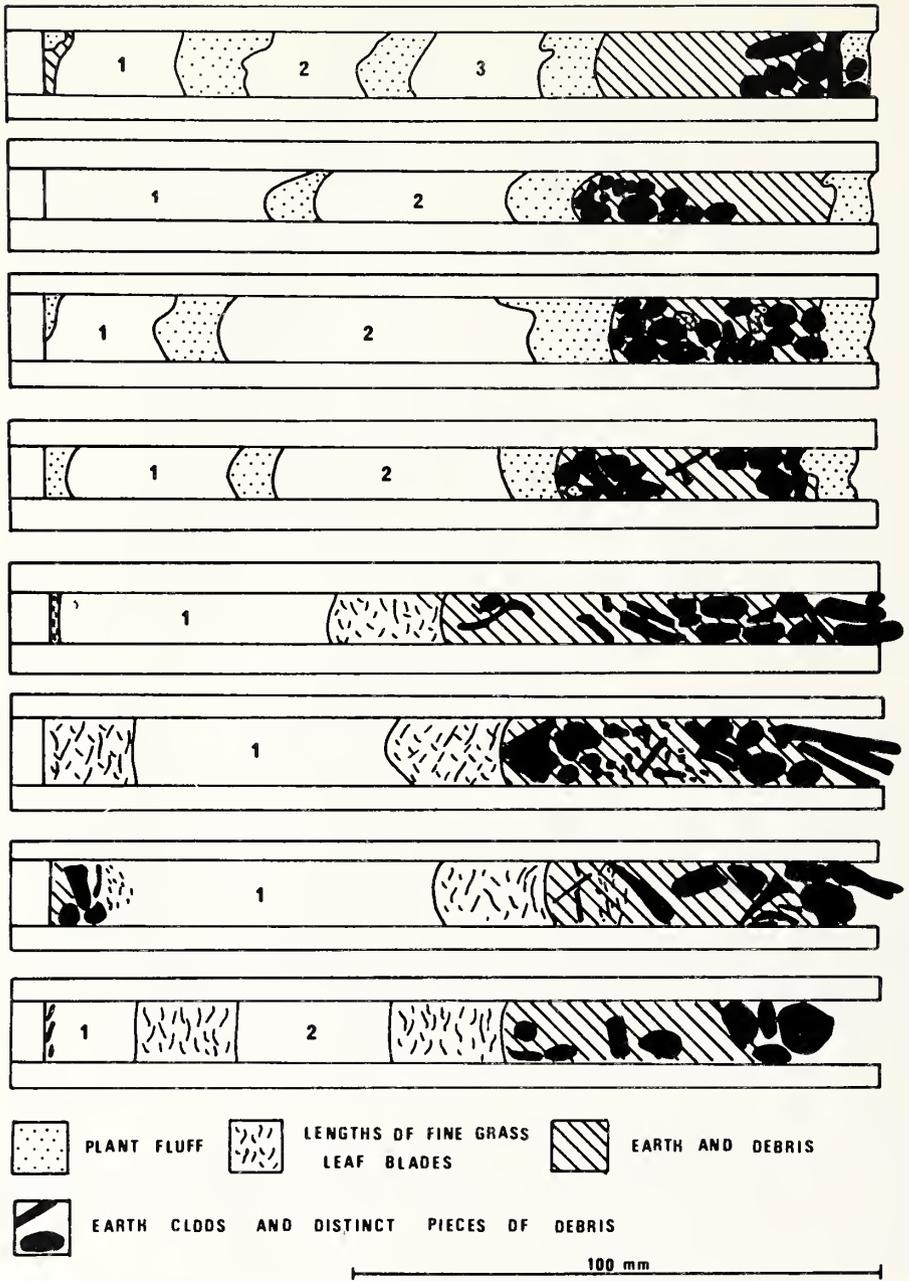


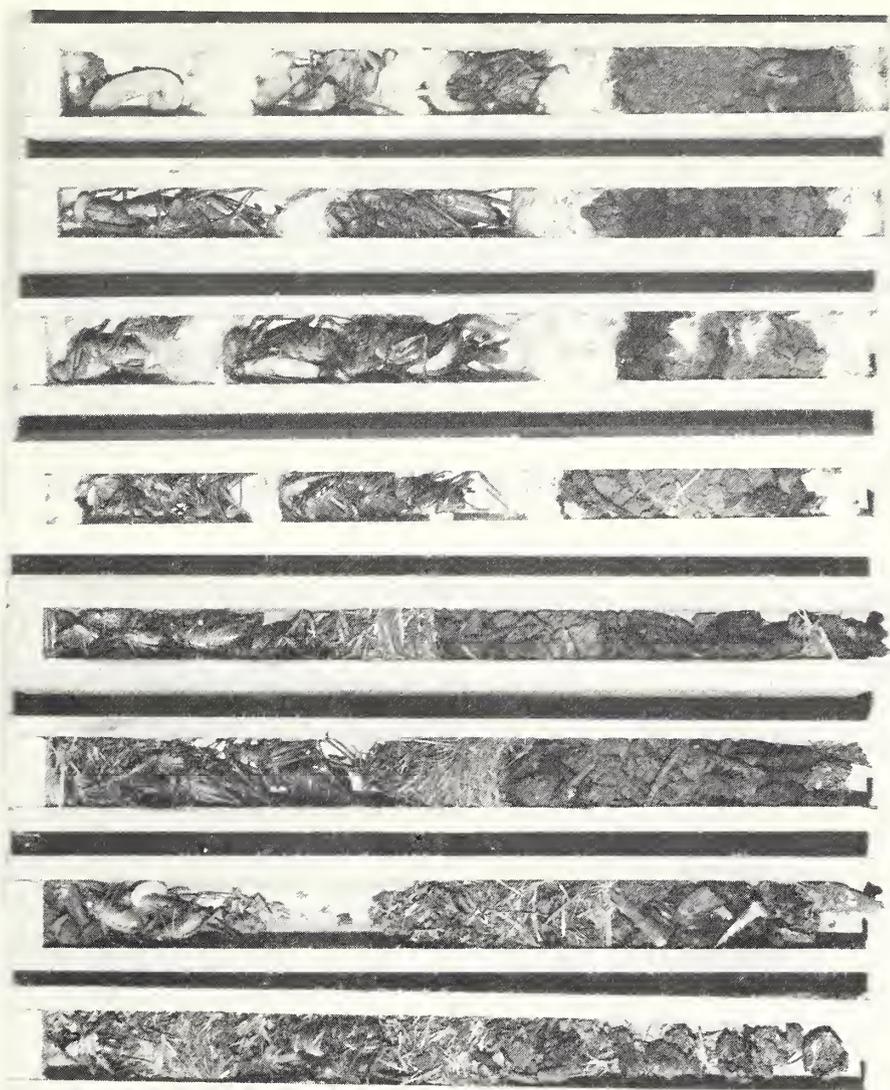
Fig. 5. Plans of four nests of *I. simoni*, a, b and d incomplete, c with final closure of dung.

trap-nests preliminary plugs were present in six and ranged in thickness from 1–32 mm. Material, be it fluff, debris or grass, for the construction of this and succeeding plugs is collected by the female with her mandibles and held by them is carried in flight by her to the nest. In all three species, whilst the nesting female is compacting the materials, buzzing sounds can be heard within the nest. Collecting of nesting materials from source by *I. pelopoeiformis* females was observed. They were gathering debris from the ground in close proximity to their nests and collecting fluff from inflorescence heads on which they alighted. Collection and positioning of material by this species is very rapid, each cycle of departure from the nest, collection of material, return to the nest and compaction of the material taking an average 1,3 minutes. The wasp usually pauses on the threshold of the nest entrance to groom her antennae before each excursion.

After the cavity has been prepared for the reception of the first prey, loosely packed material, fluff in the case of *I. simoni* and *I. pelopoeiformis* and grass in the case of *I. stanleyi*, is assembled at a distance between the nest entrance and the closed end of the cavity to form a temporary closure through which the wasp will pass on entering and leaving the cell during provisioning. Hunting is then commenced. A prey katydid is captured, subdued by stinging and its antennae are pruned. The wasp then holds it with her mandibles and legs and flies with it held beneath her, head forwards and dorsum uppermost. In the trap-nesting species it was observed that having arrived at the nest the wasp puts down the prey within the entrance, en-



Figs 6 and 7. Plans and photographs of eight completed nests of *I. pelopoeiformis* in trap-nests.



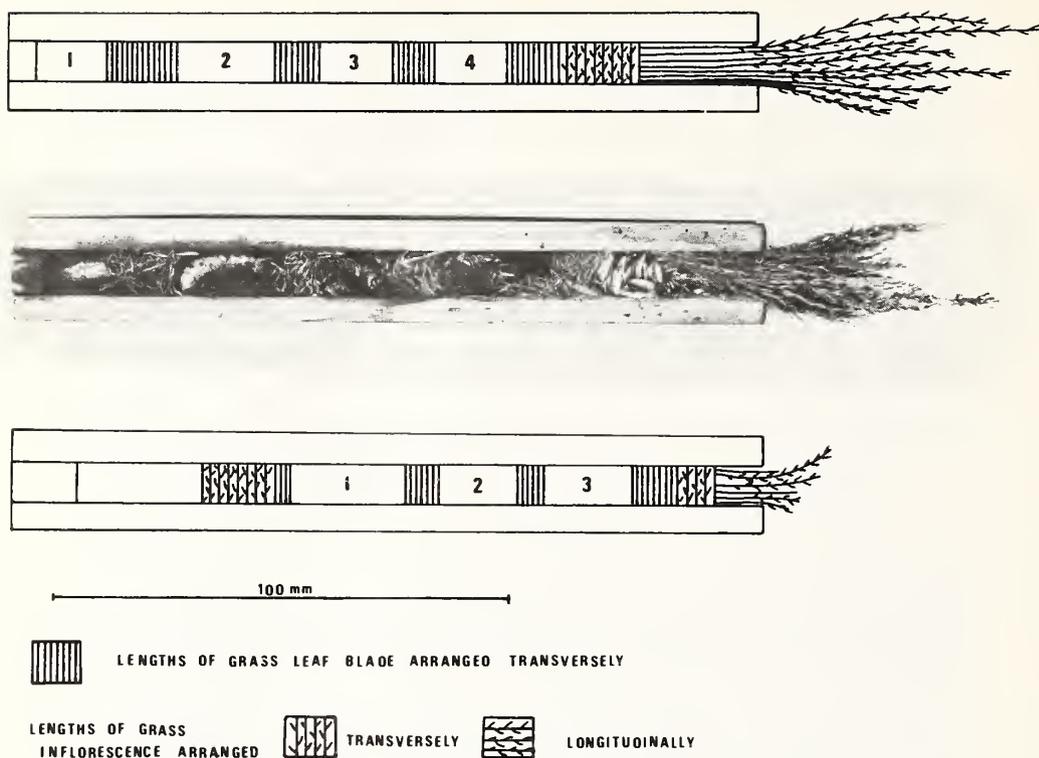


Fig. 8. Plan and photograph of one completed nest of *I. stanleyi* in a trap-nest and plan of a second.

ters, turns around and pulls the prey in towards her. She positions it in the cell so that it faces the inner end and lies either on its back or on one of its sides. She usually oviposits on this prey before leaving the nest to hunt for a second prey. If an egg is not laid on the first prey to be introduced into the cell, it will be laid on the second. In the four nests of *I. simoni* examined the prey were found to lie horizontally across the cells. Due to the smallness of the prey in relation to the diameter of the cell this was probably inevitable as it would only be possible to position larger prey vertically. It appeared that oviposition had been on one of the first prey.

The egg is yellowish and slightly curved in all three species. Dimensions are given in Table 3. In all three species the egg is cemented to the prey by its anterior end. It is positioned in front of the right or left mesothoracic coxa and lies transversely across the venter extending beyond it from the side away from the point of attachment.

The number of prey per fully provisioned cell is governed by the size of the prey and the total weight of provision required. Thus, if the prey are large a smaller number is required than if the prey are small. In Fig. 9 the numbers of prey per completed cell are plotted against frequency for 111 cells of *I. pelopoeiformis* in trap-nests. As the range in number of prey is from 1-10 and a peak is shown at 5 it is clear that an average sized prey is preferred but that when not available a single large prey may be taken or conversely at the other extreme ten very small prey. The prey taken by *I. simoni* and *I. stanleyi* were consistently smaller than

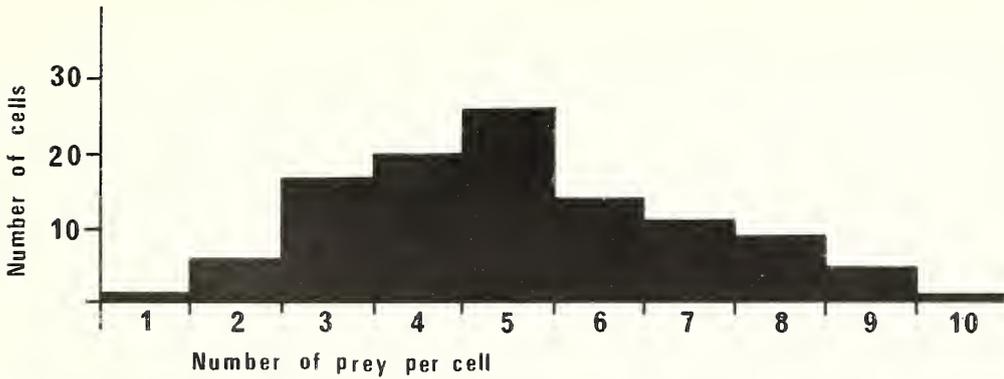


Fig. 9. Numbers of prey per completed cell plotted against frequency for 111 cells of *I. pelopoeiformis* in trap-nests.

those taken by *I. pelopoeiformis* and therefore, although these two wasps are smaller and consequently have a smaller prey requirement measured by weight the actual number of prey per cell tended to be larger than in cells of *I. pelopoeiformis* (Table 4).

The full provision for a cell having been supplied the wasp closes the cell. *I. simoni* seals the cell with compacted clods of earth mixed with a little fluff leaving the temporary closure intact. However, *I. pelopoeiformis* and *I. stanleyi* close their cells by compacting the material which formed the temporary closure and adding to this further material of the same nature. In these two species if a further cell is to be constructed, a new temporary closure is formed. The thickness of the cell closure varies. The range was 7–40 mm in a sample of 132 *I. pelopoeiformis* cells (63 per cent being between 10 and 20 mm), 1–32 mm in a sample of 7 *I. stanleyi* cells and 3–11 mm in a sample of 4 *I. simoni* cells. After the closure of the last cell has been completed the remaining space between it and the cavity entrance is filled by the construction of the closing plug. The length of the closing plug varies. The range was 26–100 mm in a sample of 77 nests of *I. pelopoeiformis*, 10–96 mm in a sample of 4 nests of *I. stanleyi* and 48 mm in a single sealed nest of *I. simoni*.

TABLE I.

Measurements of all sealed cells of *Isodontia pelopoeiformis* and of *Isodontia stanleyi* constructed within trap-nests, showing the relationship between length of cell lumen and boring diameter and how it differs between the two species.

Boring diameter (mm)	Cells constructed by <i>Isodontia pelopoeiformis</i>			Cells constructed by <i>Isodontia stanleyi</i>		
	No. of cells	Range in length of cell lumen (mm)	Average length of cell lumen (mm)	No. of cells	Range in length of cell lumen (mm)	Average length of cell lumen (mm)
9,5	47	28–67	40	3	18–26	21
12,7	89	10–62	31	13	8–30	18

TABLE 2.

Measurements of sealed cells of *Isodontia pelopoeiformis* constructed within trap-nests and from which wasps were reared, showing the relationship between length of cell lumen, boring diameter and the sex of the wasp for which the cell was constructed.

Boring diameter (mm)	Cells from which male wasps were reared			Cells from which female wasps were reared		
	No. of cells	Range in length of cell lumen (mm)	Average length of cell lumen (mm)	No. of cells	Range in length of cell lumen (mm)	Average length of cell lumen (mm)
9,5	38	28-60	40	0	—	—
12,7	30	10-58	29	29	20-55	36

TABLE 3.

Dimensions of the eggs of the three *Isodontia* species.

<i>Isodontia</i> sp.	Dimensions of eggs		
	Average length (mm)	Average diameter (mm)	Size of sample
<i>simoni</i>	3,61	0,88	3
<i>pelopoeiformis</i>	4,01	0,94	12
<i>stanleyi</i>	4,0	0,87	1

LIFE HISTORY

The life history of *I. pelopoeiformis* has been described in detail by Smithers (1955). Stages in the development from egg to fully developed larva are shown in Fig. 10. In the present study hatching of the larva of this species was found to take place from two to four days after oviposition with most larvae hatching after three days. From four to eight days were taken by the larva to consume the cell's provision and to reach the full-grown state. The outer loosely woven cocoon of yellow silk was completed within a day after the cessation of feeding and the inner cocoon of mahogany to black parchment-like material was completed within a further one or two days. The total length of time from oviposition to the construction of the inner cocoon by the full grown larva therefore ranged from eight to fifteen days. The scant data for *I. stanleyi* indicated similar times for this species. No data are available for *I. simoni*.

TABLE 4.
 Number and weight of prey making up the provision of completed *Isodontia* cells, and weights of adult female wasps.

<i>Isodontia</i> sp.	No. of prey in completed cells		Weight of provision of a single completed cell		Weight of ♀ wasp.	
	Sample size (= no. of cells)	Range	Sample size (= no. of cells)	Range (mg)	Sample size (= no. of ♀♀)	Range (mg)
<i>simoni</i>	7	5-12	6	154-602	3	84-107
<i>pelopoeiformis</i>	111	1-10	6	338-1431	1	—
<i>stanleyi</i>	11	7-19	—	—	1	—
						86

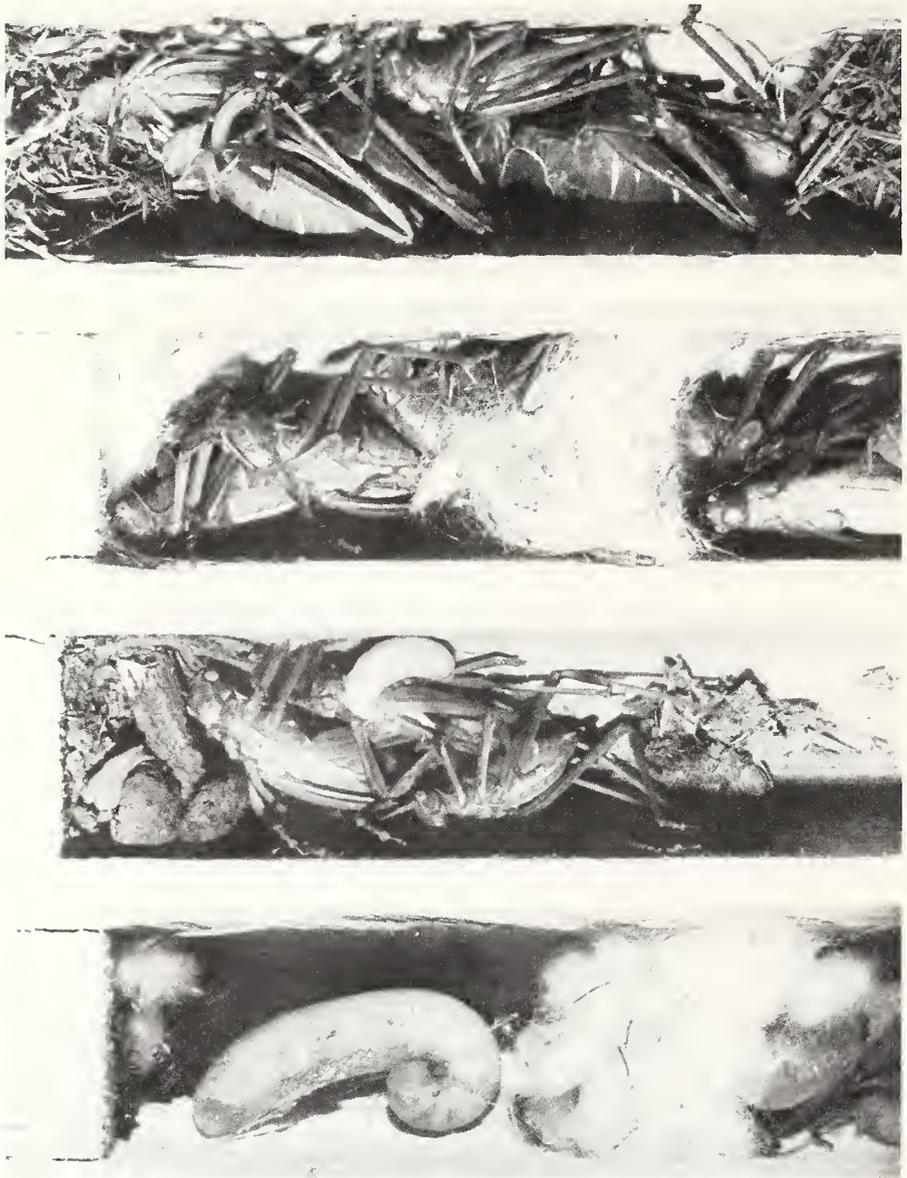


Fig. 10. Stages in development of *I. pelopoeiformis* from egg to fully developed larva ($\times 2,2$).

Development periods, from oviposition to emergence of the adult, were calculated for a total of 45 males and 12 females of *I. pelopoeiformis* reared from trap-nests taken from the field when completed and thereafter kept indoors at room temperature. Wasps developing from eggs laid during the period from late December through to February of one summer season emerged as adults during the period from January to March of the following summer season. Developmental periods of 321–407 days (average 365 days) were recorded for males and 351–431 days (average 401 days) were recorded for females. From these figures, unsatisfactory as they are (see below), it is apparent that *I. pelopoeiformis* is univoltine under the climatic conditions prevailing in the Eastern Cape Province. This conclusion is supported by the relatively short flight season observed for this species in the field. The greater part of the year, including the winter months, is therefore spent in a state of prepupal diapause. This situation is different from that reported by Smithers (1958) for *I. pelopoeiformis* in Southern Rhodesia (now Zimbabwe) where the species was found to be bivoltine at least.

As *I. pelopoeiformis* in the field flies and nests during the same weeks each summer, it is clear that under natural conditions the development period from oviposition to adult emergence must be considerably shorter than 365 days to allow for the length of the pre-oviposition and pre-nesting period and for at least part of the length of the nesting period itself. The development periods obtained during the present study are therefore unnaturally long and must be ascribed to the fact that the trap-nests containing the developing wasps were kept indoors and were therefore not subjected to the temperature and humidity conditions prevailing in the field. The figures nevertheless show that the developmental period for males is shorter than that for females. This is confirmed by the proterandry observed in the field.

When handled, newly emerged specimens of *I. pelopoeiformis*, both males and females, have a very strong odour, somewhat akin to that of guava fruits or to that of the leaves of some *Eucalyptus* species.

SEQUENCE OF SEXES IN NESTS

Certain species of aculeates which construct serially arranged cells within pre-existing cavities commonly show a fixed sequence of sexes in nests in which both males and females develop. This has been shown by Krombein (1967: 29) for species of Vespidae and some Megachilidae in which females develop in cells at the inner or blind end of the cavity and males in cells at the outer or open end. To establish whether this is true also of *I. pelopoeiformis*, an analysis of completed nests constructed within 12.7 mm trap-nests and from which at least some wasps were reared was undertaken (Table 5).

Of the 33 nests analysed, seven were one-celled and therefore yielded no information concerning the correlation between the position of a cell within the nest and the sex of the wasp produced within that cell. Of the 26 two- and three-celled nests half included cells in which the wasp egg had not hatched or in which the larva died before spinning its cocoon. In the remaining 13 nests, all larvae had developed at least to the cocoon-spinning stage and 21 of the 31 cells had yielded adult wasps which were available for sexing. Notwithstanding the failure of the 10 other wasps to develop beyond the cocoon-spinning stage, these individuals were also available for sexing by virtue of the difference in length between the inner cocoons of males (21–24 mm) and of females (27–29 mm).

Six nests each produced wasps of one sex only, 3 two-celled nests producing only females and 1 two-celled nest and 2 three-celled nests producing only males. Seven nests, 4 two-celled and 3 three-celled produced wasps of both sexes. In these, the females had without exception developed within cells constructed and provisioned before those from which males developed. Female-producing cells were therefore sited towards the inner or blind end of the trap-nest and male-producing cells towards the outer or open end of the trap-nest. Though incomplete, the data from the 13 nests in which only some wasps had reached the cocoon-spinning stage shows

TABLE 5.

Analysis of completed *I. pelopoeiformis* nests constructed within trap-nests having a boring diameter of 12,7 mm and from which at least some wasps were reared. The correlation between the position of a cell within the nest and the sex of the wasp produced within that cell is shown for two- and three-celled nests. Number of nests = 33; number of cells = 68; number of sexed wasps = 53.

Nature of nest	Cells in positional order and sex of wasp produced within each			Frequency within sample
	Cell 1	Cell 2	Cell 3	
One-celled	♀	—	—	2
	♂	—	—	5
Two-celled	♀	♀	—	3
	♀	♂	—	4
	♀	?	—	6
	?	♂	—	3
	♂	♂	—	1
Three-celled	♀	♀	♀	0
	♀	♀	♂	1
	?	♀	♂	1
	♀	?	♂	1
	♀	♂	♂	2
	♀	?	?	1
	?	♂	?	1
	♂	♂	♂	2

the same trends and are in no instances contradictory. It follows from the above that, if the first cell in a nest is male-producing, all subsequent cells constructed within that nest by the female will also be male-producing.

CANNIBALISM

Four of the 132 cells of *I. pelopoeiformis* examined were found to contain not one egg-bearing katydid but two. In their dimensions and provisioning these cells were not unusual: all were in 12,7 mm trap-nests, cell lumens ranged in length from 32–59 mm, and the number of prey ranged from 4–8. In the 59 mm long cell, however, the arrangement of the prey was atypical in that the katydids were divided into two distinct groups of four each as if belonging to separate cells from which the dividing partition had been omitted. One katydid of both groups bore an egg.

In one of the four cells the first-laid egg was not viable. In the remaining three cells (including the cell with two groups of prey) the first-laid egg, identified as such by the position within the cell of the katydid to which it was cemented, hatched before the second-laid egg. In two instances hatchings were separated by one day and in the third instance by three days. The two larvae co-existed in the cells for as long as the older larva was feeding on its first katydid—

that is, the katydid to which the egg had been cemented. However, after leaving this prey and before starting to feed on a second katydid the older larva in all three instances located the younger larva and ate it. Thereafter the older larva proceeded to feed on the katydid with which the younger larva had been associated. It would appear that a larva having devoured its first katydid actively seeks out any conspecific larva in the cell for in all three instances, and in the cell with the divided provision in particular, the larvae were well separated spatially.

PARASITES AND OTHER ASSOCIATED INSECTS

Parasitic and other associated insects were recorded from the nests of *I. pelopoeiformis* only. Undoubtedly this was due to the fact that the number of nests of this species that was available for examination was far greater than that of the other two species. Nine of the 85 nests (10.6 per cent) were affected.

Most common and affecting six completed and sealed nests was an unidentified species of scavenger fly (Sarcophagidae: Miltogramminae). The cleptoparasitic maggots, up to 17 per nest, developed on the provision stored in the cells and in multicellular nests generally moved from one cell to the next thus destroying the contents of all. In one three-celled nest, however, only the second and third cells were affected, the first in time yielding a wasp. Developmental periods were short, the larvae feeding for about a week after which they pupated in or near the nest closure. The adult flies emerged from the puparia after about a further fifteen days.

Also cleptoparasitic was a species of Chrysididae affecting one nest. Four adults were reared, the development time, from oviposition to emergence of the adult, being about 325 days.

Two nests were invaded and robbed by small black ants of the genus *Crematogaster*.

SHELTERING AND SLEEPING HABITS OF ADULT WASPS

During the period of nest construction, when nesting activities had ceased for the day and during unfavourable weather, females of *I. stanleyi* utilizing trap-nests were frequently found sheltering in a temporary closure of an incomplete nest or between such a closure and the trap-nest entrance. However, despite the far greater number of nests of *I. pelopoeiformis* obtained in trap-nests, females of this species were never found sheltering in nests and would therefore appear to shelter elsewhere. No information on this facet of behaviour is available for *I. simoni* females nor for males of any of the three species.

DISCUSSION

Some aspects of the nesting of 14 of the 54 species of *Isodontia* recognized by Bohart and Menke (1976) have been published to date. Grouped by zoogeographical region, the 14 species and the publications relevant to each are:

AFROTROPICAL REGION—*I. pelopoeiformis* (Dahlbom) (Smithers, 1958; Heinrich, 1969; Gess, 1981) and *I. stanleyi* (Kohl) (Gess, 1981);

NEARCTIC REGION—*I. auripes* (Fernald) (Packard, 1869; Rau and Rau, 1918; Rau, 1926 and 1928; Krombein, 1967 and 1970), *I. elegans* (Smith) (Ashmead, 1894; Davidson, 1899; Fernald, 1906; Ainslie, 1924; Bohart and Menke, 1963; Parker and Bohart, 1966; Krombein, 1967), *I. exornata* Fernald (Bequaert, 1930), *I. mexicana* (Saussure) (often under the name *harrisi* Fernald) (Ashmead, 1895; Hubbard, 1896; Jones, 1904; Engelhardt, 1929; Rau, 1935 and 1943; Suehiro, 1937; Swezey, 1947; Lin, 1962 and 1966; Medler, 1965; Krombein, 1967) and *I. philadelphica* (Lepeletier) (Bohart and Menke, 1963; Krombein, 1967);

NEOTROPICAL REGION—*I. costipennis* (Spinola) (Mayer and Schulthess, 1923; Bristowe, 1925; Richards, 1937) and *I. paranensis* (Berland) (Berland, 1929);

PALAEARCTIC REGION—*I. harmandi* (Pérez) (Tsuneki, 1963 and 1964), *I. maidli* (Yasumatsu) (Tsuneki, 1957, 1963 and 1964), *I. nigella* (Smith) (Piel, 1933; Tsuneki, 1963 and 1964), *I.*

paludosa (Rossi) (De Stefani, 1896 and 1901; Rudow, 1912; Berland, 1929 and 1959) and *I. splendidula* (A. Costa) (Nicolas, 1894; Berland, 1929).

In addition to the zoogeographic distributions given above, *I. nigella* occurs in the Oriental and Australian Regions and *I. mexicana* in Central America. The latter has also become established in Hawaii and France.

Characteristic of all the above species is that nesting takes place in pre-existing cavities situated above ground level. The actual height above the ground appears to be immaterial as is evidenced by the positional range given above for trap-nests utilized by two species at Hilton. Most frequently the records concern the use of cavities associated with plants, less frequently with vertical banks and their man-made counterpart, walls.

Records pertaining to nesting in association with plants may be divided into three broad categories. The first category concerns nests made within tubes formed by leaves—*I. costipennis* in a curled-up leaf, *I. mexicana* in folded dead leaves of yucca, in the open-ended tube-like leaves of pitcher plants (*Sarracenia* spp.) and in the exposed hollow mid-ribs of dead fronds of *Pandanus* palms, and *I. nigella* in a holed leaf of *Allium*.

The second category concerns nests made in hollow stems the ends of which have been broken off or in which holes have been made by other animals. Records include the use of stems of dicotyledonous plants such as white sage by *I. elegans*, thistles by *I. paranensis* and probably an umbellifer by *I. exornata*. However, of greater frequency are records concerning the use of culms of robust perennial Gramineae such as *Arundo donax* by *I. splendidula*, *Phragmites australis* by *I. stanleyi* and in particular bamboo by *I. costipennis*, *I. elegans*, *I. harmandi*, *I. mexicana* and *I. nigella*. Most records for bamboo pertain to culms which have been cut and incorporated into man-made structures.

The third category concerns nests constructed in pithy of woody stems (including timber) within abandoned nesting galleries of *Xylocopa* species by *I. auripes*, *I. mexicana* and *I. stanleyi*, and in old borings of cerambycid larvae by *I. auripes*, *I. harmandi*, *I. maidli*, *I. nigella* and *I. stanleyi*. *I. philadelphica* is recorded from borings of unspecified origin.

Records pertaining to nesting within vertical clayey banks concern the use of the abandoned burrows of mining bees, those of *Anthophora* and *Melitoma* species by *I. auripes* and those of the former only by *I. elegans*. *I. paludosa* is recorded nesting in a cavity in a stone wall.

In view of the variety of naturally occurring pre-existing cavities utilized by the wasps it is not surprising that no fewer than eight species have been recorded as accepting trap-nests of various designs; similarly that records exist of bizarre nesting situations such as the metal tubes of laboratory gas burners chosen by *I. nigella* (Iwata, 1976: 206) and the shot-gun barrel and bicycle handle bars used by *I. pelopoeiformis* (Heinrich, 1969: 113 and present authors, respectively).

With regard to wasps and bees which do not excavate or hollow out their nests themselves but modify pre-existing cavities, a recent community study at Hilton (Gess, 1981) showed that at least some species are shared between vertical banks and plant tissue. This finding is believed to be of general application and appears relevant with respect to the above reviewed *Isodontia* species. These appear to exhibit little specificity with regard to the nature of the pre-existing cavities chosen for nesting provided these cavities are situated above the ground level. For example, individuals of a single population of *I. auripes* in Missouri were recorded by Rau (1926: 200) as utilizing both the abandoned galleries of carpenter bees in the wooden rafters of a porch above a clay bank and the old burrows of mining bees in the clay bank itself. All the nesting situations listed in the above review may therefore be considered to be homologous as to type and it may be expected that any one species would, given the opportunity, nest in the situations recorded for any of the others.

The nesting of *I. simoni* as described for the first time in the present publication is of con-

siderable interest in that the pre-existing cavities used by this species are situated in level (that is, horizontal) ground, a nesting situation hitherto unknown for any *Isodontia* species. Level ground as a nesting situation does not represent merely yet another site to be added to those listed above but rather represents one that is fundamentally different. This is indicated by the finding in the already mentioned community study that the difference in the angle of presentation of a soil surface, vertical as opposed to horizontal, has a very profound influence on the nesting of wasps and bees. In the community studied it was found that, with the possible exception of one species (*Pison allonymum*), there was no sharing of species between level ground and vertical banks and that indeed both nesting situations are characterized by communities of species unique to themselves. Nesting in pre-existing cavities in level ground must therefore be considered to be characteristic for *I. simoni* and it is highly unlikely that the species will ever be found nesting elsewhere. Certainly at Hilton it was very striking and, before the nesting site was established, indeed puzzling that, in contrast to *I. pelopoeiformis* and *I. stanleyi*, *I. simoni* was never found to utilize trap-nests suspended in bushes and trees.

In their discussion of the tribe Sphecini Bohart and Menke (1976: 106–108) pointed out that most wasps in this tribe are fossorial and that the genus *Isodontia* (as also *Chilosphex*) which nests in pre-existing cavities is presumed to have evolved from fossorial forms. Similarly, Tsuneki (1963: 71) is of the view that burrow- or tube-renters like *Isodontia* are more advanced than burrowing species like *Sphex*. In order to derive the nesting typical of the majority of *Isodontia* species from that of the fossorial type as exhibited by species of *Sphex* the following evolutionary stages in nesting behaviour may be postulated:

Digging of burrow in friable soil of horizontal aspect.	→	Use of pre-existing burrow (or other cavity) in preferably non-friable soil of horizontal aspect.	→	Use of pre-existing burrow (or other cavity) in a vertical bank.	→	Use of a pre-exist- ing burrow (or other cavity) asso- ciated with plants.
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Within this evolutionary sequence the nesting of *I. simoni* clearly belongs to the second step whereas that of all the other species here reviewed belongs to the third and fourth steps. On this basis the nesting of *I. simoni* must be seen as being more primitive than that of the other species.

In view of the suggested primitiveness of the nesting of *I. simoni* it is of interest that Bohart and Menke (1976: 120 and 121) list this species, together with *I. pelopoeiformis* and two other species for which details of nesting are lacking, as among the least specialized, structurally primitive species.

A structural character used by the above authors in assessing the degree of specialization of various species is the form of the female mandibular apex. They point out that there is a progression from the bidentate (primitive) to the tridentate (specialized) condition.

As the form of the mandibular apex is determined by function it is relevant to examine the identity of the nesting materials that are manipulated by the mandibles during their collection, transport and incorporation into the structure of the nest. From the relatively scant data available it would appear that the use of grass leaf blades and grass inflorescences is typical of those species with trifid mandibles, such as *I. auripes*, *I. elegans*, *I. mexicana*, *I. nigella*, *I. splendida* and *I. stanleyi*, though the first three of these species as also *I. hermandi* are known to use also bark fibres. Moss is in addition used by *I. hermandi* and *I. maidli*.

Plant fluff from the fruits of Compositae and Asclepiadaceae on the other hand is collected by those species with bifid mandibles such as *I. simoni* and *I. pelopoeiformis* though the latter is known very occasionally and exceptionally to use also very soft grass leaf blades, probably when pappus is not available. With respect to *I. paludosa* which is recorded as using both

thistle pappus and grass inflorescences it is perhaps significant that the form of the mandibular apex is described by Bohart and Menke (1976: 120) as being more nearly bidentate than tridentate and as illustrating the intermediate state. Recorded nesting materials of *I. costipennis* are similarly asclepiadaceous or apocynaceous seed hairs: it would seem likely that this species has a bifid mandible but this could not be confirmed.

On the basis of the correlation between the form of the mandibular apex and the nature of the plant-derived nesting materials it is apparent that the use of plant fluff is primitive and the use of grass is advanced. The primitiveness of the nesting of *I. simoni* suggested by the situation of its nest is therefore confirmed by the nature of the plant material used for nest construction.

If, as is suggested, the nesting of *Isodontia* is to be derived from the fossorial type as exhibited by *Sphex*, then the use of clods of earth by the ground-nesting *I. simoni* is hardly surprising and is clearly more primitive than its use of plant fluff. Similarly, the retention as nesting materials by *I. pelopoeiformis* of clods of earth and the use of other objects picked up off the ground can be seen as relict behaviour carried over from the original nesting site, a pre-existing cavity in the ground, to the derived nesting site, a pre-existing cavity raised above the ground.

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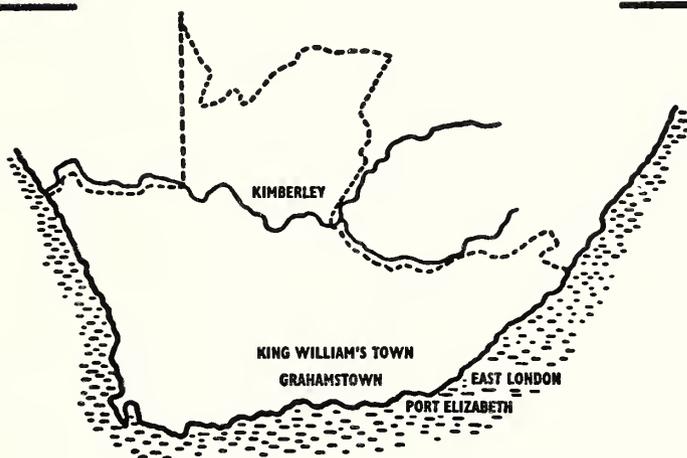
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**Historical atlas of the diurnal raptors of the Cape Province (Aves:
Falconiformes)**

by

A. F. BOSHOFF

(The Lakes Nature Conservation Station, Private Bag X6546, George, 6530)

C. J. VERNON

(East London Museum, 319 Oxford Street, East London, 5201)

and

R. K. BROOKE

(Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch,
7700)

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ABSTRACT

Maps showing the past and present (1970s) distribution of 55 taxa of breeding and non-breeding diurnal raptor occurring in the Cape Province, South Africa, are presented. The com-

pilation of the maps is such that any major range fluctuations which have taken place on a temporal basis are indicated. Almost a quarter of the taxa show a decrease, most show no change and only two indicate an increase. The value of this information for long-term monitoring studies and for conservation purposes is mentioned. The limitations of the survey are discussed.

UITTREKSEL

Kaarte word vertoon wat die vorige en huidige (1970s) verspreiding van 55 soorte telende en nie-telende dags-aktiewe (diurnal) roofvoëls wat in die Kaapprovinsie, Suid-Afrika, voorkom, aandui. Die samestelling van die kaarte is sulks dat enige grootskaalse gebiedsveranderinge wat oor 'n tydperk plaasgevind het, aangedui word. Ongeveer 'n kwart van die soorte toon 'n afname, die meeste wys geen verandering en slegs twee het toegeneem. Die waarde van hierdie inligting vir lang-termyn monitorstudies en vir bewaringsdoeleindes word genoem. Die beperkings van die opname word bespreek.

INTRODUCTION

This paper documents the past and present distribution and status of the breeding and non-breeding diurnal raptors, all members of the Falconiformes, of the Cape Province. In terms of the conservation requirements of the breeding birds of any area, it is necessary to define and monitor their status. As a group raptors require detailed study as they are located at the ends of various food chains and reflect major fluctuations taking place along such chains. Thus they are considered to be reliable indicators of the state of the environment. There is little doubt that the various agricultural practices employed throughout the Cape Province (and elsewhere in southern Africa) have greatly altered the habitat and that this must have a marked effect on raptor populations. Due to their predatory and, in the case of vultures, carrion eating habits, raptors suffer as a result of various forms of indirect persecution, e.g. poisoning and trapping for jackals, *Canis mesomelas*, and other mammalian "vermin". Whereas pesticide levels appear to be low in southern African raptor populations, mortality caused by electrocution is a recent and increasing factor. In addition many raptors are accused of causing death and damage to domestic livestock and poultry and as a result are directly persecuted by farmers.

Whereas certain species may be able to adapt to these changes, *viz.* the "generalists", others have become extinct or face extinction, *viz.* the "specialists". Some of the changes that have already taken place in raptor populations in the eastern Cape Province have been described by Skead (1967) and Vernon (1978). A further indication of their parlous conservation state is the relatively large number of raptors included in the *South African Red Data Book: Aves* (Siegfried *et al.* 1976).

It is hoped that an overall broad-based survey will allow for the ranking of the raptors of the Cape Province in terms of priority for detailed research and conservation action. In particular the survey was seen as an attempt to update the two most frequently used works which present distribution maps for the diurnal raptors of the Cape Province, *viz.* McLachlan & Liversidge (1978) and Snow (1978).

One way of determining the dynamic status of a taxon is to monitor its distribution (= range). Here two categories could be applied. Firstly those with a drastically reduced range and therefore also a reduced total population. This situation can be caused by both direct and indirect persecution and in terms of conservation species in this category provide the most cause for concern. Secondly there are those taxa with an unchanged or slightly reduced range but with a reduced total population. This situation can be caused mainly by direct persecution although indirect persecution remains an important factor. In the cases where there is no reduction in range and where population levels have remained stable there is little cause for concern at present. In other words, it is the authors' contention that an unaltered range may rep-

resent a relatively stable population whereas a marked decrease in range may represent a real decrease in numbers. Whereas it may be possible to obtain some idea of distributional changes for certain taxa, it is virtually impossible to make any detailed statement on changes in population levels because of the lack of data.

SURVEY METHODS

All available published and unpublished sources containing references to raptors in the Cape Province were consulted, records were extracted and entered into the computer databank scheme outlined by Boshoff *et al.* (1978). Where possible the following information was coded: taxon, locality, date, relative and actual abundance, sex, age and breeding data. Attempts were made to ensure the accuracy of the contents of the databank, but it became clear that many records, from both published and unpublished sources, were suspect. Where possible records were awarded a "reliability" category (cf. Boshoff *et al. op cit.*) but in many cases this was not possible. In the event of an obvious error the record concerned was rejected; often this was not easy and some subjective decisions were made. Taxa which had 50 or fewer records for the entire 1700 – 1979 period were particularly carefully scrutinised. Maps were prepared with symbols indicating presence per locus (= one "quarter-degree square").

On a map one symbol per locus may represent one or more records for the particular locus. Where several records were made for one species in one locus for one period this has been

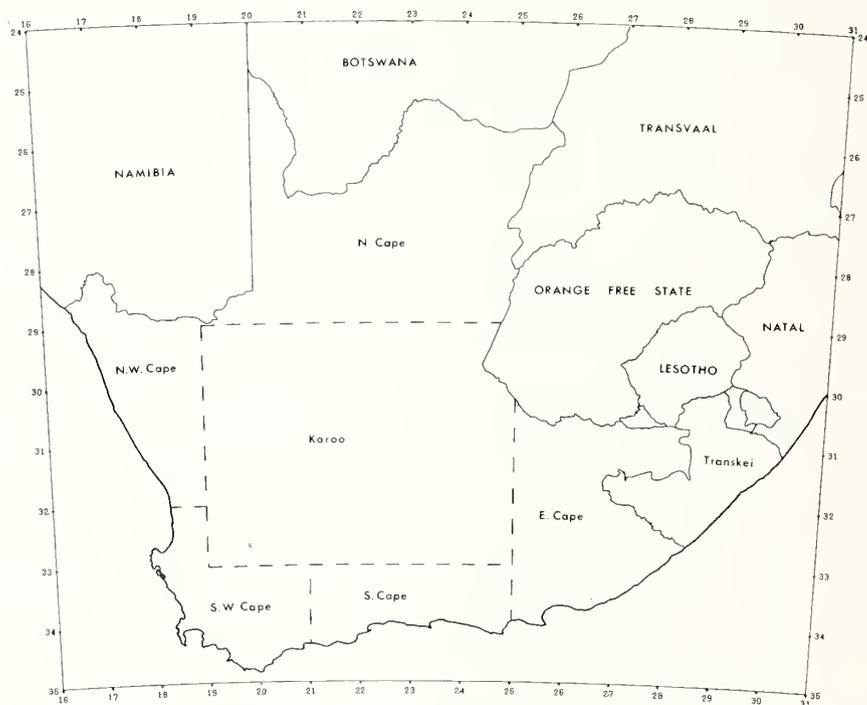


Fig. 1. The Cape Province of South Africa, showing the various regions referred to in the text, and the Transkei.

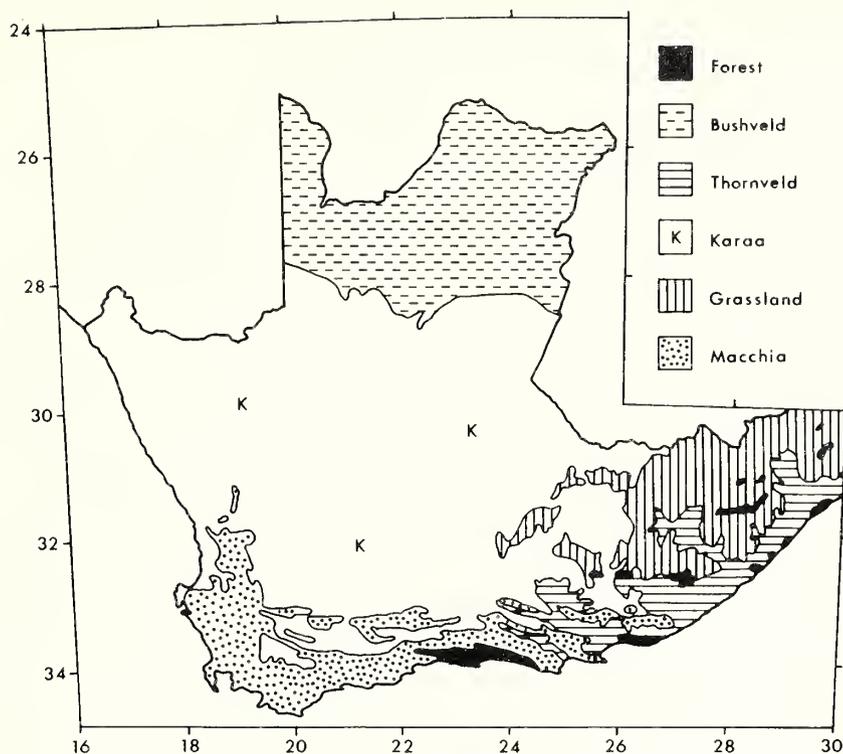


Fig. 2. Broad vegetation categories of the Cape Province, adapted from Acocks (1975) (see text).

taken as a single observation. The term “resident”, as used in this paper, refers to a taxon living and breeding in the Province, however, confusion is possible where a taxon is not sedentary but undergoes local migration or is nomadic. Degree of abundance has been limited to three subjective categories, *viz.* “common”, “scarce” and “rare”.

The general regions of the Cape Province referred to in the text, *viz.* E. Cape, N. Cape, N.W. Cape, S. Cape, S.W. Cape and Karoo, are outlined in Fig. 1. These regions were named for convenience and coincide approximately with the major vegetation types of the Province (Fig. 2). In Fig. 2 the broad veld types shown incorporate the following veld types, as described by Acocks (1975):

Forest	Nos 1, 2, 4
Thornveld	Nos 7, 21, 22, 23
Bushveld	Nos 16, 17
Macchia	Nos 47, 69, 70
Karoo	Nos 24 to 43
Grassland	Nos 44, 48, 50, 59, 60

Although no fieldwork has been carried out by the Cape Department of Nature and Environmental Conservation in the Transkei since independence was granted to that territory in

1976, all available data from that area, as well as from the Ciskei and Bophuthatswana, have been included in the databank. This was done because much of the early ornithological work was carried out in the Transkei, then part of the Cape Province.

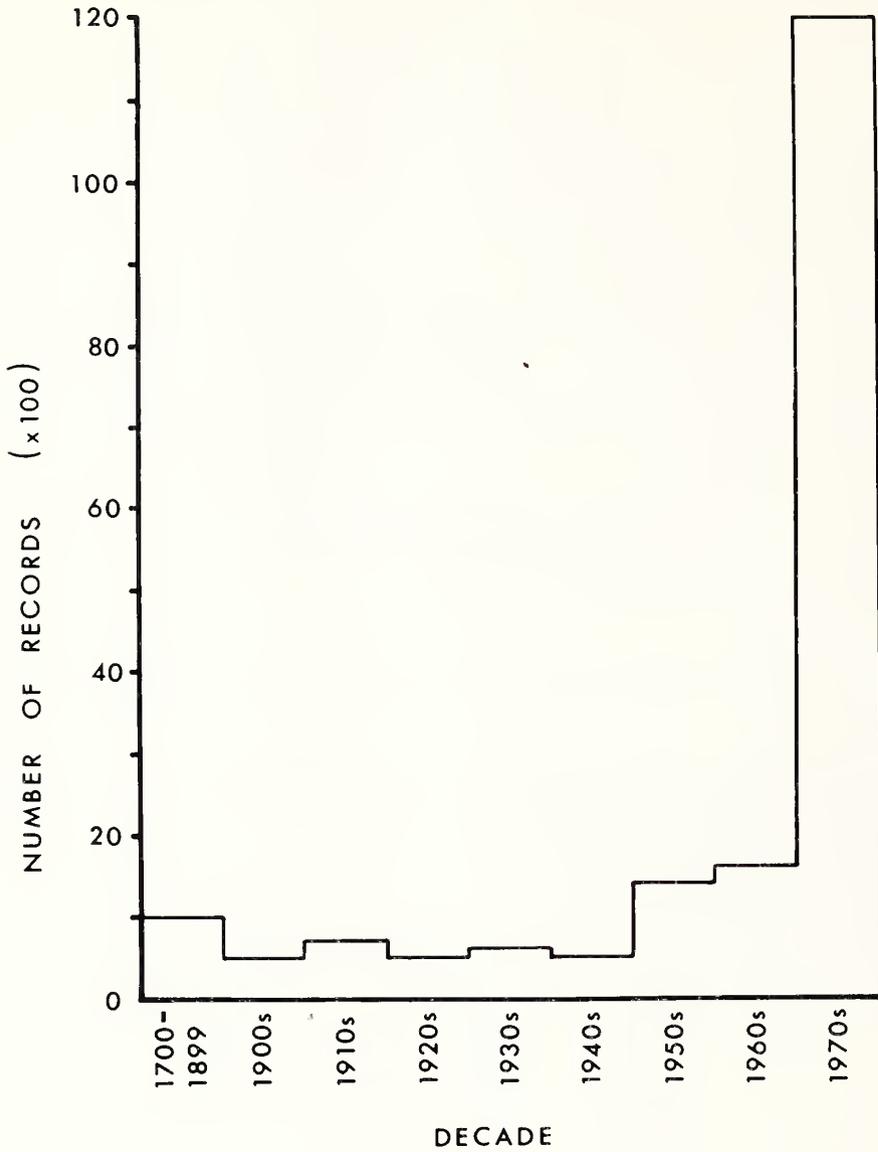


Fig. 3. The number of published and unpublished raptor records (to nearest 100) for the Cape Province and Transkei, per decade, up to 1979. 1700 - 1899 taken as one decade.

BOSHOFF ET AL.: HISTORICAL ATLAS OF DIURNAL RAPTORS (AVES: FALCONIFORMES)

TABLE 1

The number of published and unpublished records of species of diurnal raptor per decade in the Cape Province and Transkei up to the 1970s. 1700 – 1899 taken as one decade.

Species	Number of records per decade									Total
	1700 – 1899	1900 – 1909	1910 – 1919	1920 – 1929	1930 – 1939	1940 – 1949	1950 – 1959	1960 – 1969	1970 – 1979	
Secretary Bird	36	16	33	18	25	19	71	60	351	629
Palmnut Vulture	—	—	—	—	2	1	1	3	2	9
Lammergeyer	22	7	4	6	3	4	15	64	53	178
Egyptian Vulture	29	2	2	2	1	1	3	2	4	46
Hooded Vulture	3	1	—	1	—	—	3	—	1	9
Cape Vulture	41	15	13	21	51	25	91	207	483	947
Whitebacked Vulture	1	—	—	—	—	1	5	16	50	73
Lappetfaced Vulture	13	2	1	1	2	—	13	9	25	66
Whiteheaded Vulture	4	—	—	1	—	—	—	3	4	12
Black Kite	1	—	—	—	1	—	5	2	31	40
Yellowbilled Kite	13	8	45	39	73	25	88	43	500	834
Blackshouldered Kite	65	46	105	59	87	67	96	132	1 799	2 456
Cuckoo Hawk	3	6	14	5	2	4	3	10	20	67
Honey Buzzard	—	—	2	1	1	1	—	3	—	8
Black Eagle	41	12	10	10	8	13	82	108	666	950
Tawny Eagle	18	5	5	1	3	2	11	14	65	124
Steppe Eagle	—	—	—	—	—	1	—	—	4	5
Wahlberg's Eagle	1	—	—	—	1	—	2	3	5	12
Booted Eagle	13	5	5	3	5	—	4	38	470	543
Hawk Eagle	1	—	—	—	—	—	1	—	1	3
Ayres' Eagle	2	2	1	—	—	—	—	1	—	6
Longcrested Eagle	21	8	33	2	2	1	6	3	16	92
Martial Eagle	30	15	18	20	22	18	38	59	303	523
Crowned Eagle	36	15	13	13	16	14	35	57	251	450
Brown Snake Eagle	3	—	—	1	—	—	3	1	8	16
Blackbreasted Snake Eagle	17	3	2	1	1	1	21	6	39	91
Bateleur	12	5	23	6	2	3	8	10	41	110
Fish Eagle	30	9	6	4	8	26	56	88	328	555
Steppe Buzzard	28	19	45	31	30	22	62	57	786	1 080
Mountain Buzzard	1	7	1	1	1	2	4	14	74	105
Jackal Buzzard	54	37	56	20	34	35	74	74	1 169	1 553
Redbreasted Sparrowhawk	38	15	21	2	4	10	23	13	82	208
Ovambo Sparrowhawk	—	—	—	—	—	—	1	—	1	2
Little Sparrowhawk	22	15	19	8	8	9	18	13	31	143
Black Sparrowhawk	15	4	4	1	—	6	4	26	27	87
Little Banded Goshawk	2	—	1	—	1	—	1	—	4	9
African Goshawk	47	34	20	24	10	21	43	48	155	402
Gabar Goshawk	16	3	2	6	2	4	14	12	32	91
Pale Chanting Goshawk	26	17	14	12	5	3	55	38	850	1 020
African Marsh Harrier	25	7	10	5	9	16	88	60	297	517
Montagu's Harrier	8	1	4	1	3	—	7	2	2	28
Pallid Harrier	12	3	14	18	27	7	5	6	6	98
Black Harrier	31	6	3	2	3	3	26	47	470	591
Gymnogone	18	11	13	5	6	4	28	33	151	269
Osprey	6	1	5	7	7	17	27	19	116	205
Peregrine	23	6	2	4	3	2	19	15	86	160
Lanner	27	23	18	10	9	17	52	48	318	522
Hobby	9	—	—	2	—	1	4	8	9	33
African Hobby	1	—	—	1	—	—	—	1	2	5
Rednecked Falcon	2	—	—	—	—	—	5	5	4	16
Eastern Redfooted Kestrel	4	—	20	1	3	—	1	6	7	42
Common Kestrel	52	60	51	43	77	63	80	61	1 481	1 968
Greater Kestrel	10	12	4	16	2	2	35	24	169	274
Lesser Kestrel	2	3	64	29	25	28	52	24	221	448
Pygmy Falcon	10	—	—	—	1	—	7	35	41	94
Total	945	466	726	464	586	499	1 396	1 631	12 111	18 824

It should be emphasised that the concept of the present atlas was actively promoted only from early 1978 and therefore field surveys connected with other projects prior to this date did not involve the recording of distributional data for all raptor taxa. Thus on certain field surveys prior to 1978 the very common taxa were not recorded in the field. Attention is drawn to this in the relevant taxon accounts.

Nomenclature and order of taxa follow Clancey (1980). As much of the data interpretation methodology was decided on a *post hoc* basis this aspect is discussed below.

DISTRIBUTION, HABITAT AND STATUS OF INDIVIDUAL TAXA

In total some 18 824 records of 55 taxa were obtained from the various sources with the 1970s having 1,8 times the number of records as for the entire pre-1970s period (Table 1 and Fig. 3). Of the 55 taxa surveyed, some 34 are considered to breed in the Province. On a *post hoc* basis it was decided to present two maps for each taxon. These maps show, respectively, the pre-1970s and 1970s distribution of each taxon in the Cape Province and part of the Transkei; Transkei records east of 29° E are not mapped here. On the pre-1970s maps three periods

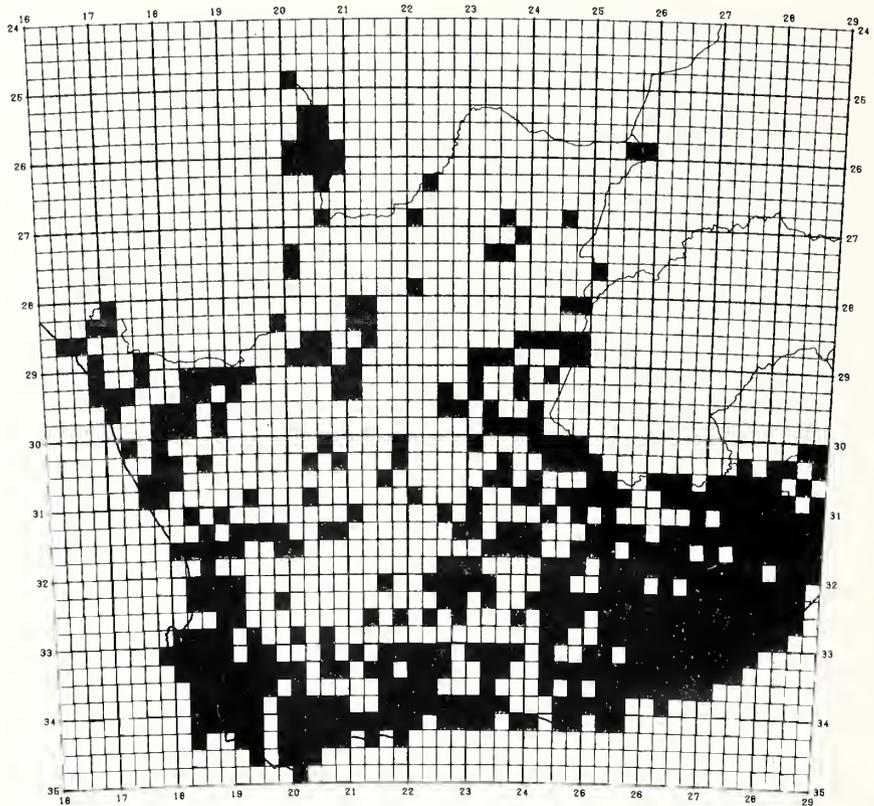


Fig. 4. Loci in the Cape Province and part of the Transkei where raptors were recorded between 1700 and 1969.

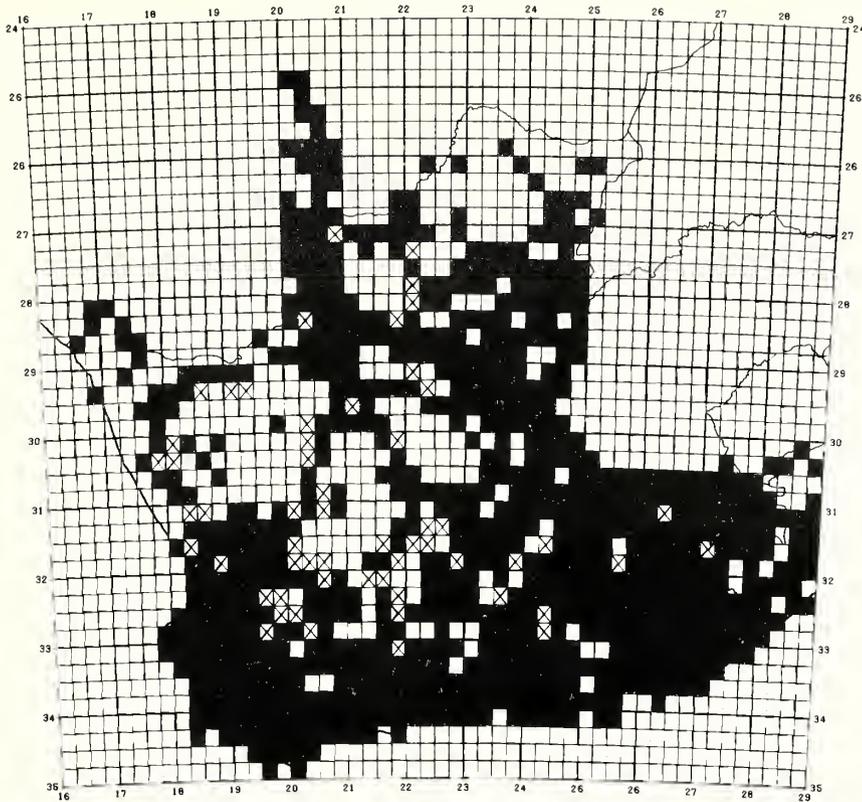


Fig. 5. Loci in the Cape Province and part of the Transkei where raptors were recorded between 1970 and 1979. "X" denotes loci visited (once) but where no raptors were recorded.

are differentiated, viz. 1700 – 1899 (open triangle), 1900 – 1949 (open circle), 1950 – 1969 (open square). On the 1970s maps a solid square symbol is used to denote presence of a taxon. Here 1949/1950 was taken as a cut-off point due to the general increase in the number of records in the 1950s and which carried through to the 1970s (Fig. 3).

The coverage obtained by the survey in terms of loci from which raptors were recorded for the pre-1970s and 1970s is shown in Figs 4 and 5 respectively and in Table 2. A comparison of the coverage between the two periods is also made (Table 2). For both periods the percentage coverage for the S.W. Cape, S. Cape and E. Cape is markedly greater than that for the N.W. Cape, N. Cape and Karoo. However, Table 2 and Figs 4 and 5 should only be referred to in terms of the constraints mentioned in the discussion.

The general range trend of each of the 55 taxa between the two periods is listed in Table 3. Individual taxon accounts follow.

TABLE 2

Number of loci in the Cape Province in which raptors were recorded in the 1700 – 1969 and 1970 – 1979 periods

	Region						Total
	N. Cape	N.W. Cape	Karoo	S.W. Cape	S. Cape	E. Cape	
Total number of loci	285	101	379	92	82	163	1 102
<i>1700 – 1969</i>							
Loci where raptors recorded	52	43	109	70	54	141	469
% coverage	18	43	29	76	67	87	43
<i>1970 – 1979</i>							
Loci where raptors recorded	159	46	252	87	79	154	775
% coverage	56	46	66	95	96	94	70
Trend or Change	***		***	**	**	*	

*** substantial increase
 ** marked increase
 * small increase

TABLE 3

General range trend of the diurnal raptors of the Cape Province between the periods 1700 – 1969 and 1970 – 1979.

Species	No change	Some increase	Some decrease	Marked decrease
Secretary Bird	*			
Palmnut Vulture	*			
Lammergeyer				*
Egyptian Vulture				*
Hooded Vulture			*	
Cape Vulture			*	
Whitebacked Vulture	*			
Lappetfaced Vulture				*
Whiteheaded Vulture	*			
Black Kite	*			
Yellowbilled Kite	*			
Blackshouldered Kite	*			
Cuckoo Hawk	*			
Honey Buzzard	*			
Black Eagle	*			
Tawny Eagle				*
Steppe Eagle	*			
Wahlberg's Eagle	*			
Booted Eagle	*	?		
Hawk Eagle	*			

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Species	No change	Some increase	Some decrease	Marked decrease
Ayres' Eagle			*	
Longerested Eagle				*
Martial Eagle	*			
Crowned Eagle			*	
Brown Snake Eagle	*			
Blackbreasted Snake Eagle	*			
Bateleur				*
Fish Eagle	*			
Steppe Buzzard	*			
Mountain Buzzard	*			
Jackal Buzzard	*			
Redbreasted Sparrowhawk		*		
Ovambo Sparrowhawk	*			
Little Sparrowhawk	*			
Black Sparrowhawk			*	
Little Banded Goshawk	*			
African Goshawk			*	
Gabar Goshawk	*			
Pale Chanting Goshawk	*			
African Marsh Harrier	*			
Montagu's Harrier				*
Pallid Harrier	*			
Black Harrier	*			
Gymnogere	*			
Osprey	*			
Peregrine	*			
Lanner	*			
Hobby	*			
African Hobby	*			
Rednecked Falcon	*			
Eastern Redfooted Kestrel	*			
Common Kestrel	*			
Greater Kestrel	*			
Lesser Kestrel		*?		
Pygmy Falcon	*			
Total (N = 55)	40	2	6	7
	(72,7%)	(3,6%)	(10,9%)	(12,7%)

Secretary Bird

Sagittarius serpentarius

Distribution (Figs 6 and 7)

The distribution for the pre-1970s and 1970s accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

Habitat

All veld types, except forest.

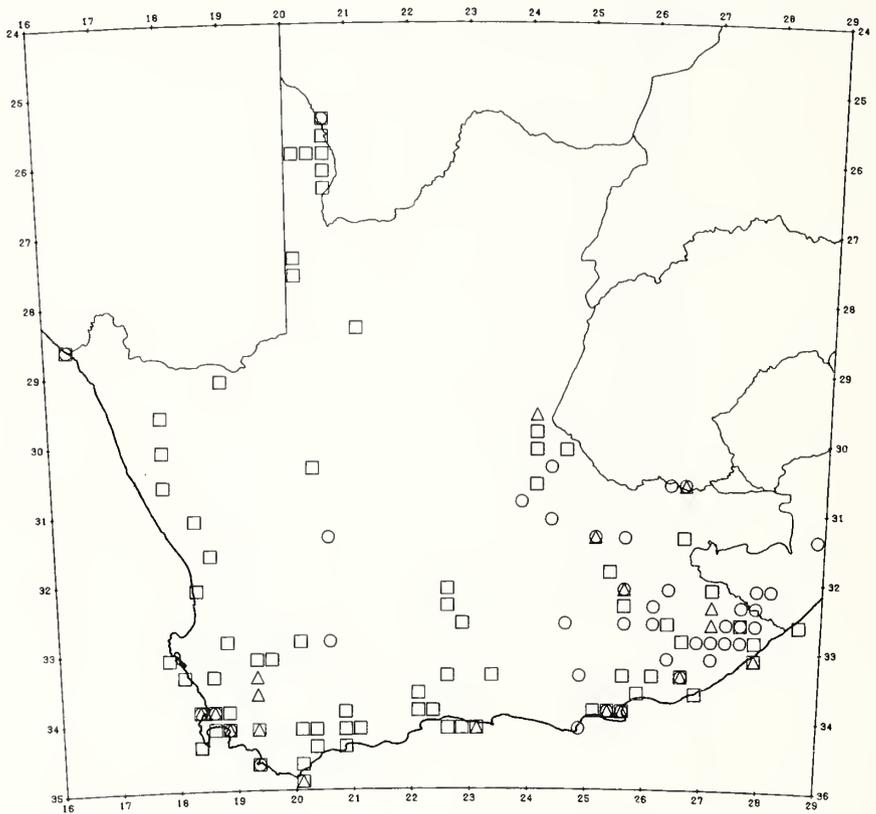


Fig. 6. Distribution of the Secretary Bird, 1700 – 1969.

Status

A scarce resident species which shows no change in range in the Province between the two periods. The large number of records from the south-eastern part of the N. Cape in the 1970s is due to increased sampling. Some decrease in numbers may have taken place in the N.W. Cape and Karoo. *S. serpentarius* is sensitive to habitat degradation due to overgrazing.

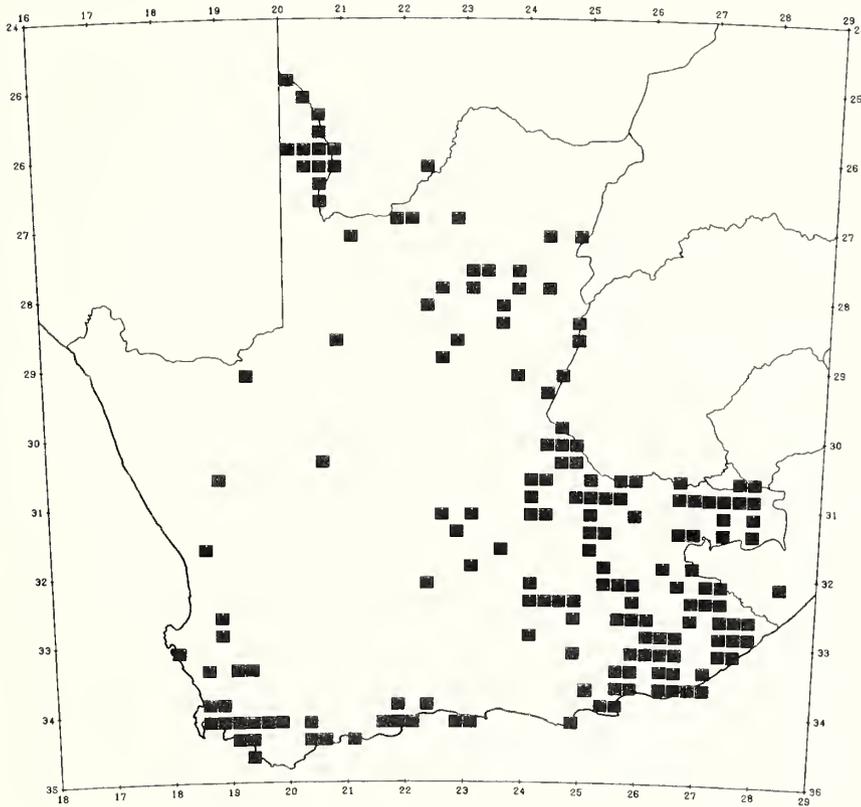


Fig. 7. Distribution of the Secretary Bird, 1970 – 1979.

Palmnut Vulture

Gypohierax angolensis

Distribution (Figs 8 and 9)

1700–1969: This distribution accords with that given by Snow (1978).

1970–1979: This distribution accords with that given by McLachlan & Liversidge (1978).

Habitat

There is no suitable habitat for this species in the Cape Province. Elsewhere in Africa the species is associated with palm trees, especially oil palms, *Elaeis*.

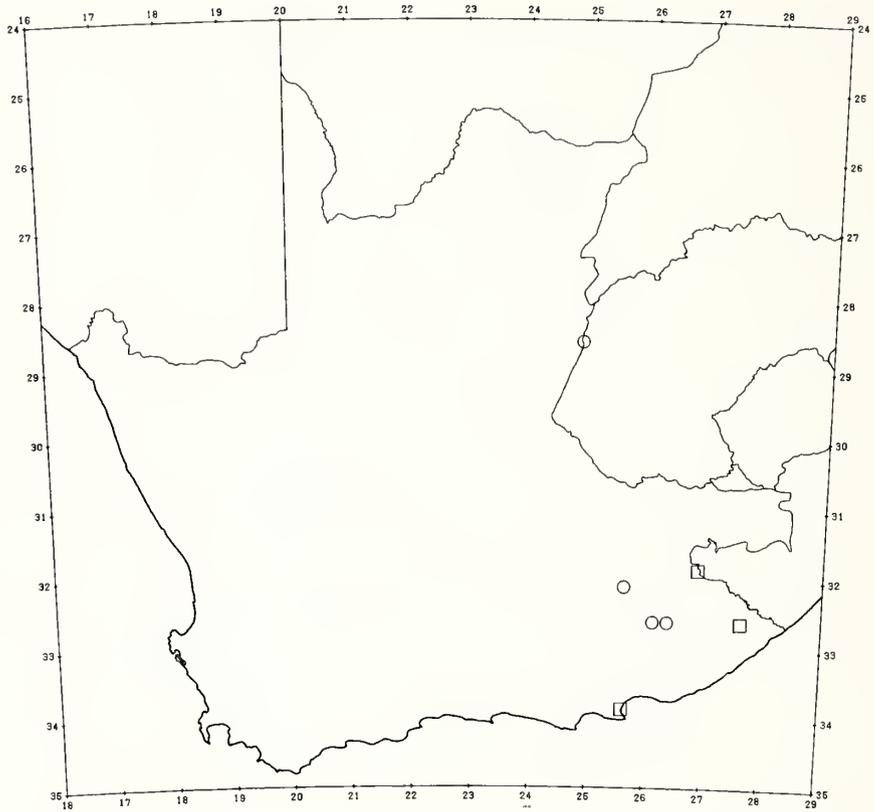


Fig. 8. Distribution of the Palmnut Vulture, 1700 – 1969.

Status

A rare vagrant for which there are only nine records over a 50 year period, from 1931 onwards. The birds recorded in the Cape Province were most often immatures and were presumably dispersing birds from the breeding populations in Zululand (Natal) and Mozambique.

G. angolensis is peripheral in the Cape Province and Transkei. This species is listed as "vulnerable" in South Africa by Siegfried *et al.* (1976). There are few records from the Transkei and E. Cape from the 1970s but it is not known to what extent this reflects the status of the southern African breeding populations. *G. angolensis* is not considered to have undergone a change in status in the Province between the two periods.

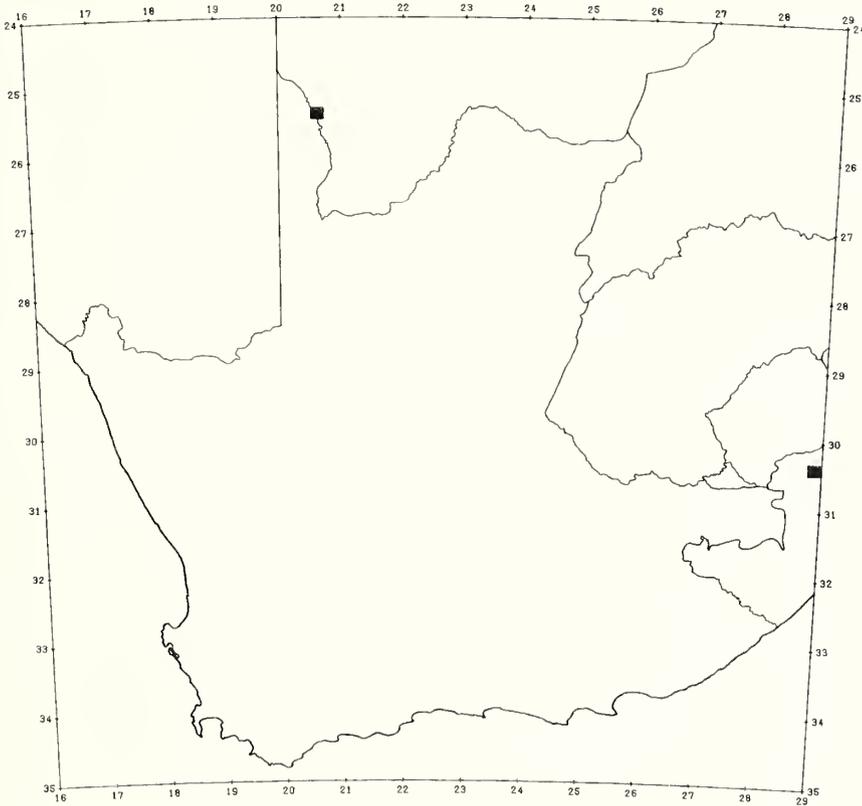


Fig. 9. Distribution of the Palmnut Vulture, 1970 – 1979.

Lammergeyer

Gypaetus barbatus

Distribution (Figs 10 and 11)

1700–1969: This distribution accords with that given by Snow (1978).

1970–1979: This distribution accords with that given by McLachlan & Liversidge (1978).

Habitat

Mountainous grassland areas. Previously extending down to the coast but now restricted to above 1 700 m above sea level.

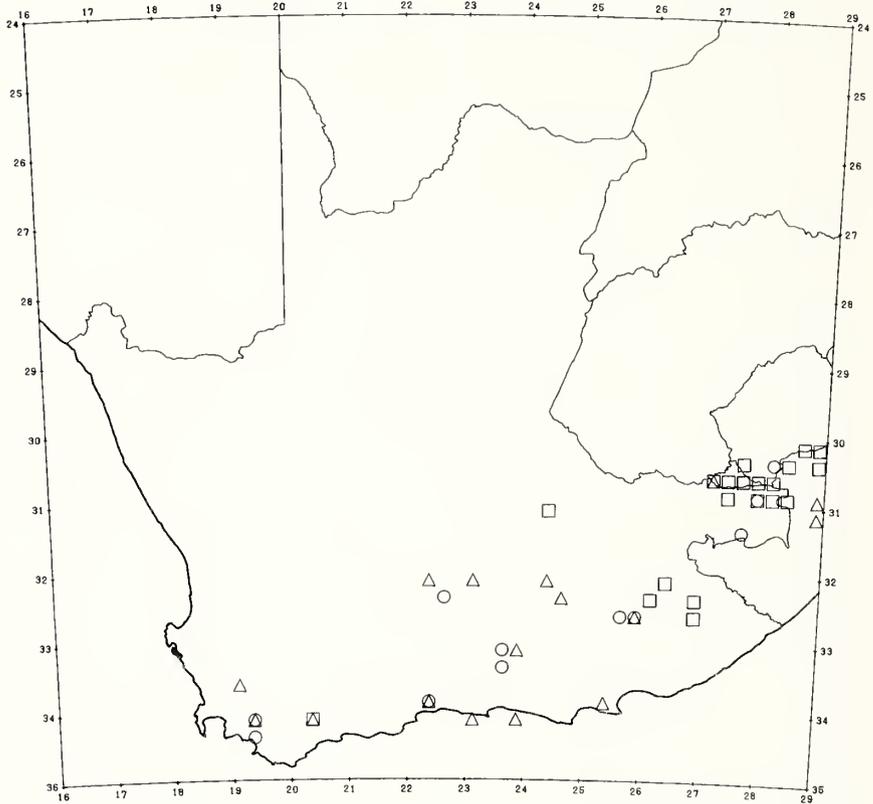


Fig. 10. Distribution of the Lammergeyer, 1700 – 1969.

Status

G. barbatus has undergone a drastic decrease in range in the Province between the two periods. Little is known of the biology of this species in South Africa and the reasons for this decrease are therefore not understood. There is a small resident population of about 120 pairs in the Drakensberg in Lesotho and outliers in Natal, Cape Province and Transkei (Brown 1977). *G. barbatus* is classified as "rare and threatened" in South Africa by Siegfried *et al.* (1976).

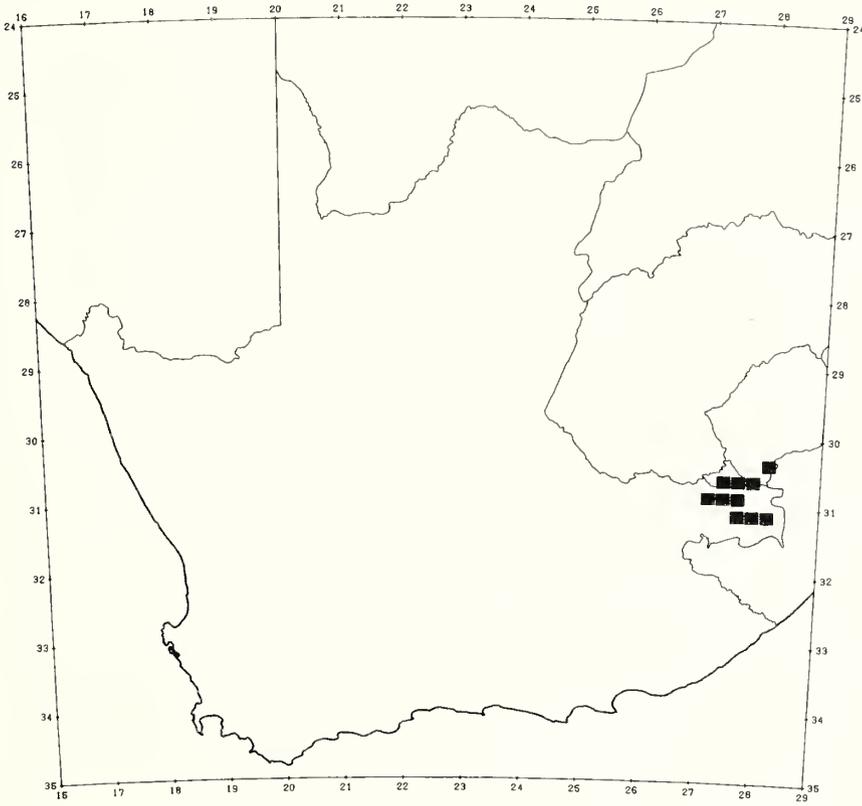


Fig. 11. Distribution of the Lammergeyer, 1970 – 1979.

Egyptian Vulture

Neophron percnopterus

Distribution (Figs 12 and 13)

1700–1969: This distribution accords with that given by Snow (1978). It is noteworthy that 29 of the 42 records for this period are between 1700 and 1900 (cf. Table 1).

1970–1979: McLachlan & Liversidge (1978) do not present a distribution map but list the species as “now very rare in our area (South Africa)”.

Habitat

Highveld open grassland and mountainous areas; also arid and semi-arid areas.

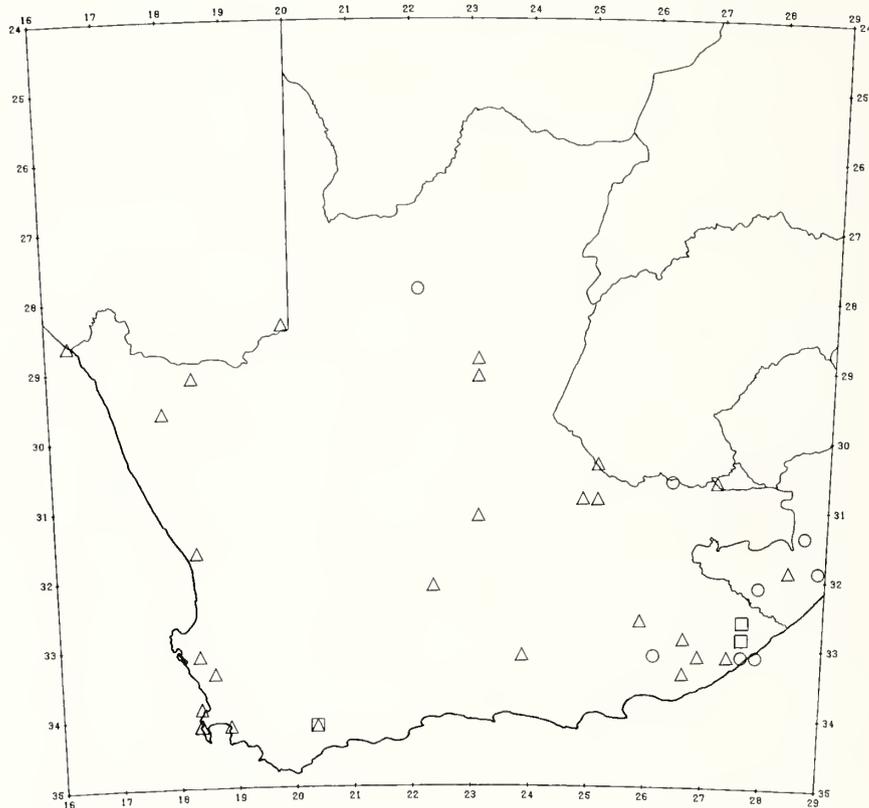


Fig. 12. Distribution of the Egyptian Vulture, 1700 – 1969.

Status

Reported to have bred at several localities in the Cape Province and Transkei in the past; last breeding record 1923, in the Transkei. *N. percnopterus* occurred throughout the Cape Province before 1900 but since then the number of records has decreased considerably with only four observations from the 1970s (Table 1). Snow (1978) states that “there is some evidence that the species spread south, colonizing South Africa between 1810 and the 1860s, and then after maintaining itself began to disappear after the turn of the century”. The status of *N. percnopterus* in southern Africa has been documented in detail by Mundy (1978), who considers that there may be a viable relict breeding population in the Transkei. The species is extinct in the Cape Province or occurs only as a rare vagrant.

Brooke (1979) and Mundy (*op cit.*) have discussed the reasons for the decrease in range and numbers of this vulture. Siegfried *et al.* (1976) list *N. percnopterus* as “endangered and possibly no longer a part of the South African (avi)fauna”.

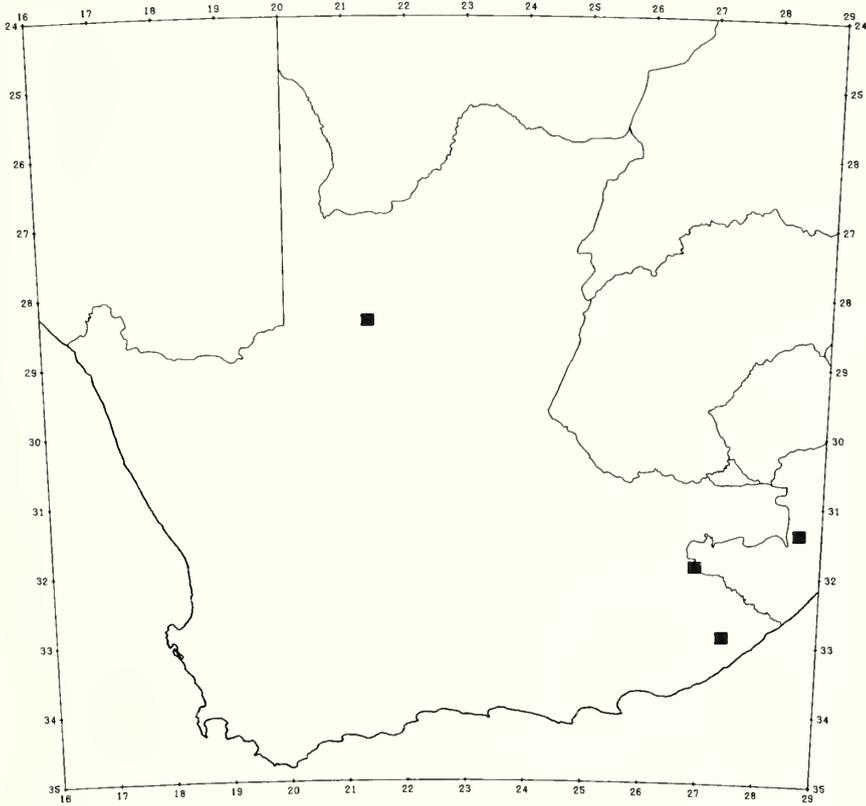


Fig. 13. Distribution of the Egyptian Vulture, 1970 – 1979.

Hooded Vulture

Necrosyrtes monachus

Distribution (Figs 14 and 15)

1700–1969: This distribution accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

1970–1979: Mills (1976) records this species as a vagrant in the Kalahari Gemsbok National Park during the early 1970s. The 1970s distribution is more restricted than that given by McLachlan & Liversidge (*op cit.*)

Habitat

Bushveld in the Cape Province. Elsewhere in Africa in savanna and both open and dense woodland; well wooded moist lowveld areas. Commensal with man north of the equator.

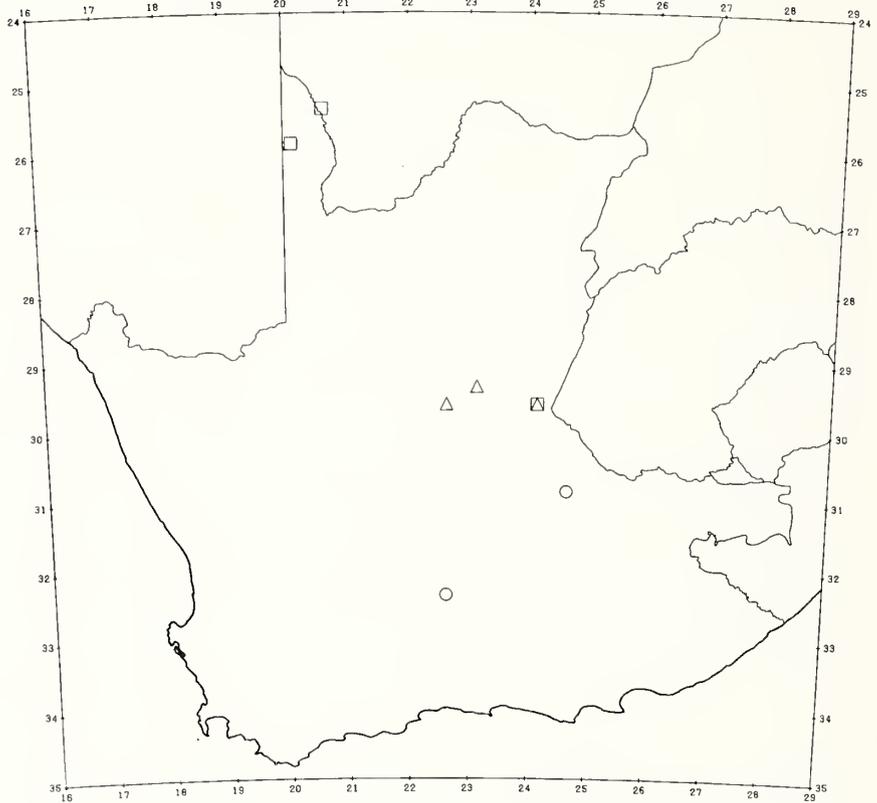


Fig. 14. Distribution of the Hooded Vulture, 1700 – 1969.

Status

Overall there is a decrease in the frequency with which the narrow-billed *N. monachus* was recorded in the 1970s as compared to the pre-1970 period. The lack of suitable habitat in the Province has prevented *N. monachus* from becoming a breeding resident. The species was, and still is, peripherally represented in the Cape Province and its range is allopatric with the other thin-billed vulture *Neophron percnopterus*, which is an ecological equivalent in so far as feeding is concerned. The paucity of records for *Necrosyrtes monachus* from the Province in the 1970s may indicate a decrease in range; the species is considered rare in the Cape Province.

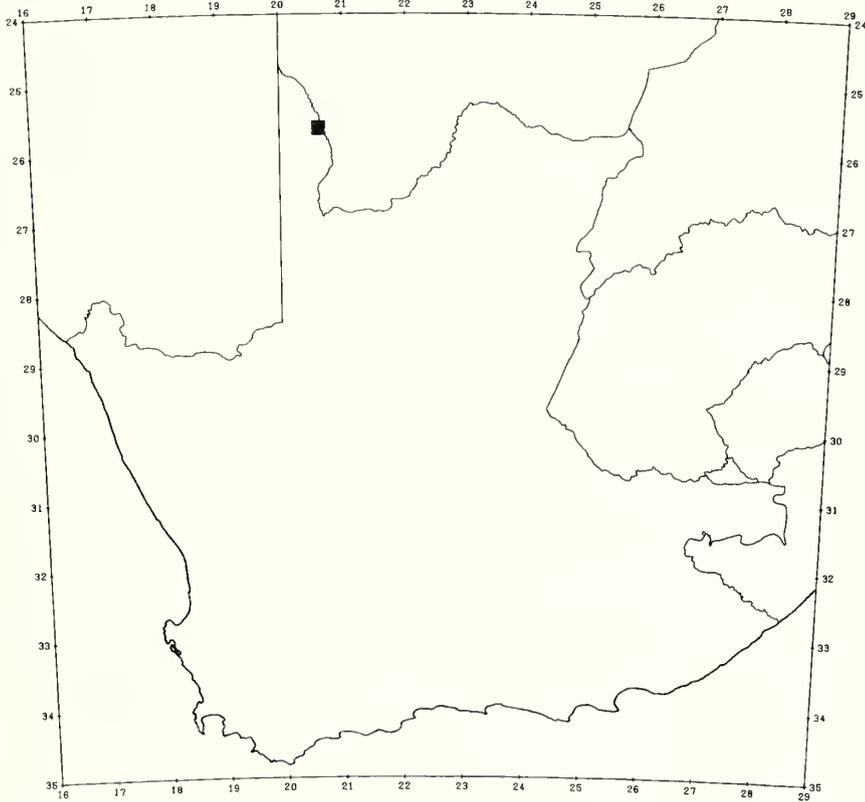


Fig. 15. Distribution of the Hooded Vulture, 1970 – 1979.

Cape Vulture

Gyps coprotheres

Distribution (Figs 16 and 17)

1700–1969: This distribution accords with that given by Snow (1978).

1970–1979: Similar to the 1700 – 1969 period but more restricted in the Karoo. This range is more limited than that given by McLachlan & Liversidge (1978).

Habitat

Breeds and roosts on cliffs. Forages over country with few trees; mainly grassland, thornveld, macchia and also the karoo at the ecotone with grassland.

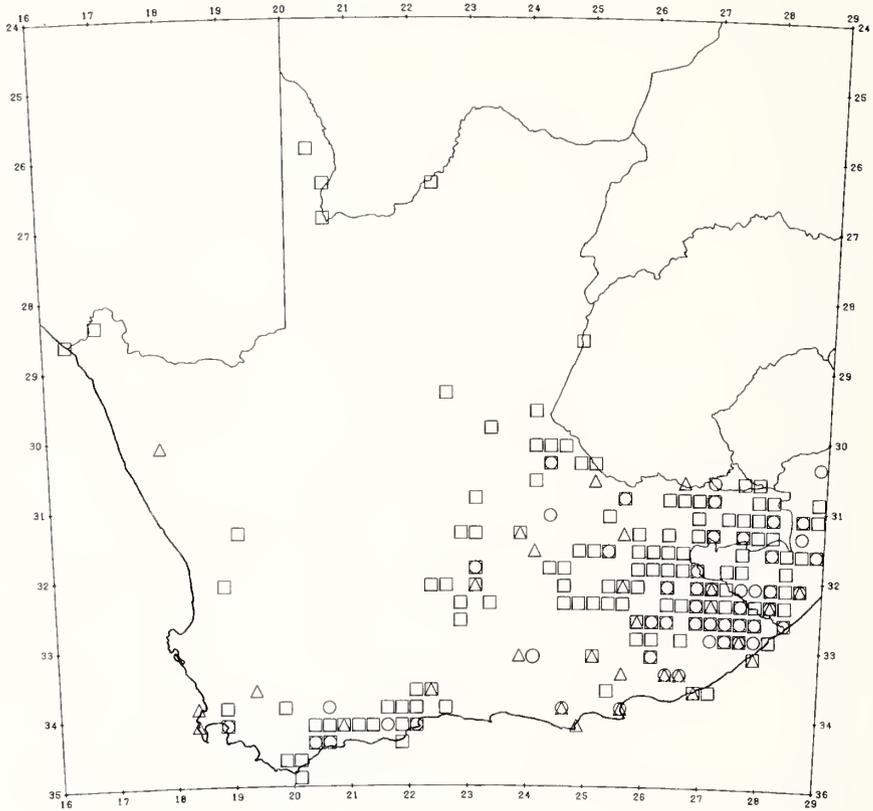


Fig. 16. Distribution of the Cape Vulture, 1700 – 1969.

Status

The past and present distribution and status of *G. coprotheres* in the Cape Province is dealt with in detail by Boshoff & Vernon (1980a). This resident species has undergone several fluctuations in range and numbers during the past 150 years and at the present time the population has stabilised at a low level which reflects the existing food supply. Additional mortality factors posing a threat to the population are drowning, electrocution and indirect poisoning. In 1979 there were only 65 breeding pairs in the Province and *G. coprotheres* is considered a scarce species in the Province. *G. coprotheres* is rightly listed as "threatened and vulnerable" in the *South African Red Data Book: Aves* (Siegfried *et al.* 1976).

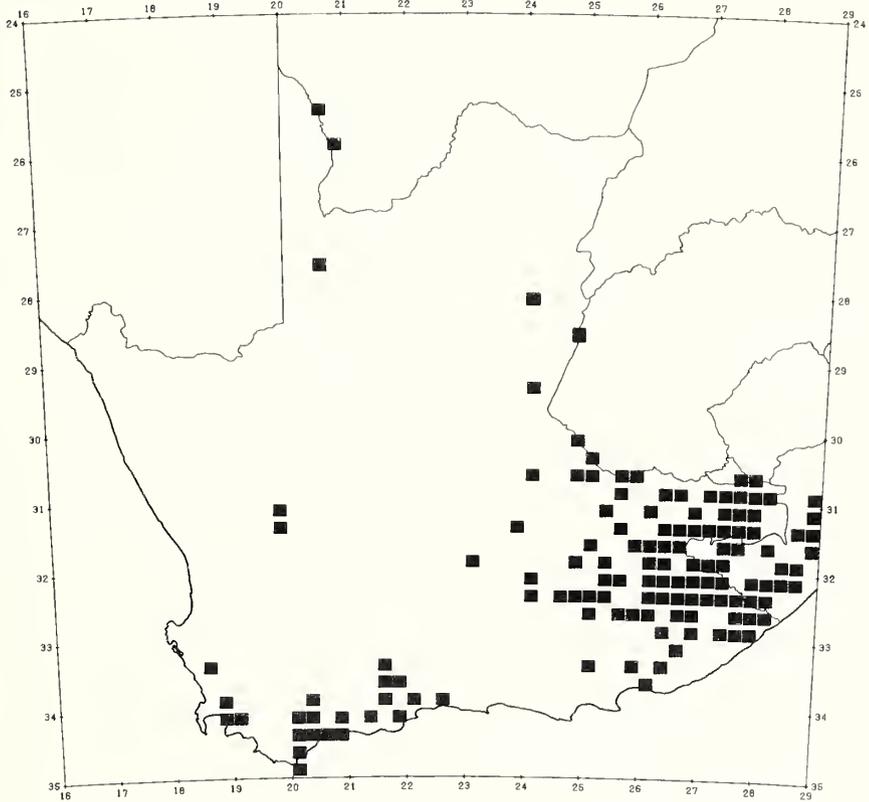


Fig. 17. Distribution of the Cape Vulture, 1970 – 1979.

Whitebacked Vulture

Gyps africanus

Distribution (Figs 18 and 19)

In view of the number of records from the 1970s, the paucity of records from the pre-1970s is noteworthy. This is due to the area being opened to farmers and travellers as late as the 1930s and 1940s, and also as a result of incorrect nomenclature (as *G. rueppelli*). The distribution of *G. africanus* for the pre-1970 and the 1970 to 1979 periods accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

Habitat

Bushveld in the Cape Province. Elsewhere in Africa in tropical and sub-tropical savanna and woodland. Breeds and roosts in trees.

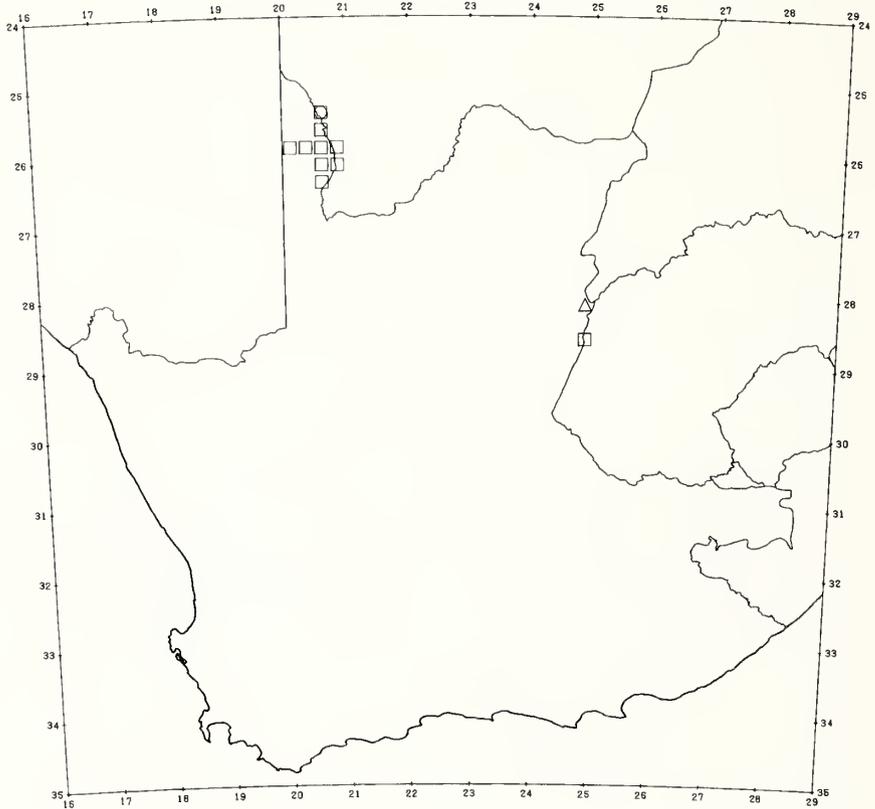


Fig. 18. Distribution of the Whitebacked Vulture, 1700 – 1969.

Status

G. africanus was undoubtedly more widespread in the N. Cape than the map for the 1700 – 1969 period suggests. At present it is the commonest vulture species in that area but it is not known whether a decrease in numbers has taken place; if so this would be due mainly to reduction in available carrion. A breeding population remains in the Kalahari Gemsbok National Park, where carrion is still freely available. The species also breeds near Kimberley (at least 75 pairs in 1979) and there is a group of unknown size which nests N.W. of Vryburg (P. J. Mundy *in litt.*). Within the Province the distribution of *G. africanus* is closely linked to that of the camelthorn *Acacia erioloba* which it finds very suitable for nesting in. There has been no change in range in the Province between the two periods.

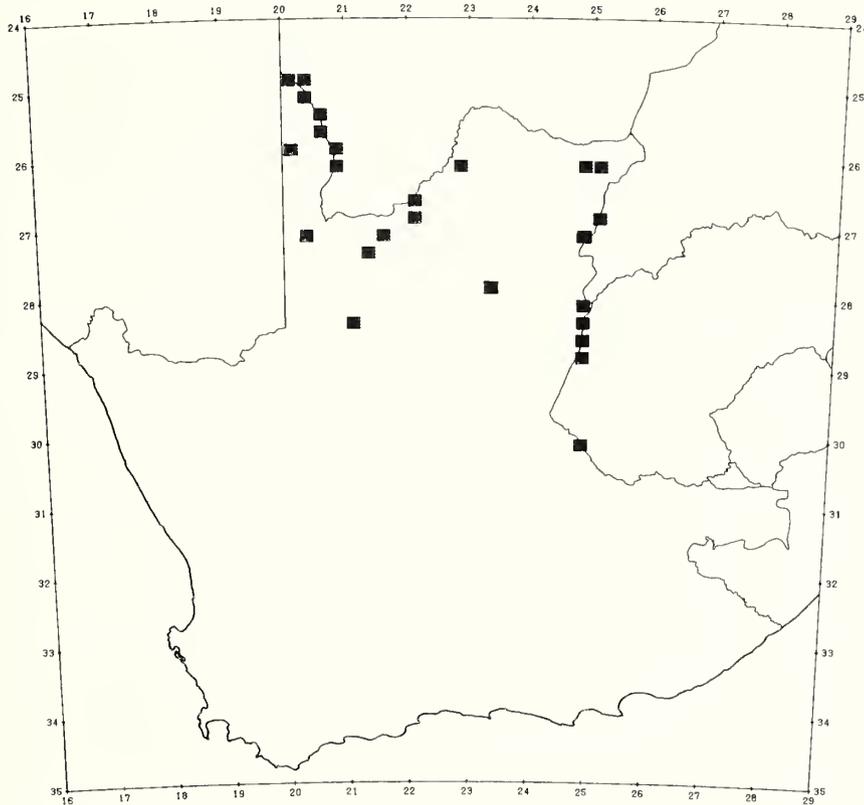


Fig. 19. Distribution of the Whitebacked Vulture, 1970 – 1979.

Lappetfaced Vulture

Torgos tracheliotus

Distribution (Figs 20 and 21)

1700–1969: Recorded as a breeding species from the S.W. Cape, S. Cape, Karoo, E. Cape and N. Cape during the 19th century. This distribution accords with that given by Snow (1978).

1970–1979: This distribution accords with that given by McLachlan & Liversidge (1978).

Habitat

Bushveld in the Cape Province. Elsewhere in Africa in tropical and sub-tropical savanna and open woodland. Particularly adapted to arid and semi-arid areas. Breeds and roosts in trees.

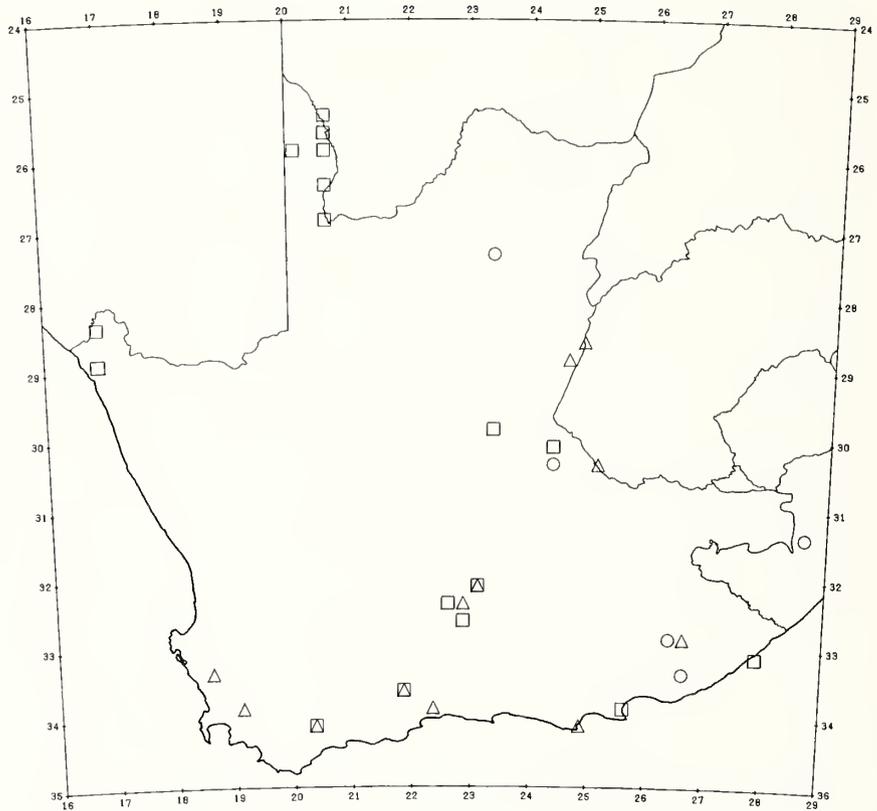


Fig. 20. Distribution of the Lappetfaced Vulture, 1700 – 1969.

Status

T. tracheliotus, a former breeding species over most of the Cape Province, has exhibited a major decrease in range and is now absent from the Province except for the N. Cape where it is a scarce but still resident species. The reasons for this decrease are not understood but may be linked to the extirpation of the indigenous game herds. Breeding is recorded from the 1970s in the Kalahari Gemsbok National Park and near Schmidtsdrif (P. J. Mundy *in litt.*) and also near Kimberley (AFB pers. rec.; R. Liversidge pers. comm.). *T. tracheliotus* should be included in a revised *South African Red Data Book: Aves*.

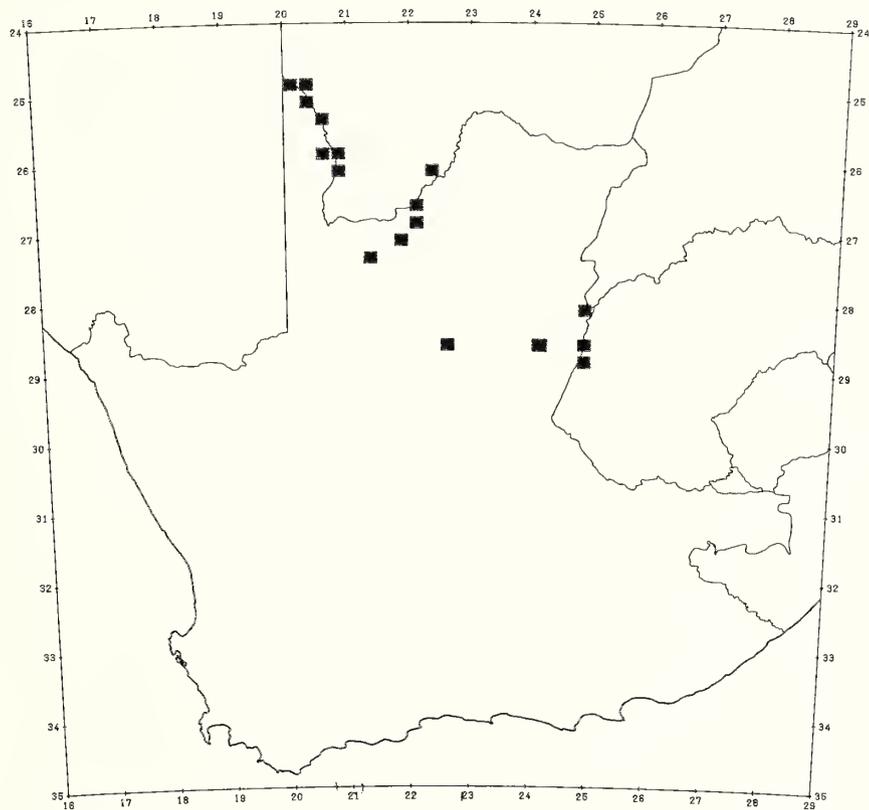


Fig. 21. Distribution of the Lappetfaced Vulture, 1970 - 1979.

Whiteheaded Vulture

Trigonoceps occipitalis

Distribution (Figs 22 and 23)

McLachlan & Liversidge (1978) and Snow (1978) exclude *T. occipitalis* from the Cape Province.

Habitat

Bushveld in the Cape Province. Elsewhere in Africa in tropical savanna and woodland.

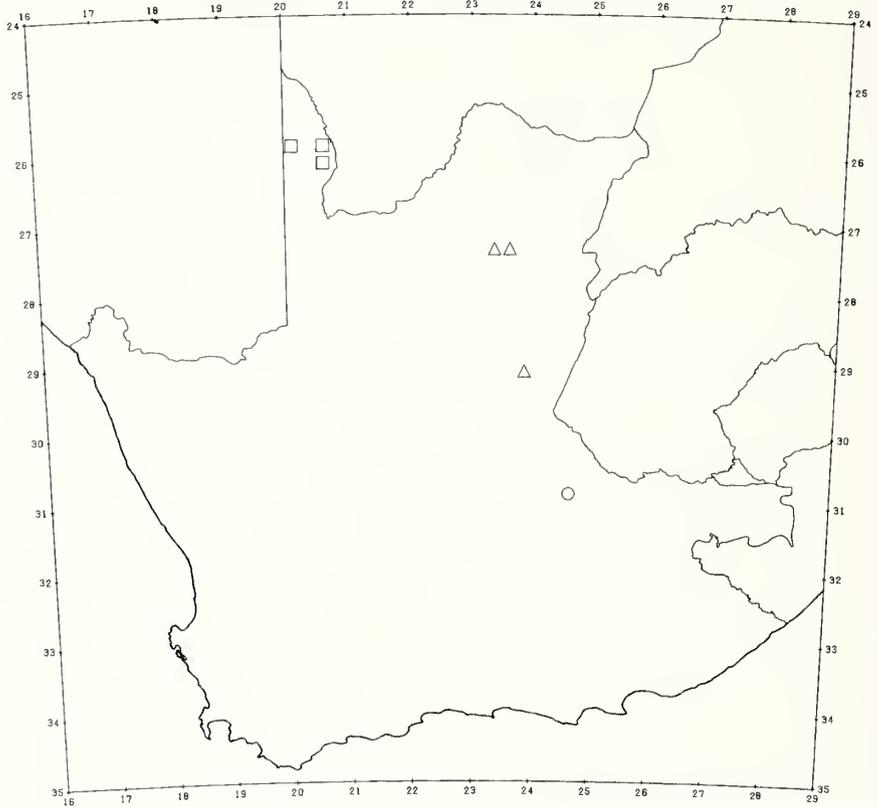


Fig. 22. Distribution of the Whiteheaded Vulture, 1700 – 1969.

Status

T. occipitalis is, and probably always has been, rare in the Cape Province, which is on the periphery of its range. The most southerly breeding records for South Africa are from Zululand, Natal. Little is known of the movements of the species in the southern parts of its range but it is considered a rare vagrant in the N. Cape, outside of the Kalahari Gemsbok National Park where adults do occur. The habitat in the Kalahari Gemsbok National Park does not suit breeding. There is, however, a record of an adult on a nest in July 1964 (Broekhuysen *et al.*, 1968). There are only 12 records from 1700 to 1969 and only four from the 1970s (Table 1). There has been no apparent change in status in the Province between the two periods.

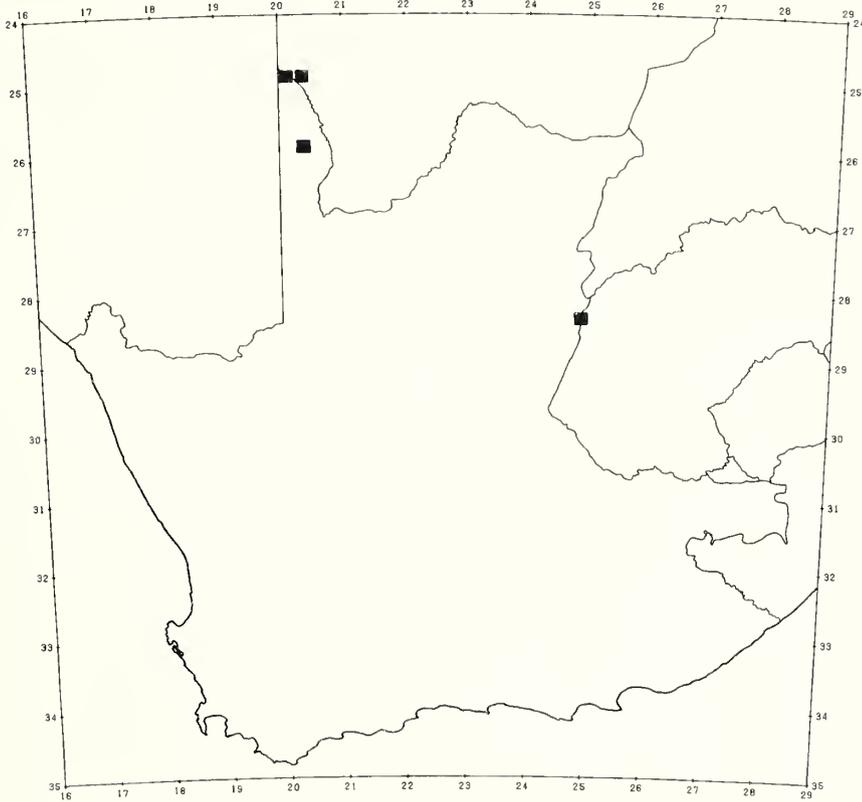


Fig. 23. Distribution of the Whiteheaded Vulture, 1970 – 1979.

Black Kite

Milvus migrans migrans

Distribution (Figs 24 and 25)

The present range (1970s) is more restricted than that given by McLachlan & Liversidge (1978). Snow (1978) does not separate *M. migrans* and *M. migrans parasitus*.

Habitat

Wide variety of habitat, with preference for open wooded country in vicinity of water.

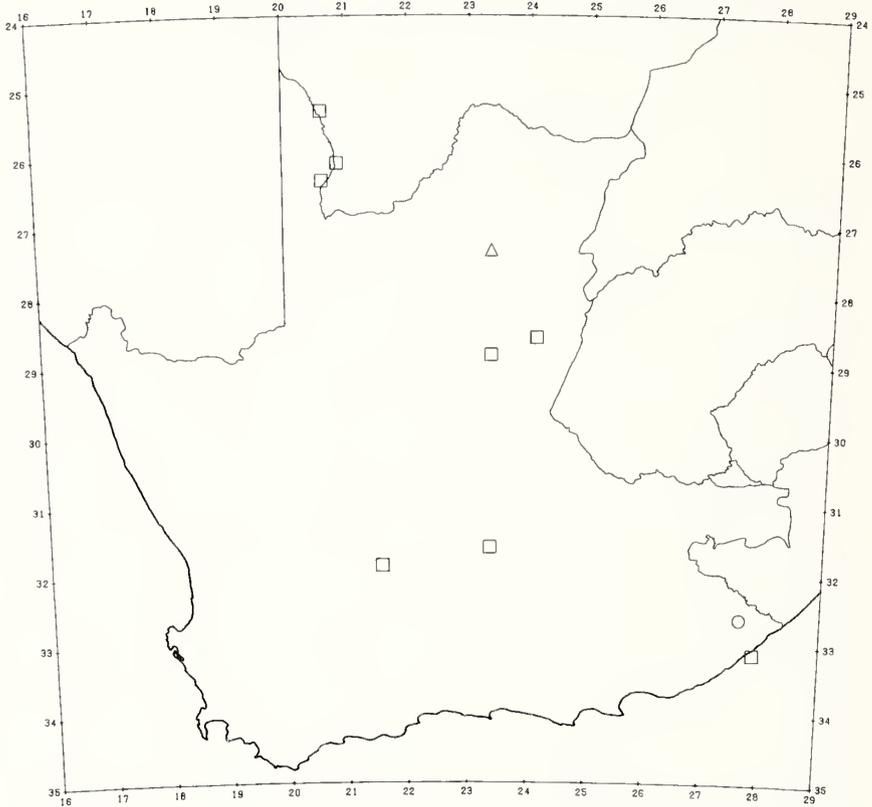


Fig. 24. Distribution of the Black Kite, 1700 – 1969.

Status

A scarce non-breeding Palaearctic migrant which is present during the austral summer. There has been no change in status in the Province between the two periods. The E. Cape and Transkei records are mapped here, however, there is a strong possibility that in these areas there have been some misidentifications as juvenile *M. m. parasitus*.

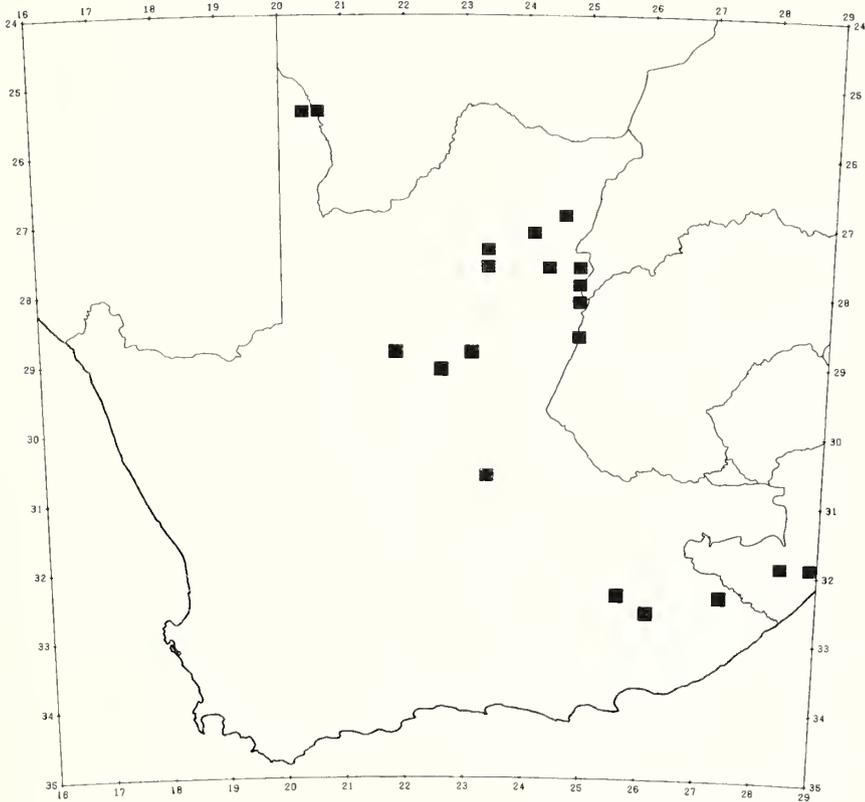


Fig. 25. Distribution of the Black Kite, 1970 – 1979.

Yellowbilled Kite

Milvus migrans parasitus

Distribution (Figs 26 and 27)

1700–1969: This distribution corresponds with that given by Snow (1978) for *M. migrans*.

1970–1979: This distribution is far more restricted than that given by McLachlan & Liversidge (1978) *sub nom.* *M. aegyptius*.

Habitat

In the E. Cape *M. m. parasitus* is found in all habitats and breeds in forests and plantations. In the S.W. Cape this taxon is found in areas of open machia and cereal crops. In both regions the taxon is frequently associated with habitation.

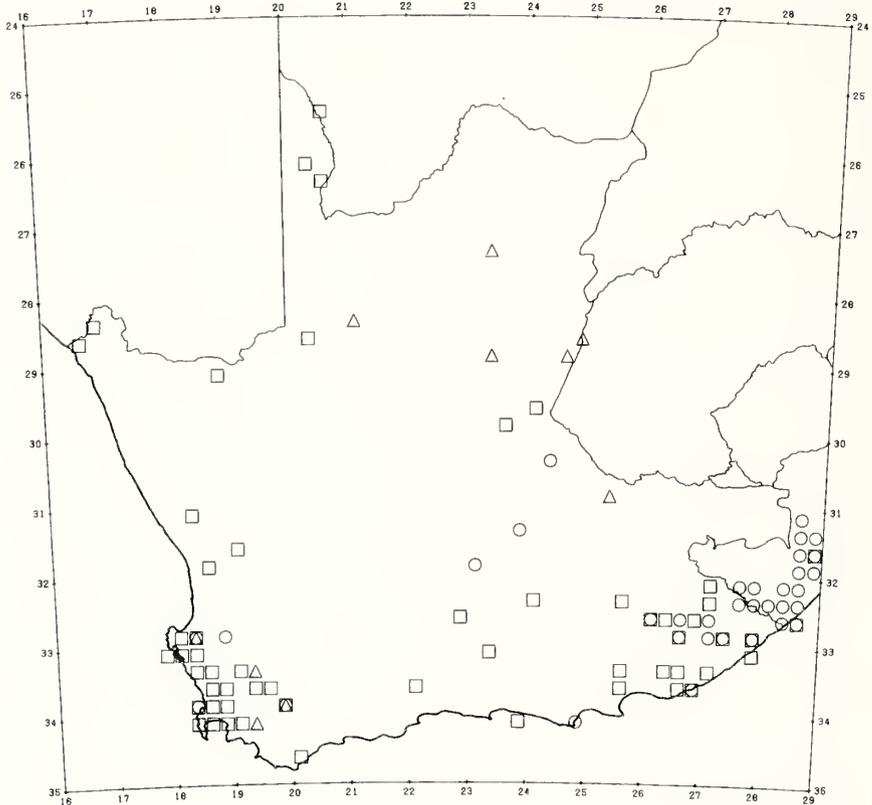


Fig. 26. Distribution of the Yellowbilled Kite, 1700 – 1969.

Status

A common breeding summer migrant which overwinters in equatorial Africa. The status of *M. m. parasitus* remained unchanged in the Province between the two periods. This study demonstrates the presence of two populations in the Cape Province.

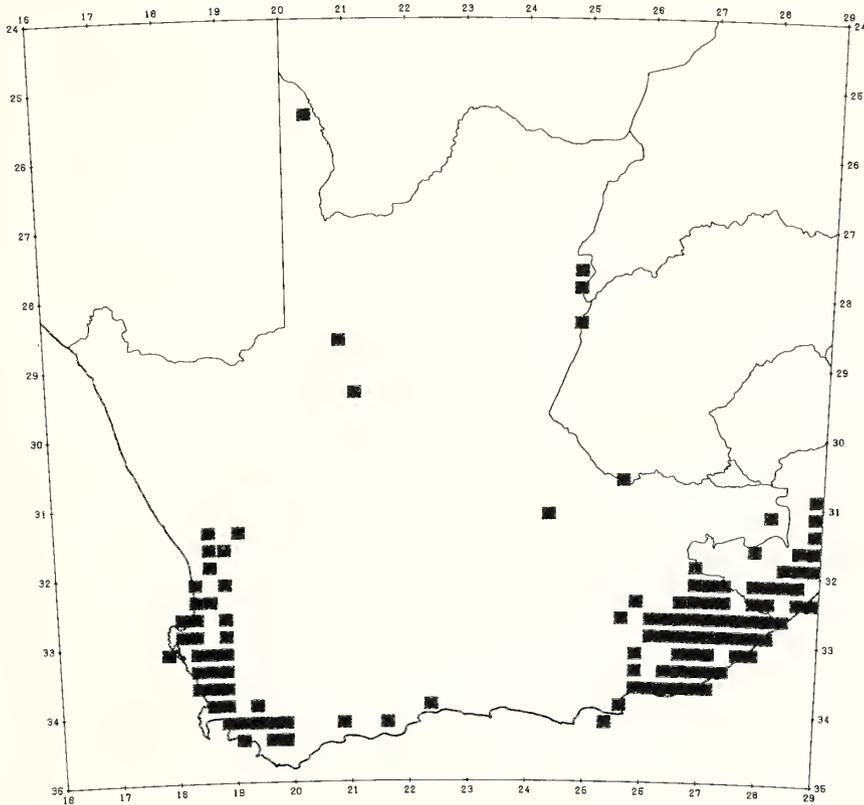


Fig. 27. Distribution of the Yellowbilled Kite, 1970 – 1979.

Blackshouldered Kite

Elanus caeruleus

Distribution (Figs 28 and 29)

Although the species may occur anywhere in the Province, it is not as evenly distributed as shown by McLachlan & Liversidge (1978). The distribution for both the pre-1970 and 1970 – 1979 periods accords with that given by Snow (1978). Known to occur in the N.W. Cape; not considered during a 1977 field survey in this region.

Habitat

Primarily grassland but found in all habitats except forest. Partial to *Pinus* and *Eucalyptus* spp. for roosting and breeding. Often found in man-made habitats, more especially croplands and town commonages.

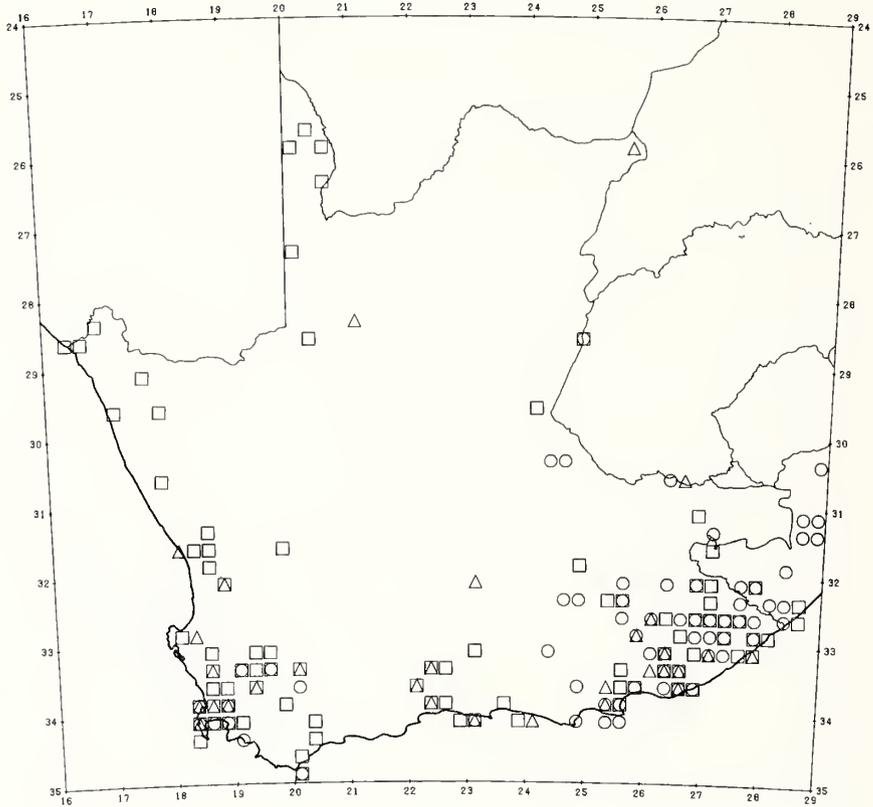


Fig. 28. Distribution of the Blackshouldered Kite, 1700 – 1969.

Status

A nomadic species which moves into suitable environments and remains there for as long as conditions are favourable. *E. caeruleus* is resident in optimal areas, however, such areas represent only a small portion of its range in the Province. There has been no apparent change in status. *E. caeruleus* is the common and most frequently recorded raptor in the Province.

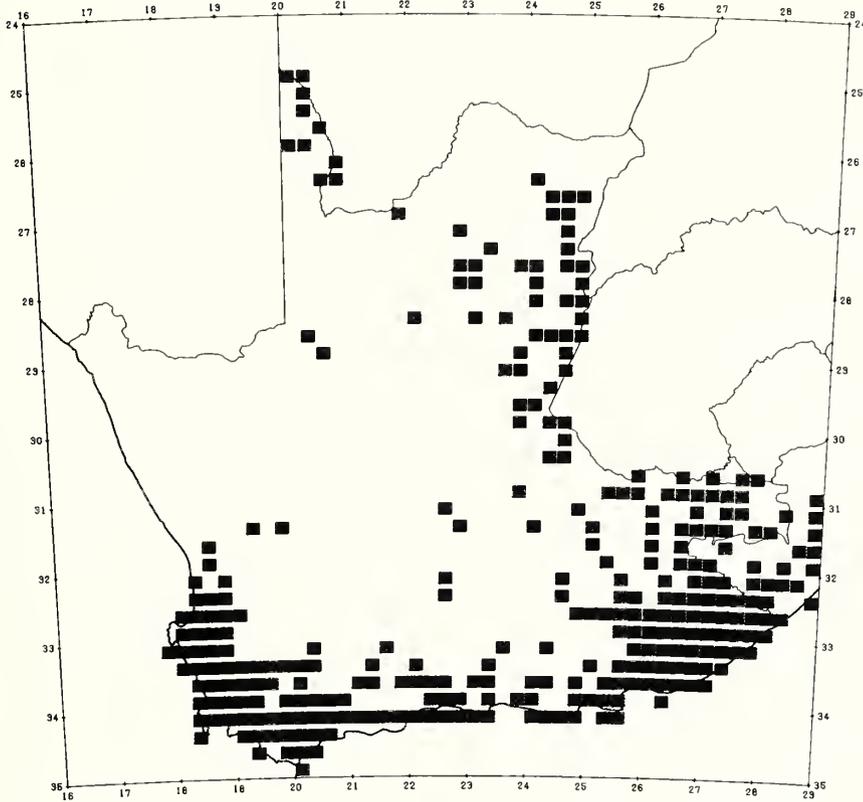


Fig. 29. Distribution of the Blackshouldered Kite, 1970 – 1979.

Cuckoo Hawk

Aviceda cuculoides

Distribution (Figs 30 and 31)

The distribution for both the pre-1970s and the 1970s accords with that given by SNOW (1978), whereas the 1970s distribution is somewhat more restricted than that given by McLACHLAN & LIVERSIDGE (1978).

Habitat

Forest and *Eucalyptus* plantations.

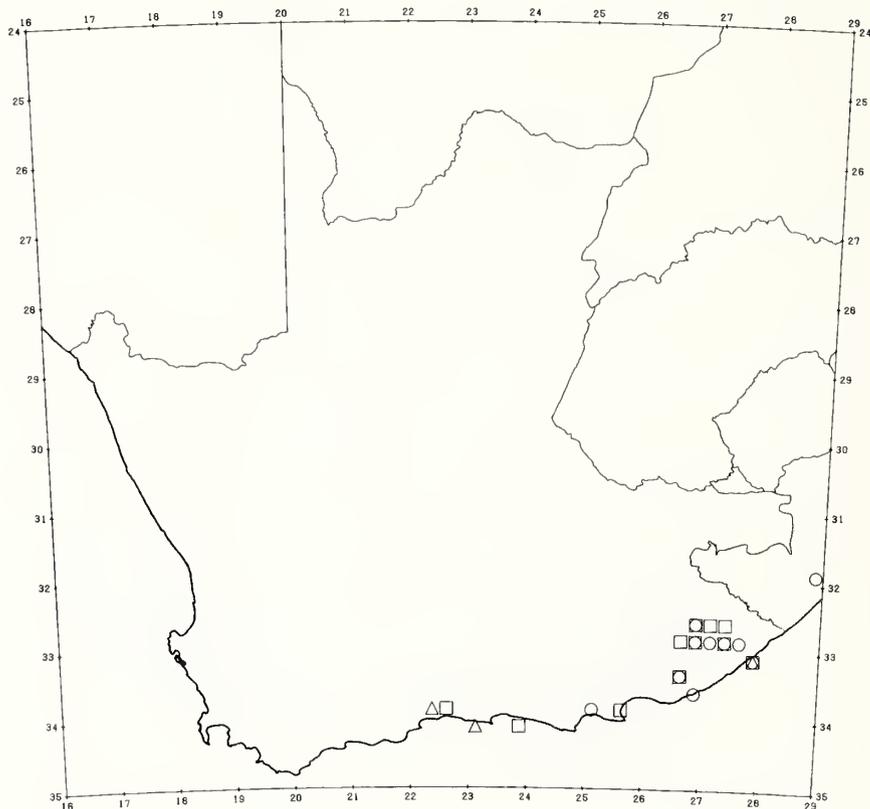


Fig. 30. Distribution of the Cuckoo Hawk, 1700 – 1969.

Status

Resident. Although there are several records of sub-adult birds there is no definite evidence that *A. cuculoides* breeds in the Province. The species is, and always has been, rare and is assigned this status by Siegfried *et al.* (1976). *A. cuculoides* may have decreased in numbers in the Province as there are fewer records for the 1970s than for the earlier period; there has been no apparent change in range in the Province between the two periods.

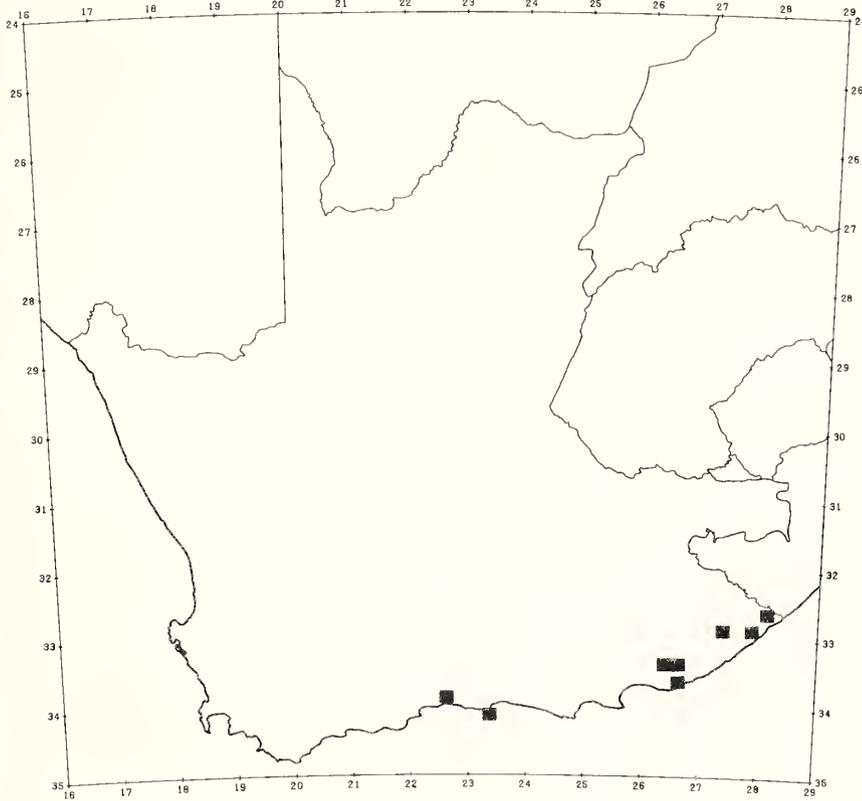


Fig. 31. Distribution of the Cuckoo Hawk, 1970 - 1979.

Honey Buzzard

Pernis apivorus

Distribution (Fig. 32)

There are no records from the 1970s and this situation accords basically with that given by McLachlan & Liversidge (1978).

Habitat

No information for the Cape Province. Elsewhere in open woodland.

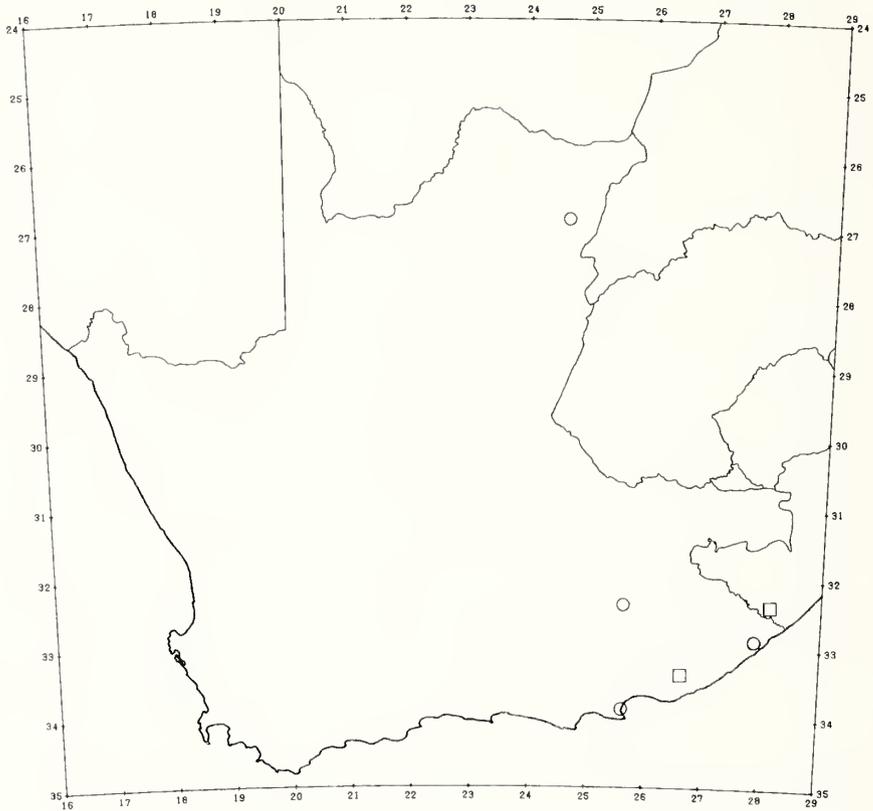


Fig. 32. Distribution of the Honey Buzzard, 1700 – 1969.

Status

A non-breeding Palaearctic migrant which is present during the austral summer. Extremely rare in the Cape Province; probably restricted to the E. Cape region. It is noteworthy that six of the eight records for *P. apivorus* are from specimens. The present authors interpret this to suggest that the species may not have undergone a decrease but simply that few ornithologists are able to identify the birds in the field. This contention is supported somewhat by the fact that Cramp & Simmons (1980) consider that *P. apivorus* has increased in numbers in its western Palaearctic range.

Black Eagle*Aquila verreauxii**Distribution* (Figs 33 and 34)

The 1970s distribution accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

Habitat

Associated with mountains and gorges where there are cliffs for eyries and abundant *Procapria capensis* prey. In the forests of the E. Cape where such conditions occur the Black Eagle is replaced by the Crowned Eagle *Stephanoaetus coronatus*. Precluded from the N. Cape through lack of suitable habitat.

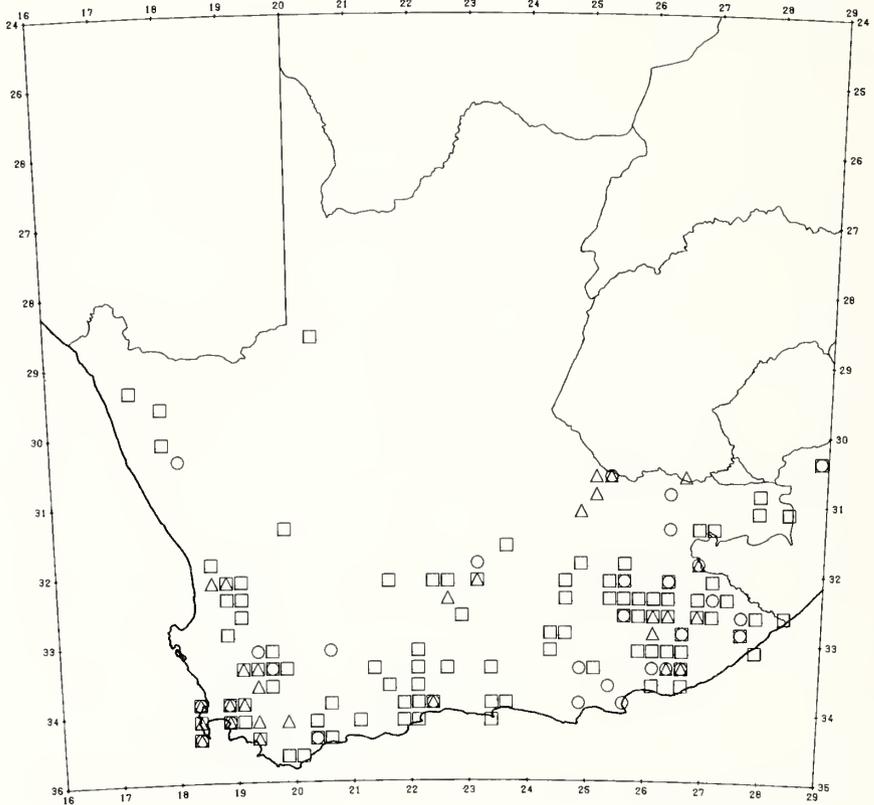


Fig. 33. Distribution of the Black Eagle, 1700 – 1969.

Status

Resident. Despite persecution by small-stock farmers *A. verreauxii* shows no change in status between the two periods. This species is the most numerous and widespread of the large eagles in the Cape Province (*vide* Boshoff & Vernon 1980b).

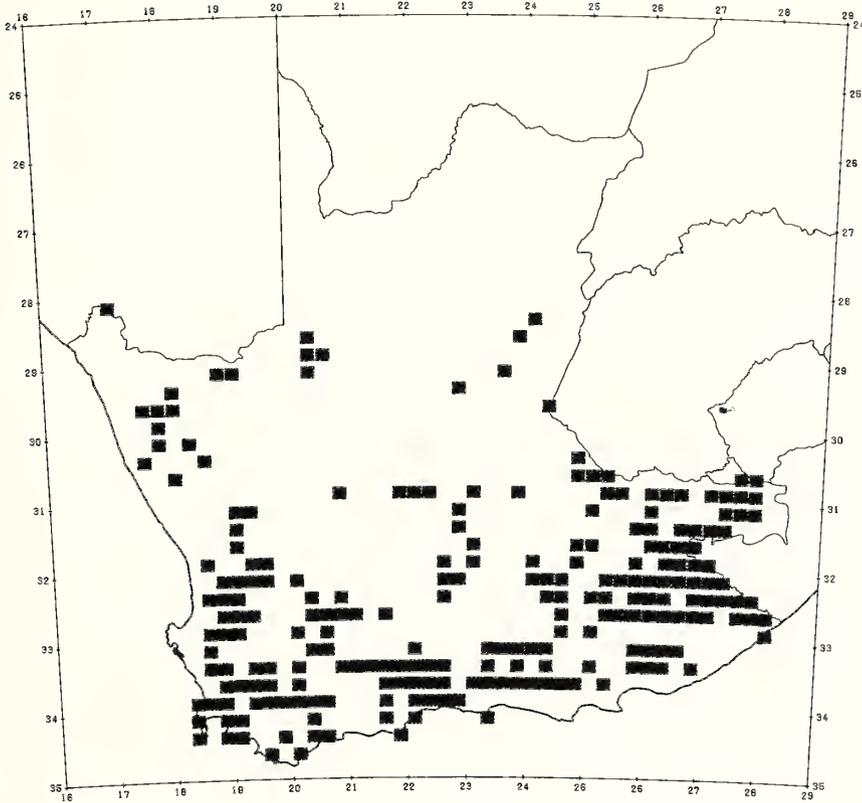


Fig. 34. Distribution of the Black Eagle, 1970 – 1979.

Tawny Eagle

Aquila rapax

Distribution (Figs 35 and 36)

1700–1969: This distribution accords with that given by Snow (1978).

1970–1979: This distribution is more restricted than that given by McLachlan & Liversidge (1978).

Habitat

Bushveld, karoo and grassland. In habitats devoid of indigenous trees the species breeds in exotic trees, e.g. *Pinus* spp., and on powerline pylons.

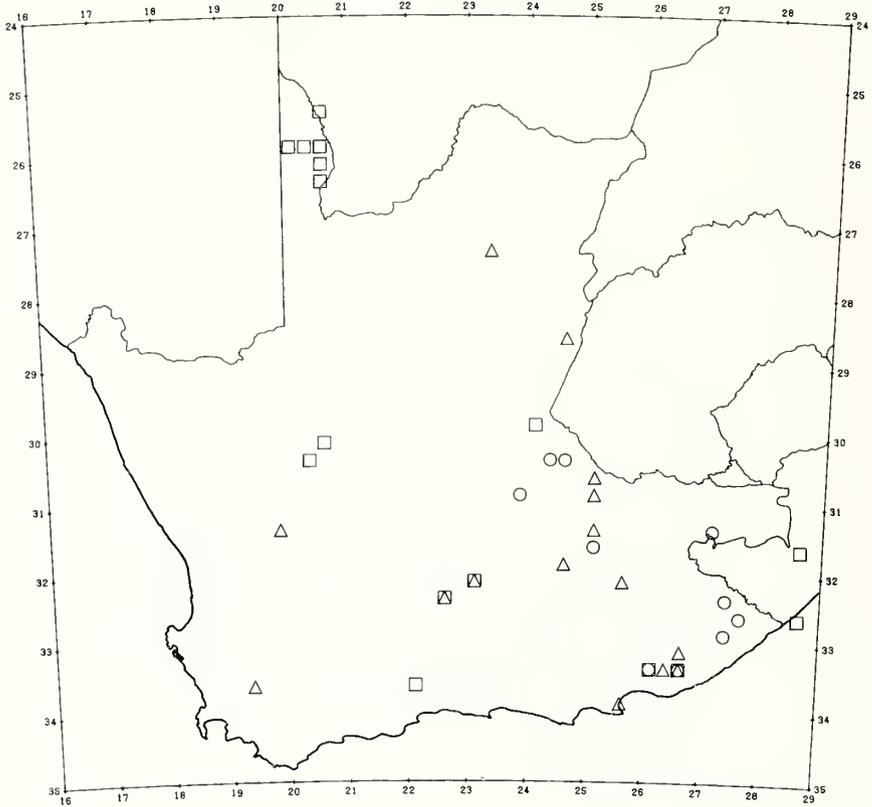


Fig. 35. Distribution of the Tawny Eagle, 1700 – 1969.

Status

Resident but scarce; the species has decreased in range in the Province. *A. rapax* is persecuted by small-stock farmers and outside the Kalahari Gemsbok National Park the total population may be relatively low (*vide* Boshoff & Vernon 1980b).

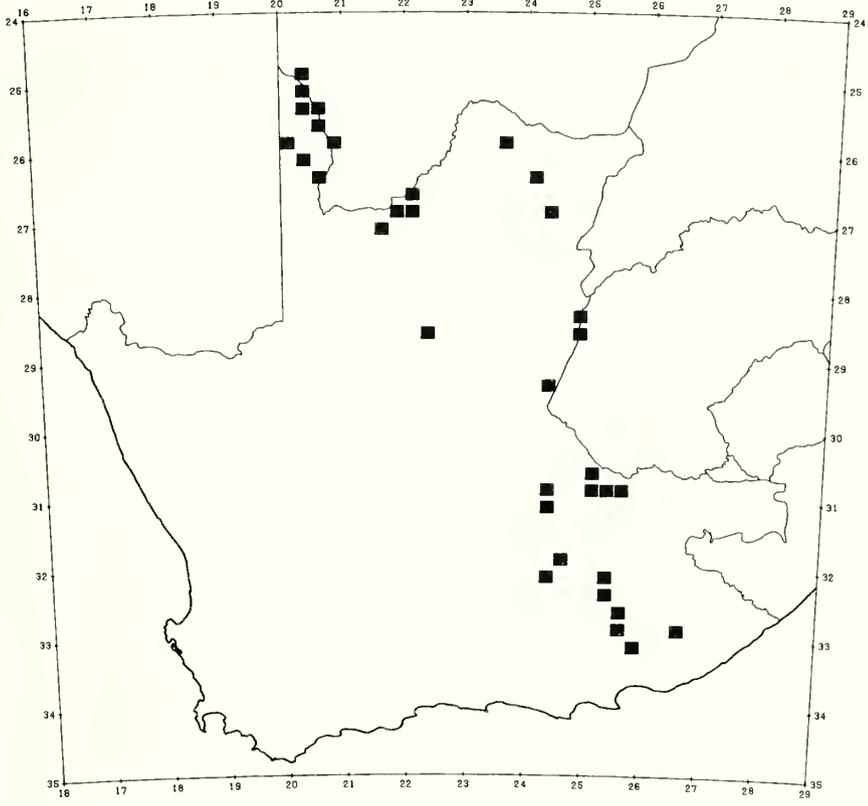


Fig. 36. Distribution of the Tawny Eagle, 1970 – 1979.

Steppe Eagle

Aquila nipalensis

Distribution (Figs 37 and 38)

McLachlan & Liversidge (1978) do not present a distribution map and only list one record, from about 1940, from Tarkastad in the E. Cape (*vide* Brooke 1974).

Habitat

Bushveld and karoo.

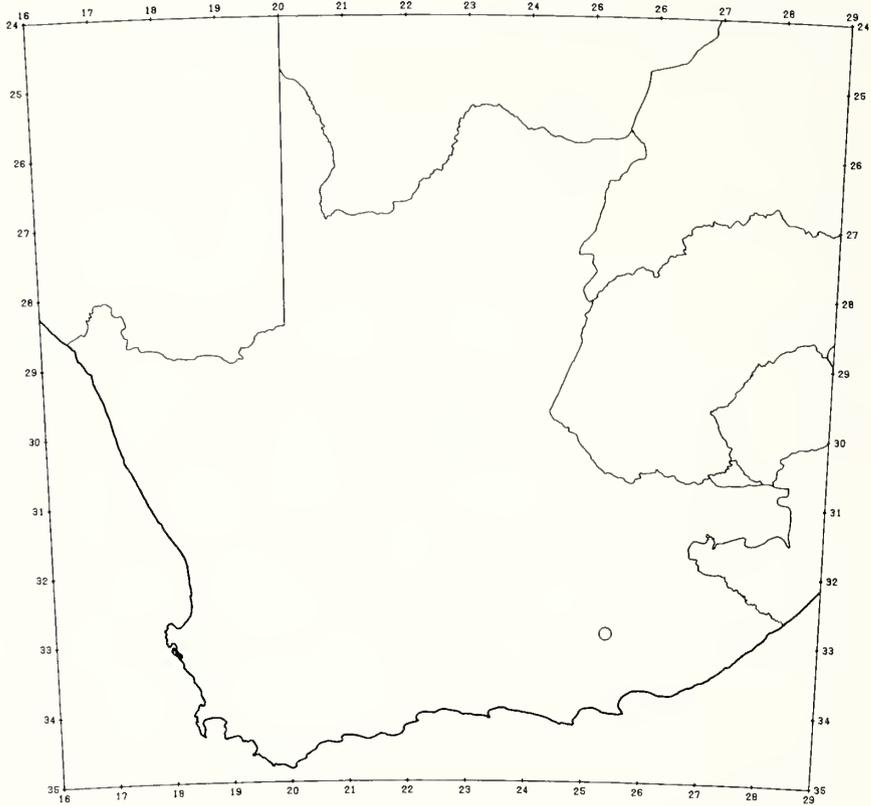


Fig. 37. Distribution of the Steppe Eagle, 1700 - 1969.

Status

A non-breeding Palaearctic migrant, which may occur in relatively large numbers in the northern parts of the N. Cape during the austral summer. To the south of this area it is a rare vagrant. The Cape Province is on the periphery of the range of this species. There has been no apparent change in status in the Province between the two periods.

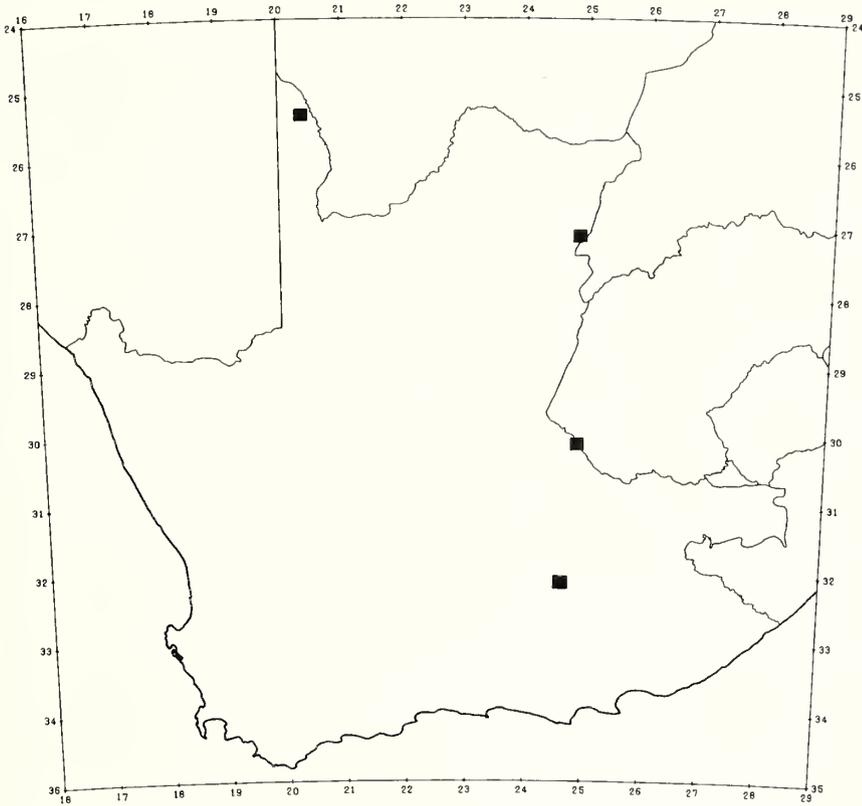


Fig. 38. Distribution of the Steppe Eagle, 1970 – 1979.

Wahlberg's Eagle

Aquila wahlbergi

Distribution (Figs 39 and 40)

The 1970s distribution is similar to that given by Snow (1978) but the S. Cape record mapped by Snow (*op cit.*) is not accepted by the present authors due to lack of substantiating evidence and atypical habitat. The distribution map given by McLachlan & Liversidge (1978) virtually excludes *A. wahlbergi* from the Cape Province.

Habitat

Bushveld in the Cape Province. Elsewhere in Africa *A. wahlbergi* is a woodland species. Where it occurs in savannas it utilises large trees along water courses.

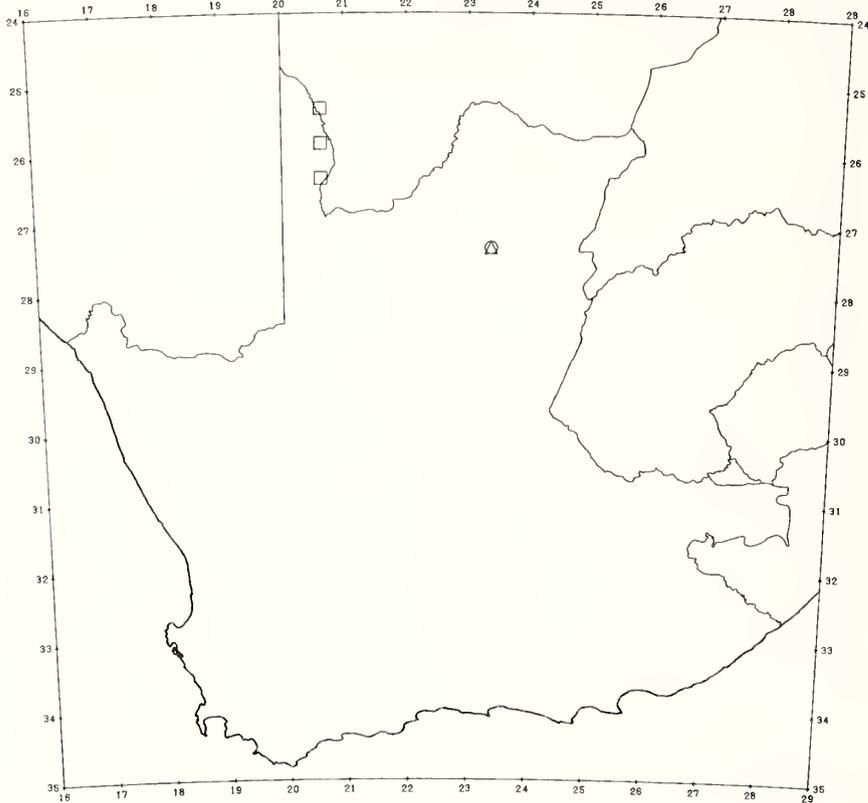


Fig. 39. Distribution of the Wahlberg's Eagle, 1700 – 1969.

Status

The status of *A. wahlbergi* in the Province is equivocal and at best can be considered a rare vagrant. It is a breeding summer migrant in southern Africa and the N. Cape is at the southern periphery of its range. There are 12 records of this species in the Province, most of them from the Kalahari Gemsbok National Park. However, none of these are substantiated and there is a possibility that misidentifications may have occurred.

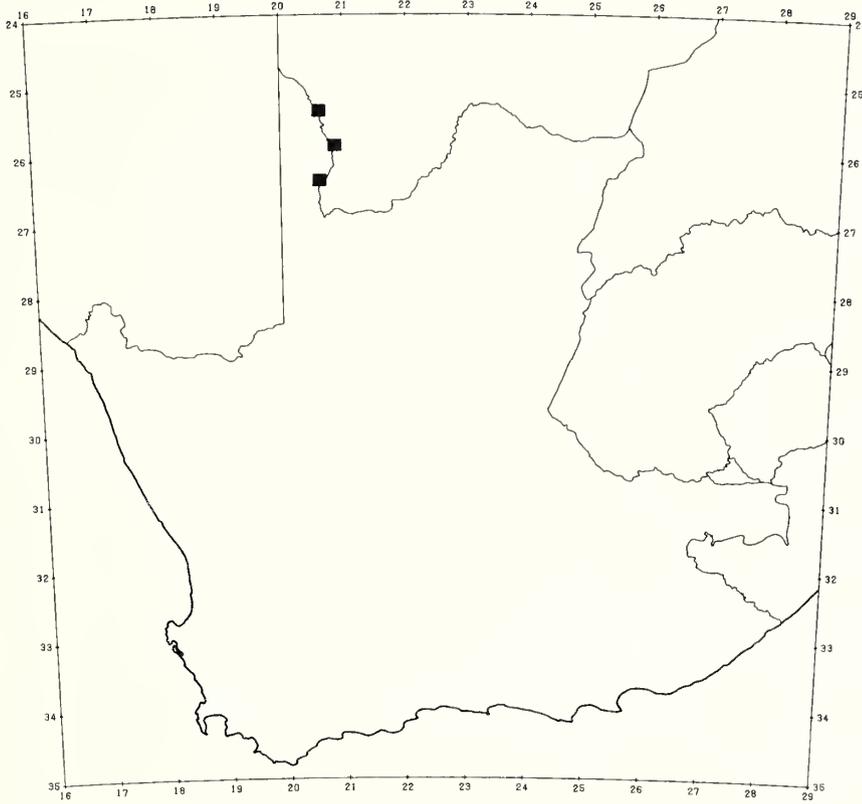


Fig. 40. Distribution of the Wahlberg's Eagle, 1970 – 1979.

Booted Eagle

Hieraaetus pennatus

Distribution (Figs 41 and 42)

The maps given for the distribution of *H.pennatus* by both McLachlan & Liversidge (1978) and Snow (1978) are inadequate.

Habitat

Karoo, macchia and grassland, especially at their ecotones. Specifically the species is found in kloofs and gorges where it breeds on cliffs, however, birds do hunt in open country well away from such sites.

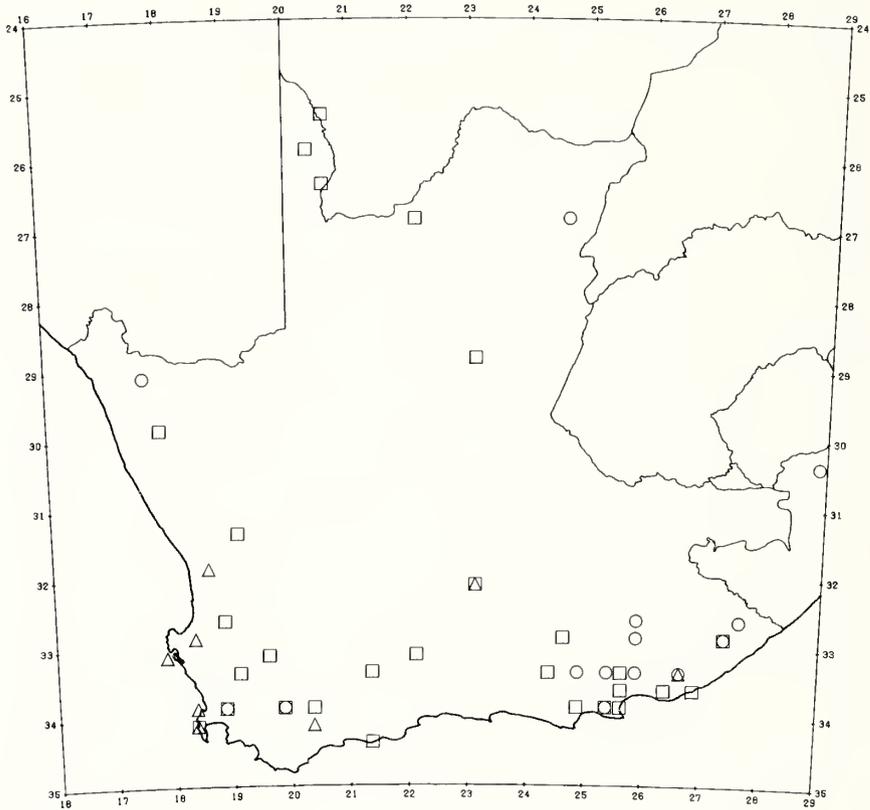


Fig. 41. Distribution of the Booted Eagle, 1700 – 1969.

Status

H. pennatus is a breeding summer migrant with nesting confined to the karoo—macchia and karoo—grassland ecotone. Non-breeding Palaearctic migrants supplement the southern African population (Brooke *et al.* 1980). Birds breeding in the southern parts of the Province move to areas north of 29° S during winter. The species was long thought to be a rare migrant and is listed as “rare and vulnerable” by Siegfried *et al.* (1976). However, recent studies have shown *H. pennatus* to be a common eagle in the Province (Brooke *et al. op cit.*). There is controversy as to whether the species has increased in recent years (Benson 1979), or has always been present but was overlooked and misidentified (Brooke *et al. op cit.*).

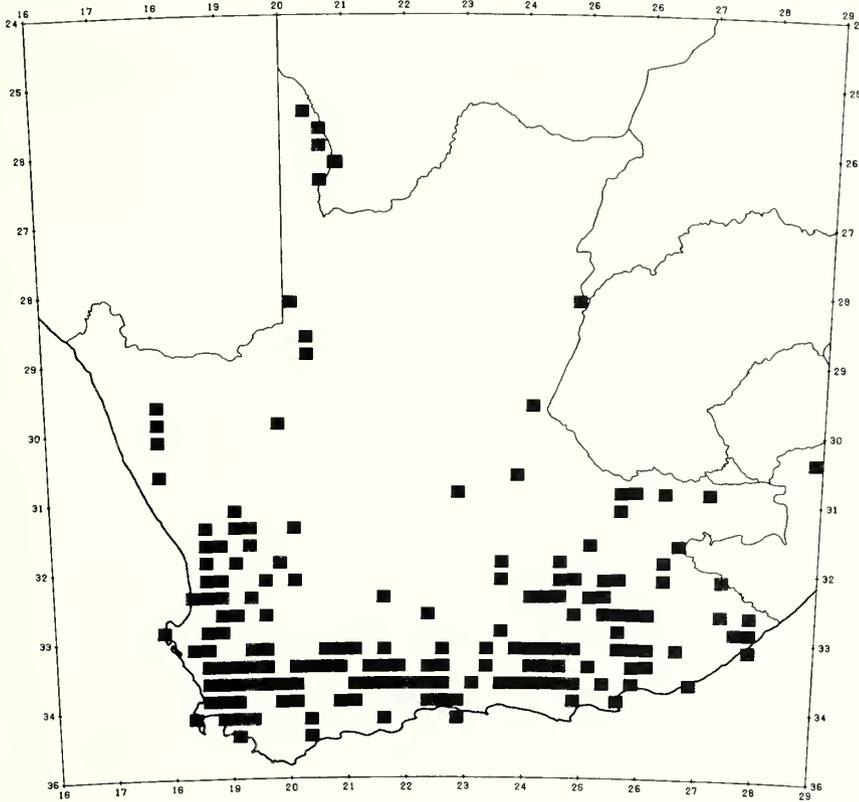


Fig. 42. Distribution of the Booted Eagle, 1970 – 1979.

Hawk Eagle

Hieraaetus fasciatus

Distribution (Figs 43 and 44)

The distribution maps presented by McLachlan & Liversidge (1978) and Snow (1978) are inadequate as none of the published records for the S.W. Cape, S. Cape and E. Cape is accepted by the present authors (see "Status").

Habitat

No information for the Cape Province but apparently bushveld. Elsewhere in Africa in woodland associated with hilly terrain.

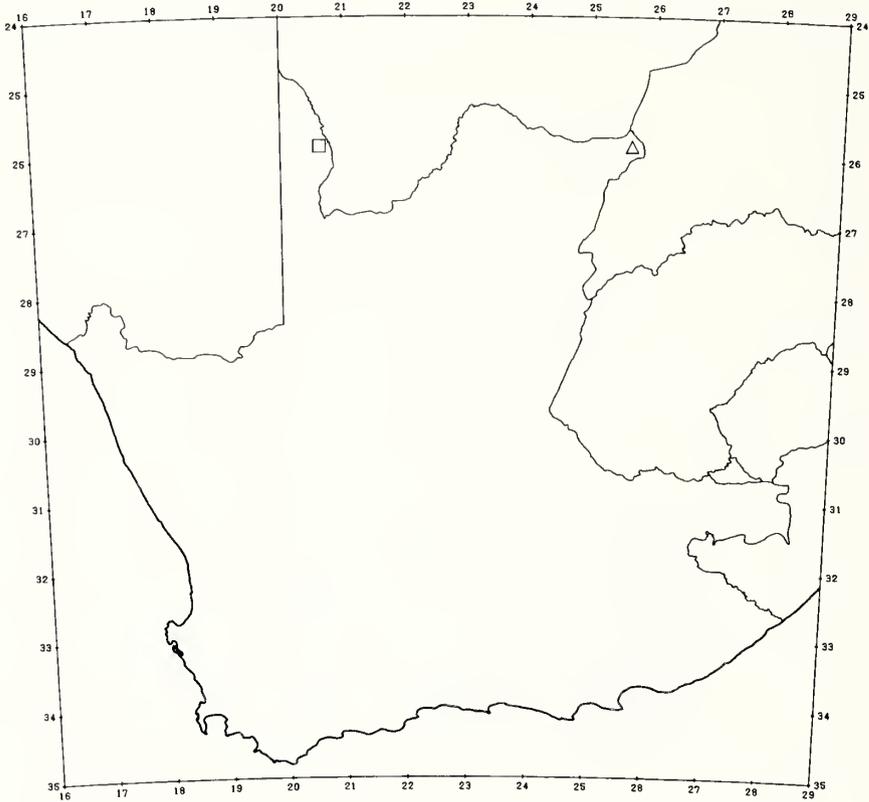


Fig. 43. Distribution of the Hawk Eagle, 1700 – 1969.

Status

With only three records for the entire 1700 – 1979 period, *H. fasciatus* is an extremely rare vagrant in the northern Cape Province, which is on the southern periphery of its range. In South Africa the furthest records to the south are from Greytown in Natal (approx. 29° S) (Cyrus & Robson 1980). There is no apparent change in the status in the Province between the two periods.

The record of a former specimen of *H. fasciatus* from the Wynberg district near Cape Town (Layard 1867) is not accepted here due to lack of substantiating data and atypical habitat. Similarly the published records of this species from the E. Cape and S. Cape (one) are not accepted due to incorrect labelling of specimens (two) and unconfirmed sight records (three).

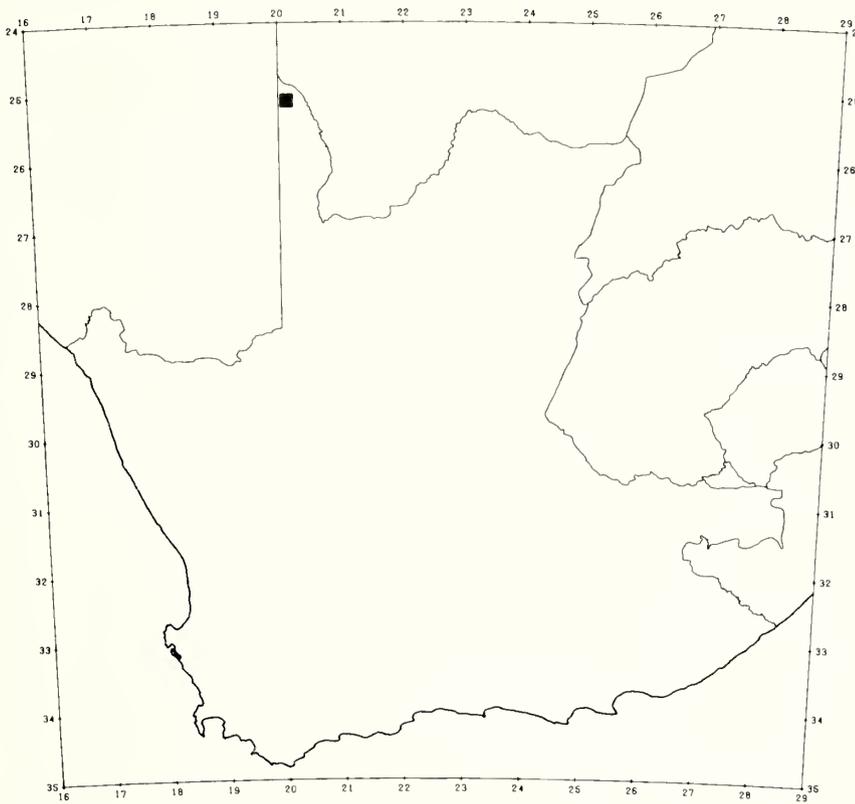


Fig. 44. Distribution of the Hawk Eagle, 1970 – 1979.

Ayres' Eagle

Hieraetus ayresii

Distribution (Fig. 45)

1700–1969: This distribution accords with that given by McLachlan & Liversidge (1978). The S.W. Cape and N.W. Cape records given by Snow (1978) *sub nom. H. dubius* are rejected (Brooke & Vernon 1981).

1970–1979: No records.

Habitat

Forest and thornveld in the Cape Province. Woodland in normal range of the species.

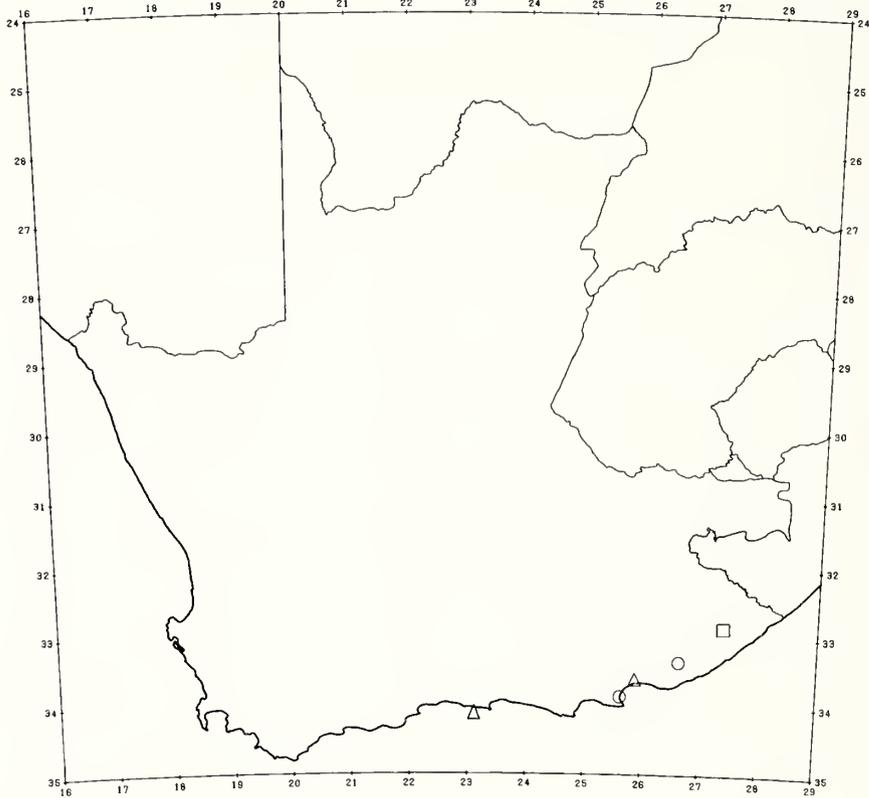


Fig. 45. Distribution of Ayres' Eagle, 1700 – 1969.

Status

A rare vagrant, well south of its normal range in Mocambique and Zimbabwe. Five of the six records from the 1700 – 1969 period are of immature birds. The earlier assumption that this species was resident in the Cape Province was based on misidentifications (Brooke & Vernon *op cit.*). Status trend in the Province indeterminate but may have ceased to occur. Siegfried *et al.* (1976) list *H. ayresii* as “rare and vulnerable” in South Africa.

Longcrested Eagle

Lophaetus occipitalis

Distribution (Figs 46 and 47)

1700–1969: The Karoo record is of a specimen from Nieu Bethesda early in the last century. This distribution accords with that given by Snow (1978) except for one S.W. Cape record mapped by that author.

1970–1979: The map in McLachlan & Liversidge (1978) fails to indicate any records for the Cape Province.

Habitat

Grassland, especially marshy areas or on the edge of forests or plantations.

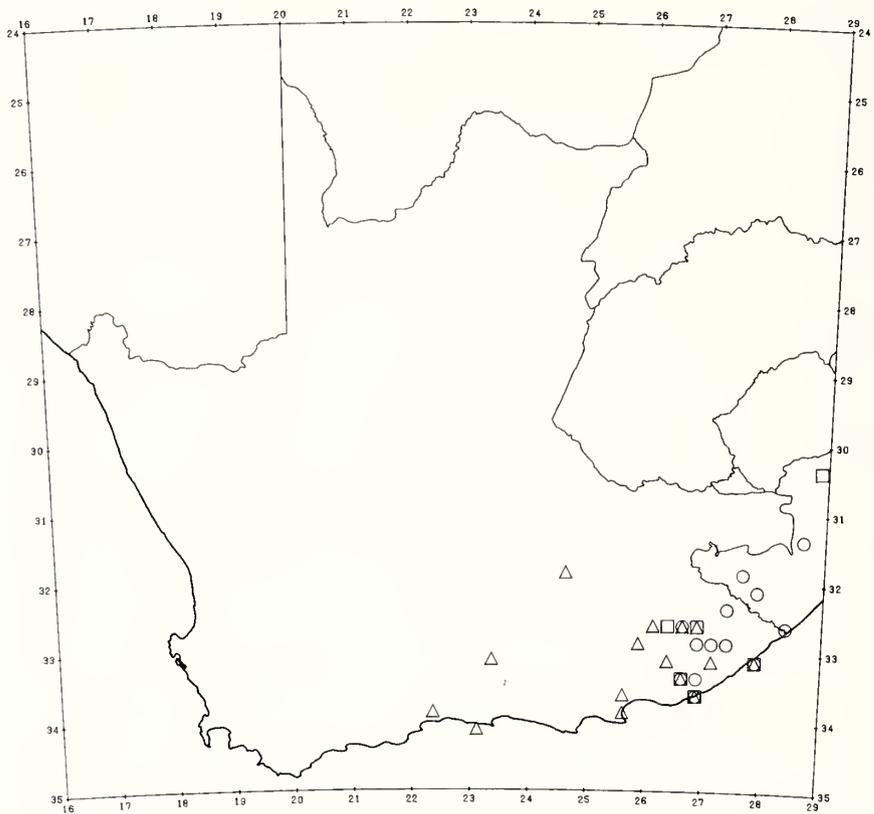


Fig. 46. Distribution of the Longcrested Eagle, 1700 – 1969.

Status

L. occipitalis has decreased in range in the Cape Province. At present its status is uncertain and at best there is only a small resident population; there are no breeding records from the Province. Individuals sighted seldom remain long in the same area. The decrease is attributed to the destruction and misutilisation of suitable habitat. The Nieu Bethesda record is considered feasible as wooded kloofs were present in the area in the past. *L. occipitalis* is listed as "rare and vulnerable" in South Africa by Siegfried *et al.* (1976).

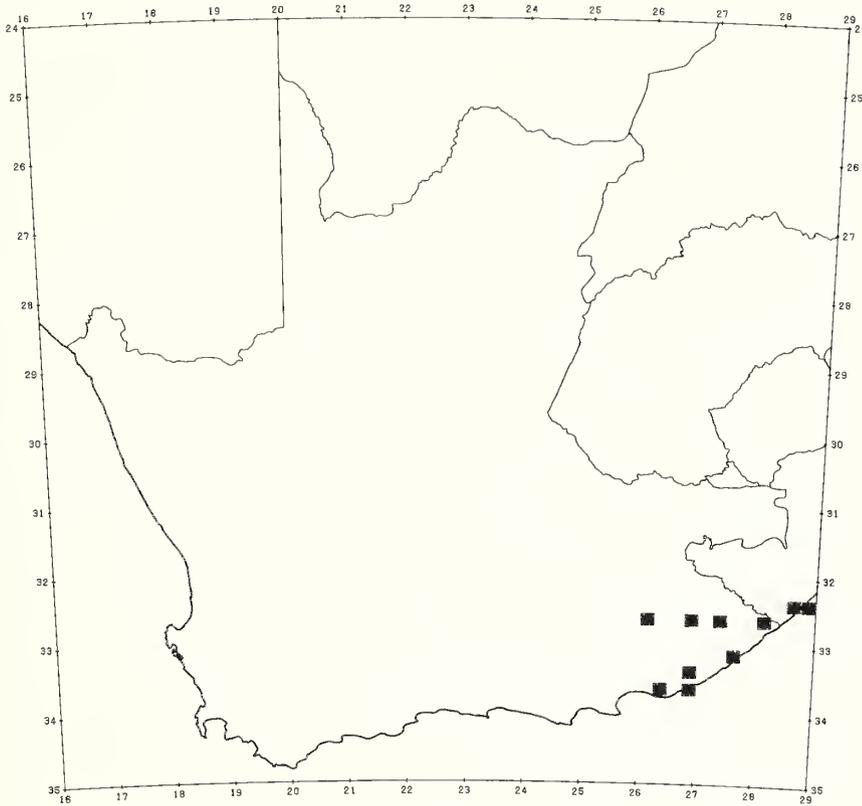


Fig. 47. Distribution of the Longcrested Eagle, 1970 – 1979.

Martial Eagle

Polemaetus bellicosus

Distribution (Figs 48 and 49)

The distribution for the pre-1970s and 1970s accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

Habitat

May be found in all habitats but more regularly in open country; seldom in forested and mountain areas.

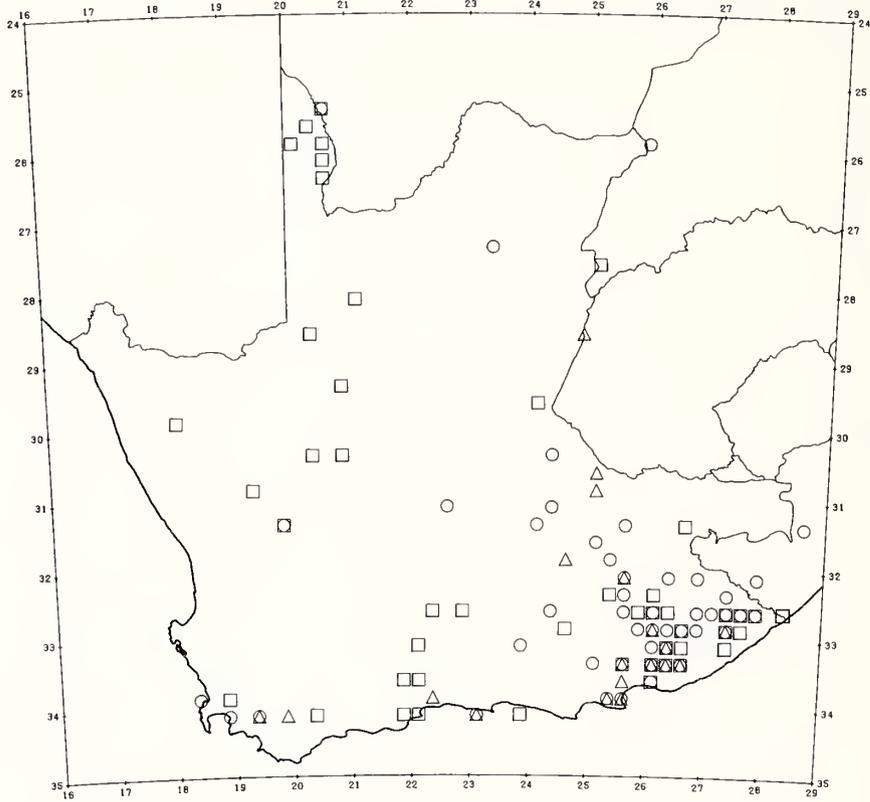


Fig. 48. Distribution of the Martial Eagle, 1700 – 1969.

Status

A scarce resident which shows no change in overall range in the Province between the two periods. *P. bellicosus* is severely persecuted by small-stock farmers (Boshoff & Vernon 1980b) but, although a decrease in numbers is considered to have taken place, there is little reliable published evidence to that effect. This species has adapted to man's activities and breeds in exotic trees, windmills and powerline pylons. *P. bellicosus* is rightly listed as "vulnerable" by Siegfried *et al.* (1976).

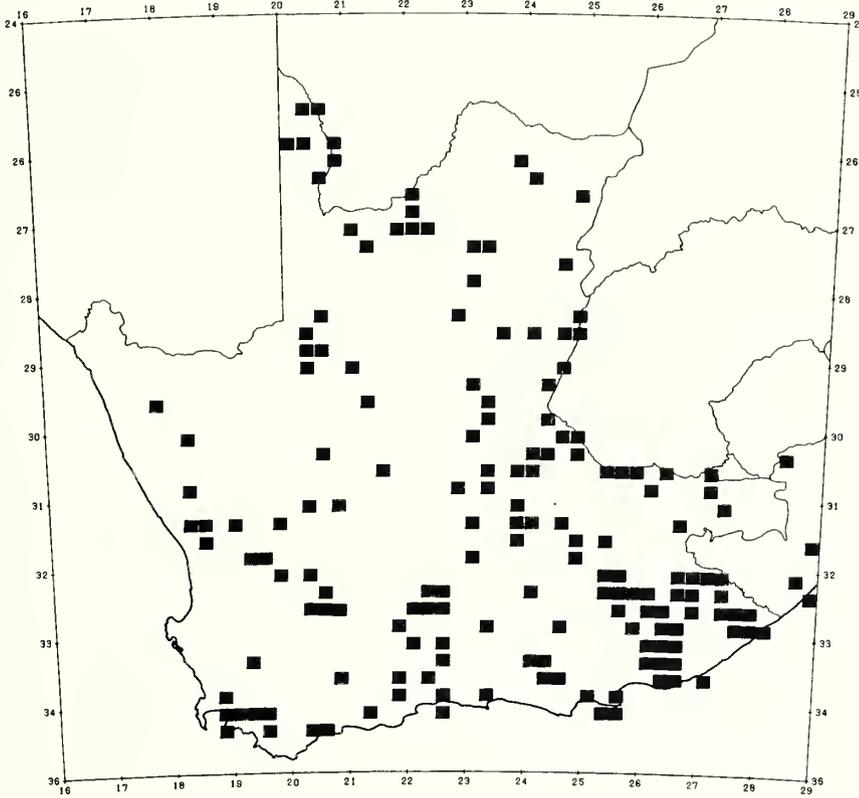


Fig. 49. Distribution of the Martial Eagle, 1970 – 1979.

Crowned Eagle

Stephanoaetus coronatus

Distribution (Figs 50 and 51)

The pre-1970 and 1970s distribution of the species accords with that given by McLachlan & Liversidge (1978) and Snow (1978) but does not extend into the Karoo *pace* McLachlan & Liversidge (*op. cit.*). The early record (breeding) from the S.W. Cape is questionable.

Habitat

Forest and also thornveld, even where such habitat is restricted to kloofs and gorges in otherwise open country.

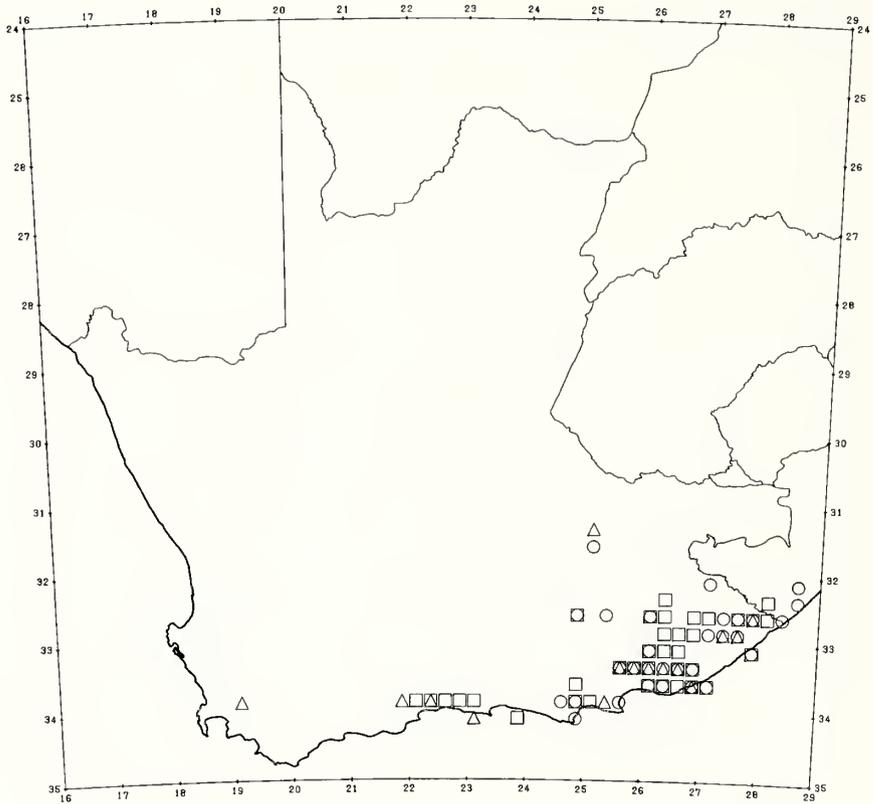


Fig. 50. Distribution of the Crowned Eagle, 1700 – 1969.

Status

A relatively scarce resident species. *S. coronatus* is directly persecuted by small-stock farmers but still has a viable population in the Province (*vide* Boshoff & Vernon 1980b). There has been no major change in range in the Province between the two periods but there may have been a disappearance from the fringes of the Karoo where the species inhabited densely wooded kloofs and ravines. The kloof vegetation was largely destroyed through misutilisation by man.

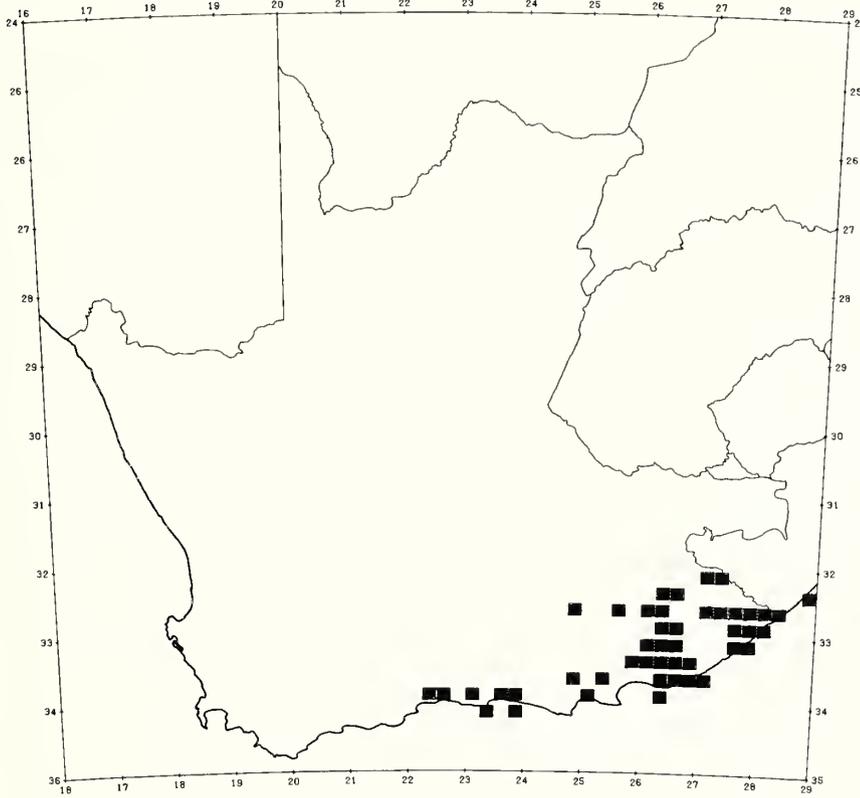


Fig. 51. Distribution of the Crowned Eagle, 1970 - 1979.

Brown Snake Eagle

Circaetus cinereus

Distribution (Figs 52 and 53)

The distribution for the pre-1970s and 1970s accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

Habitat

No information is available from the Cape Province. Elsewhere in Africa it is a woodland species.

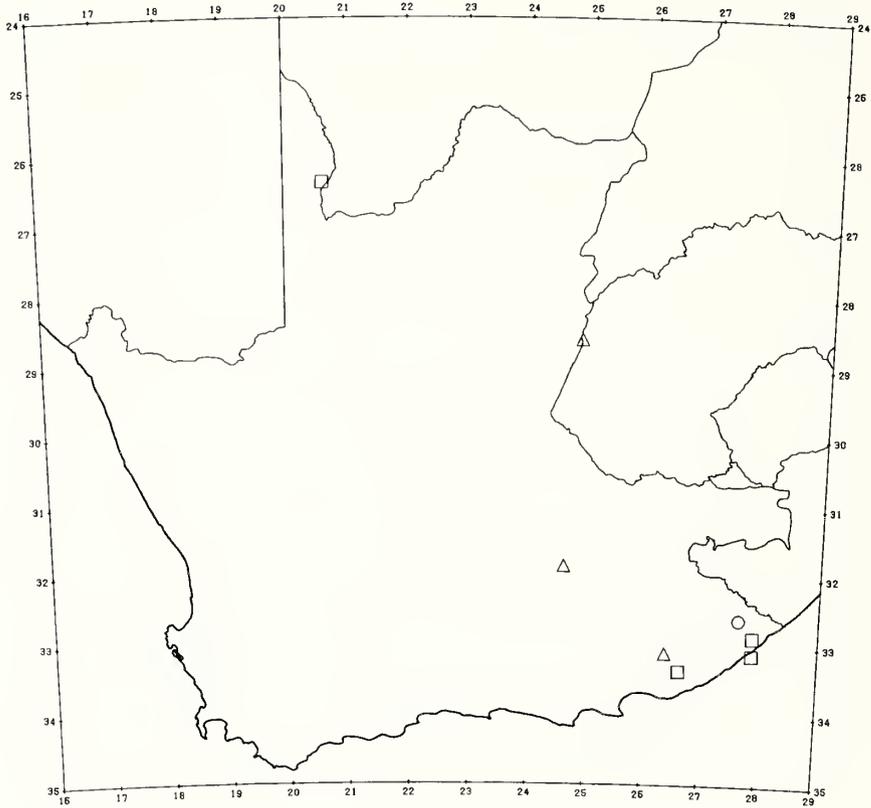


Fig. 52. Distribution of the Brown Snake Eagle, 1700 – 1969.

Status

C. cinereus is a rare vagrant to the Province and is well south of its normal range in Botswana, Transvaal, Zululand and further north. There has been no change in range in the Province between the two periods. A pre-1900 record from the Berg River is not accepted here due to lack of supporting evidence and atypical habitat.

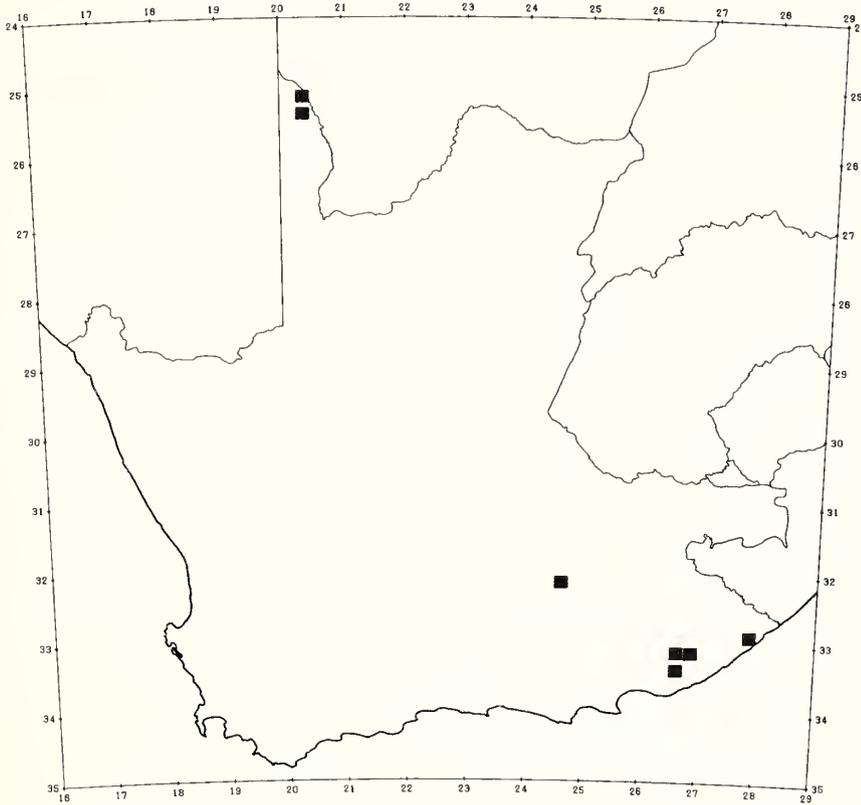


Fig. 53. Distribution of the Brown Snake Eagle, 1970 – 1979.

Blackbreasted Snake Eagle

Circaetus gallicus

Distribution (Figs 54 and 55)

The distribution for the pre-1970s and 1970s accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

Habitat

All habitats, except forest and mountain areas but most often in open country.

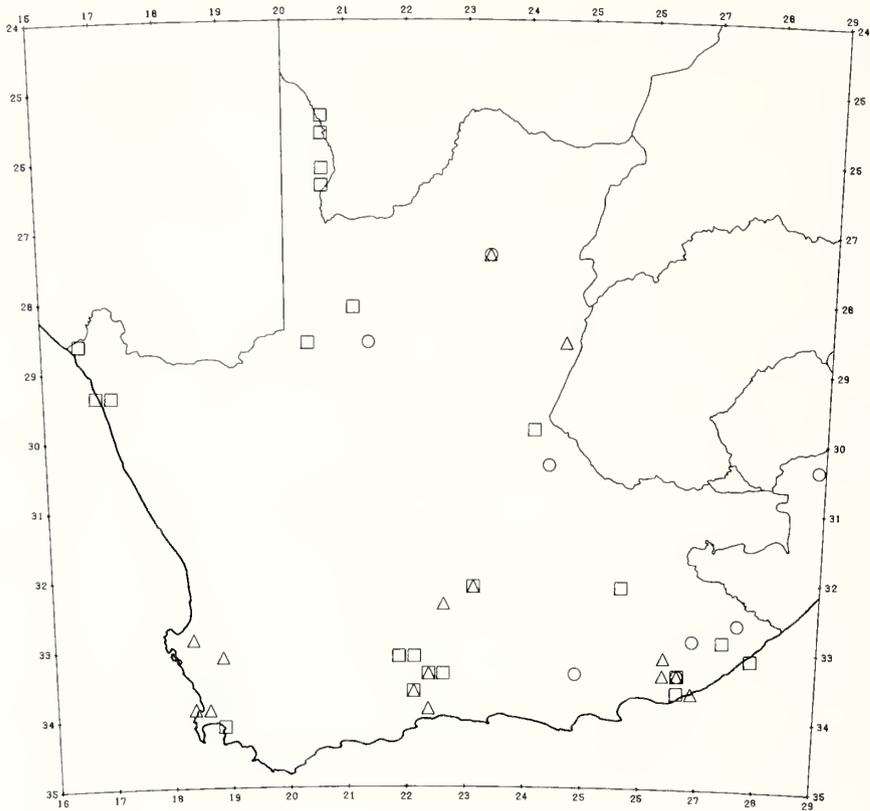


Fig. 54. Distribution of the Blackbreasted Snake Eagle, 1700 – 1969.

Status

A resident species which is, and has always been, rare. Although there are five breeding records from the Province, the majority of the birds recorded may be vagrants from Botswana, Namibia and the Transvaal. *C. gallicus* does not exhibit any change in range in the Province between the two periods.

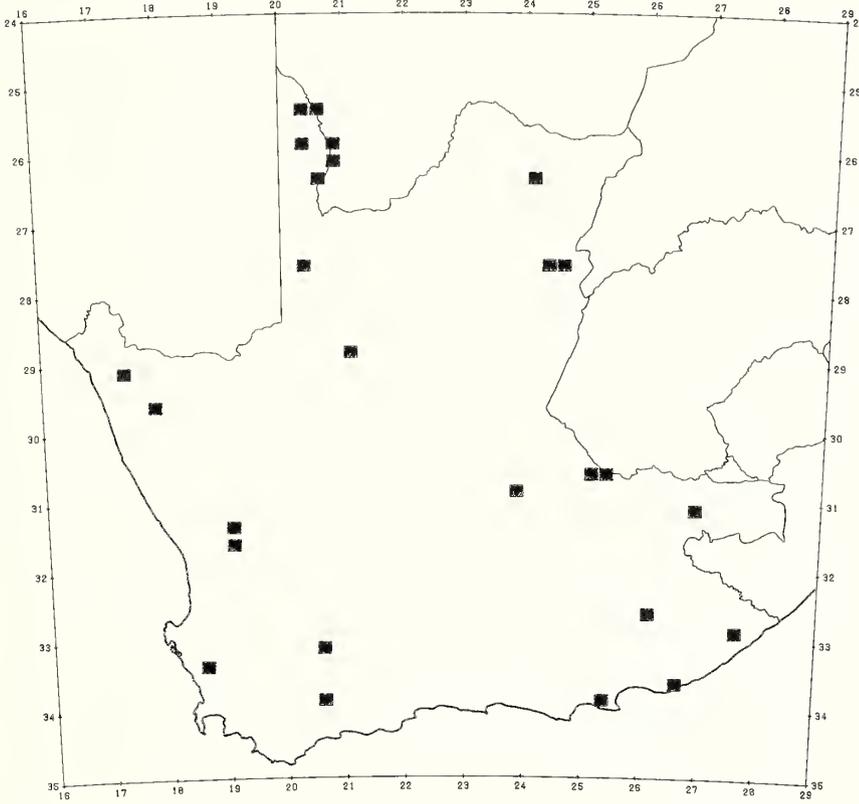


Fig. 55. Distribution of the Blackbreasted Snake Eagle, 1970 – 1979.

Bateleur

Terathopius ecaudatus

Distribution (Figs 56 and 57)

1700–1969: This distribution accords to some extent with that given by Snow (1978), except that two records from the Karoo are given by this author.

1970–1979: This distribution is far more restricted than that given by McLachlan & Liversidge (1978).

Habitat

Bushveld in the N. Cape and open country in the E. Cape. Elsewhere in its range in Africa the species is found in woodland and savanna.

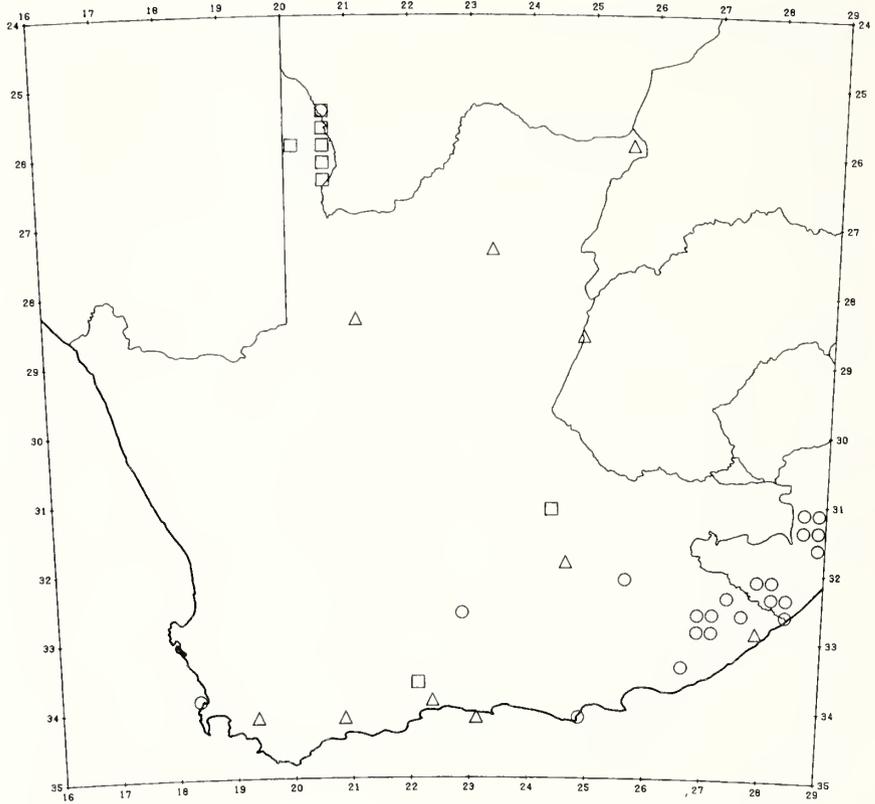


Fig. 56. Distribution of the Bateleur, 1700 – 1969.

Status

There is no satisfactory evidence that *T. ecaudatus* ever bred in the Province and so may always have been a rare vagrant. A record of a nestling from Nieu Bethesda in the early part of the last century is not accepted by the present authors. Reasons for this are given as atypical breeding habitat and the fact that it is the only breeding record of *T. ecaudatus* from the entire Province. These aspects raise suspicions of incorrect labelling or a transported captive bird. The species may be resident in the Kalahari Gemsbok National Park where regular sightings are made. Recent sight records from the S. Cape and S.W. Cape require confirmation due to possible confusion with *Buteo rufofuscus*. *T. ecaudatus* exhibits a decreased range in the Province between the two periods. The species is actively persecuted by small-stock farmers in the N. Cape. The species should be included in a revised *South African Red Data Book: Aves*.

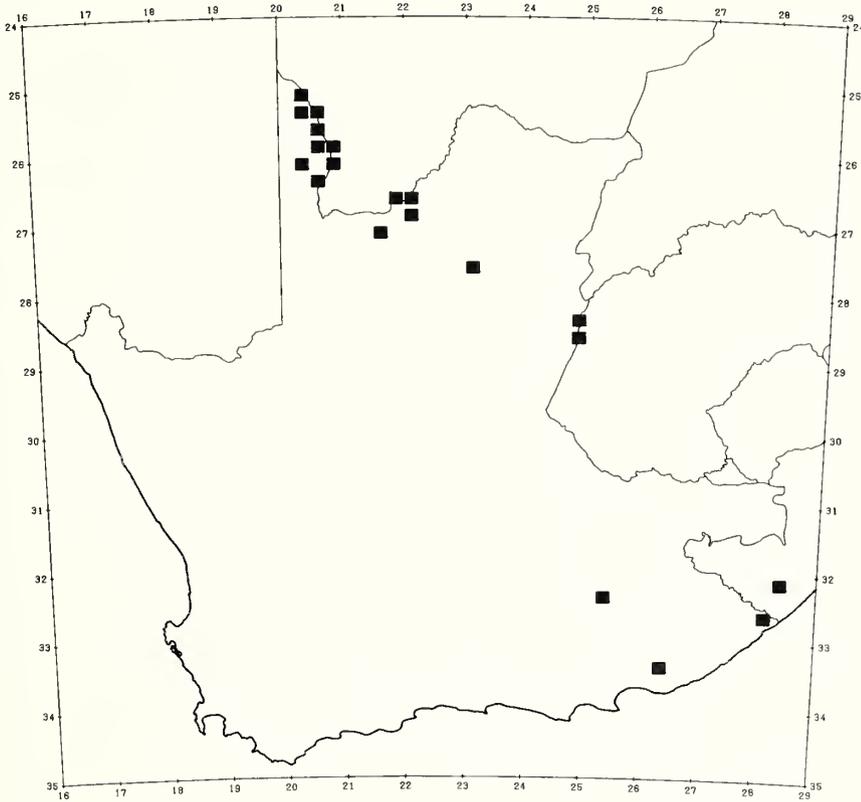


Fig. 57. Distribution of the Bateleur, 1970 – 1979.

Fish Eagle

Haliaeetus vocifer

Distribution (Figs 58 and 59)

The distribution for the pre-1970s and 1970s accords with that given by Snow (1978) but is not as widespread as that given by McLachlan & Liversidge (1978).

Habitat

Perennial rivers, lakes, dams and estuaries.

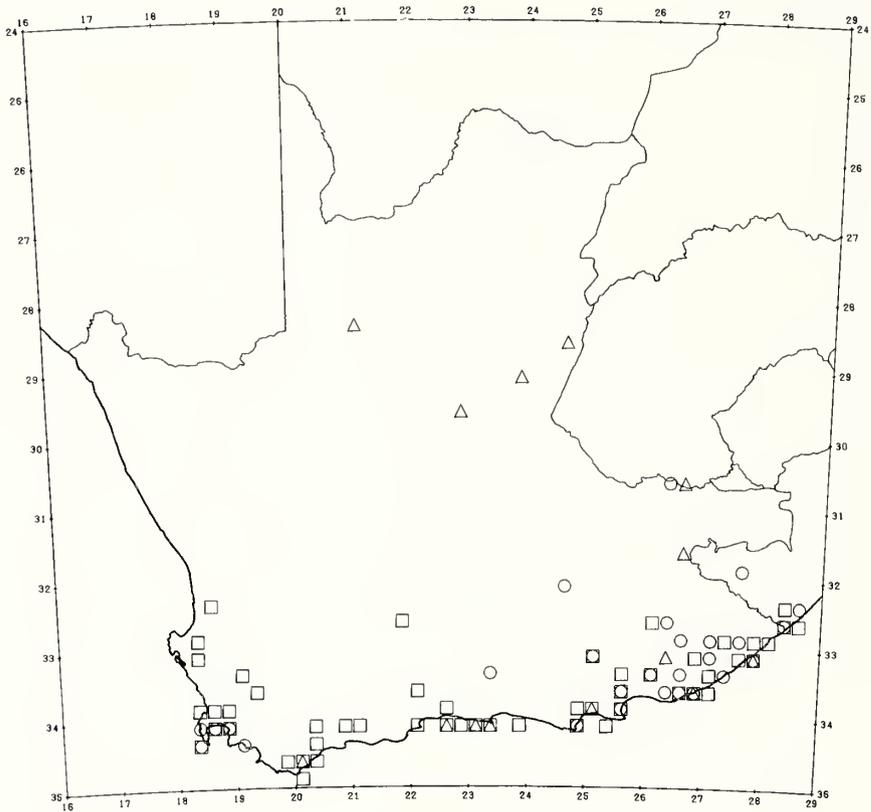


Fig. 58. Distribution of the Fish Eagle, 1700 – 1969.

Status

A common resident species which shows no change in status in the Province between the two periods (*vide* Boshoff & Vernon 1980b). Although listed as “vulnerable” in South Africa by Siegfried *et. al.* (1976), due to loss of natural habitats, this has been largely balanced by new habitats created by means of artificial water impoundments.

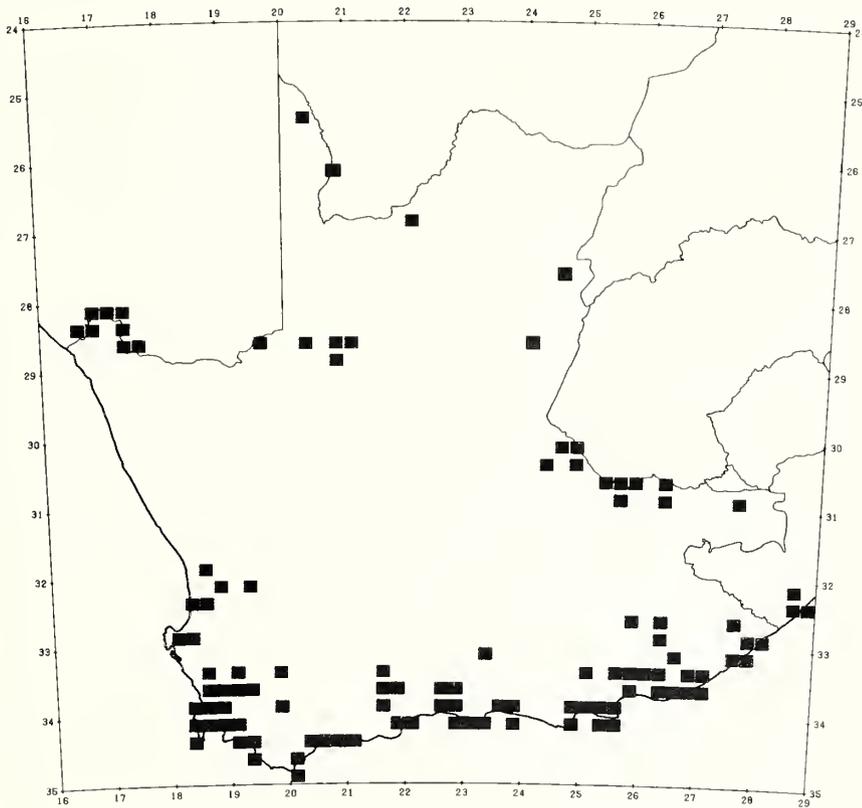


Fig. 59. Distribution of the Fish Eagle, 1970 – 1979.

Steppe Buzzard

Buteo buteo

Distribution (Figs 60 and 61)

The distribution for the 1970s is more restricted than that given by McLachlan & Liveridge (1978).

Habitat

Grassland, macchia and to some extent thornveld; particularly croplands and road verges.

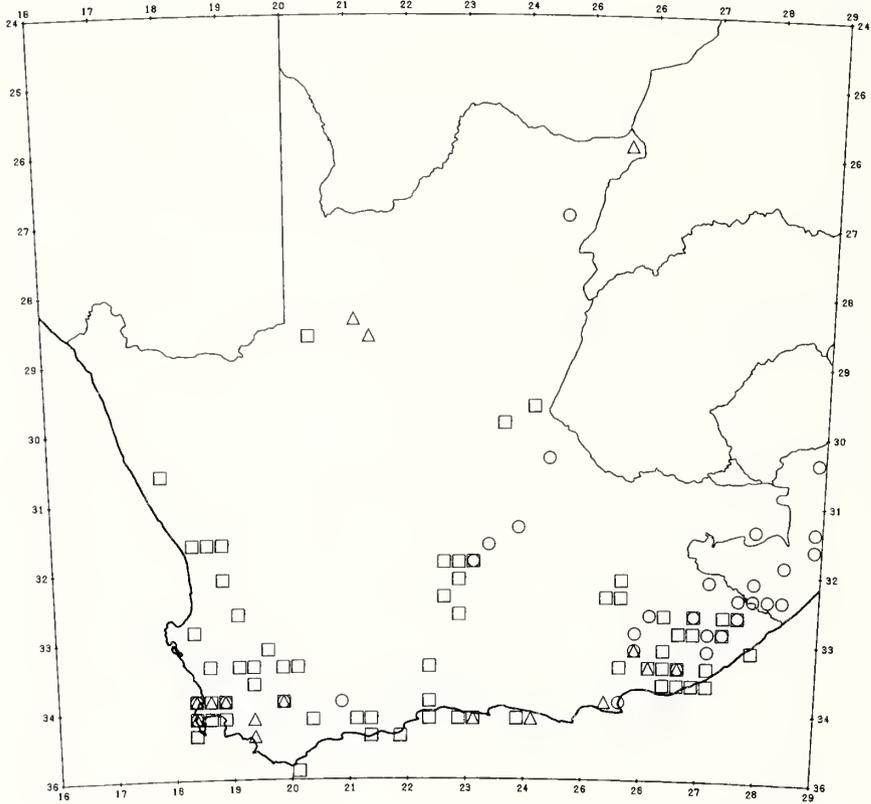


Fig. 60. Distribution of the Steppe Buzzard, 1700 – 1969.

Status

A common non-breeding Palaearctic migrant which is present during the austral summer. The species exhibits an unchanged overall status in the Province between the two periods. *B. buteo* may, however, have adjusted its distribution in the Province in accordance with changes in farming activities.

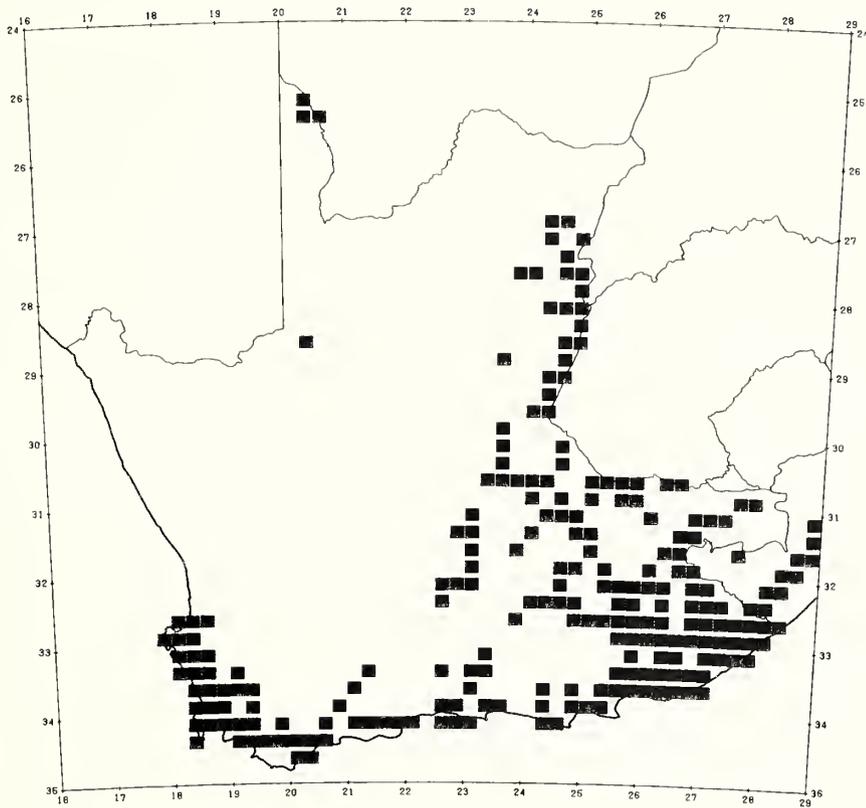


Fig. 61. Distribution of the Steppe Buzzard, 1970 – 1979.

Mountain Buzzard

Buteo tachardus

Distribution (Figs 62 and 63)

The distribution for the pre-1970s and 1970s accords with that given by Snow (1978) but is more extensive (into the S.W. Cape) than that given by McLachlan & Liversidge (1978).

Habitat

Forest and plantations of exotic species, e.g. *Pinus* spp. Despite its common name *B. tachardus* is rarely associated with mountains and, where this does occur, the birds are in or near densely wooded ravines in the footslopes.

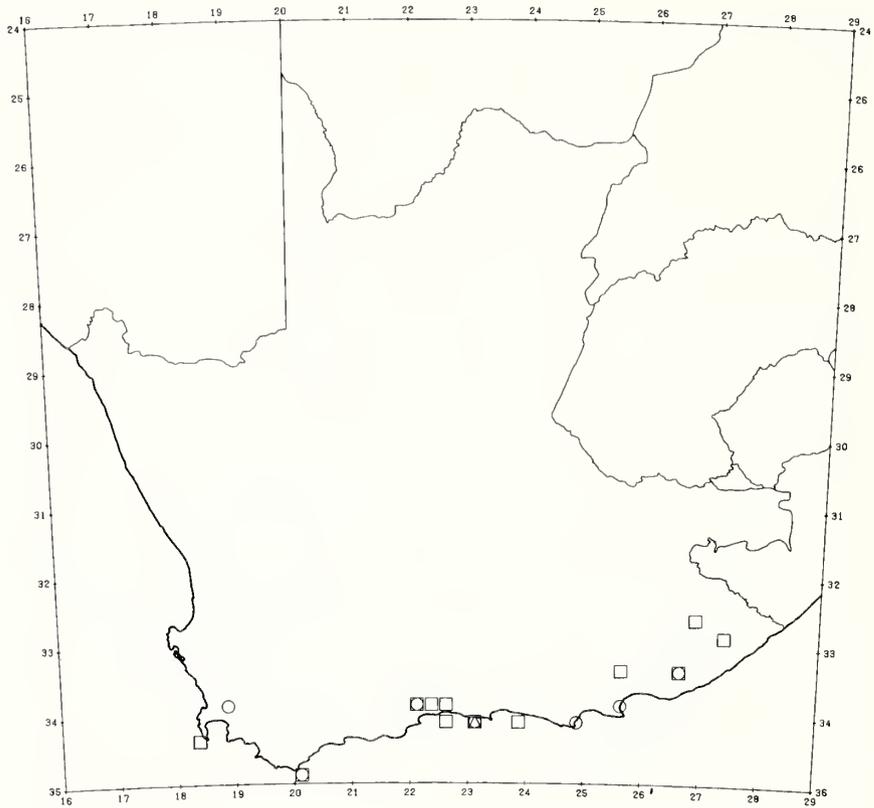


Fig. 62. Distribution of the Mountain Buzzard, 1700 – 1969.

Status

A relatively scarce resident species which shows no change in range in the Province between the two periods. In fact the species may have been overlooked in the past due to misidentification and so acquired rarity status. Although listed as "vulnerable" by Siegfried *et al.* (1976) *B. tachardus* appears to have a viable, albeit small, population in the Province. The species has adapted to plantations.

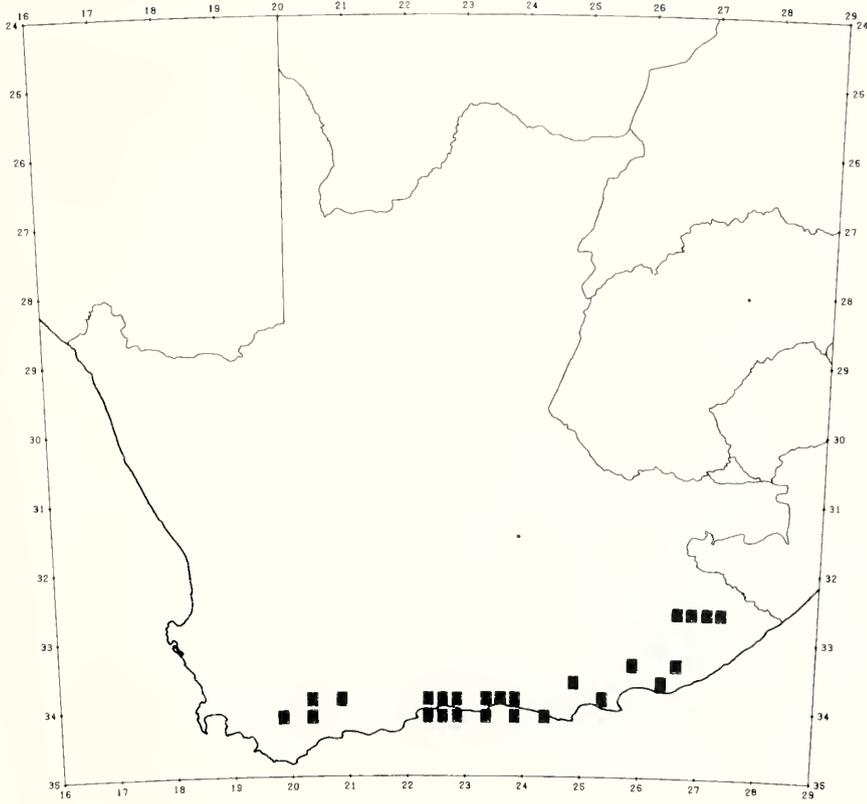


Fig. 63. Distribution of the Mountain Buzzard, 1970 – 1979.

Jackal Buzzard

Buteo rufofuscus

Distribution (Figs 64 and 65)

1700–1969: This distribution accords with that given by Snow (1978).

1970–1979: This distribution is more restricted than that given by McLachlan & Liversidge (1978).

Habitat

Found in all habitats, except bushveld, where there are cliffs and gorges. Appears to prefer open habitats e.g. macchia, grassland and karoo.

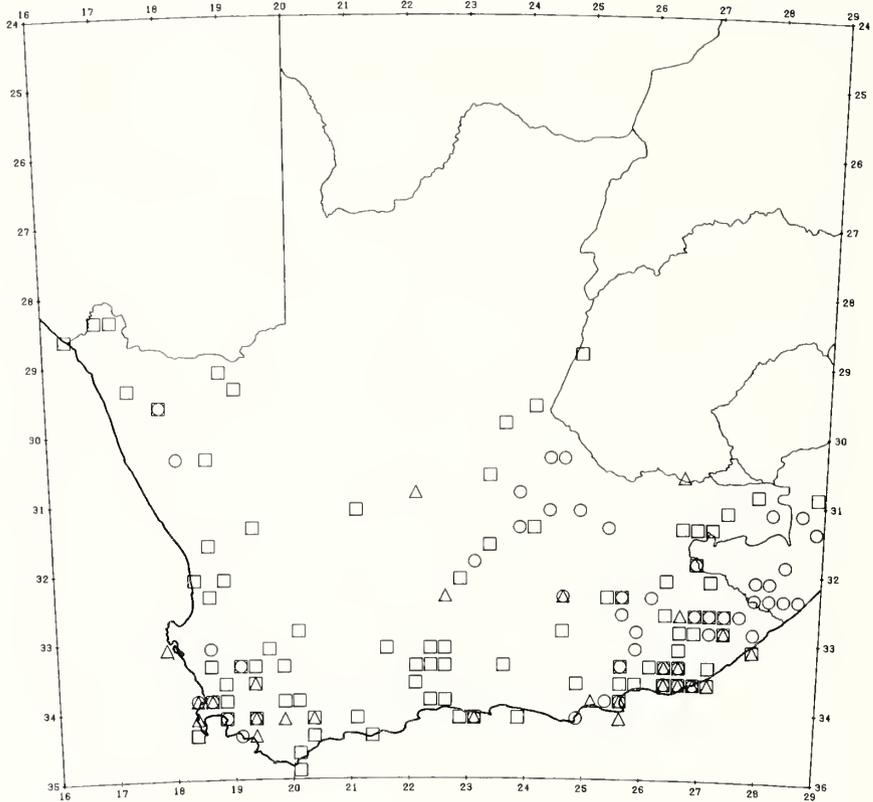


Fig. 64. Distribution of the Jackal Buzzard, 1700 – 1969.

Status

A common resident which is the third most frequently recorded raptor in the Province. There has been no apparent change in status in the Province between the two periods.

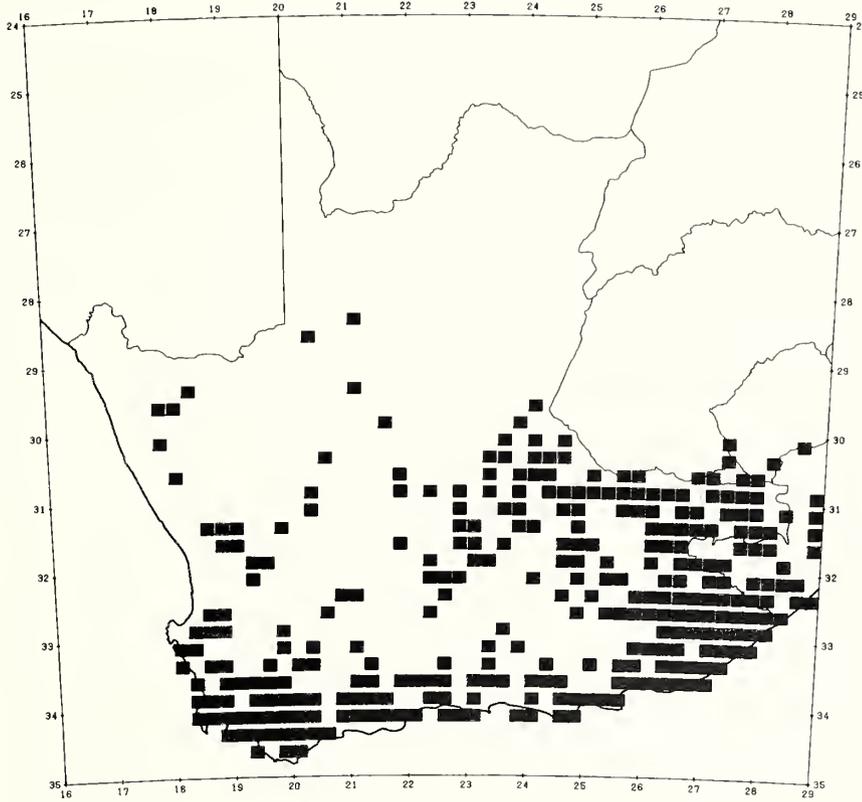


Fig. 65. Distribution of the Jackal Buzzard, 1970 – 1979.

Redbreasted Sparrowhawk

Accipiter rufiventris

Distribution (Figs 66 and 67)

The distribution for the pre-1970s and 1970s accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

Habitat

Forests, plantations and groves of exotic trees in grasslands. In the E. Cape and S. Cape the species is absent from coastal forests.

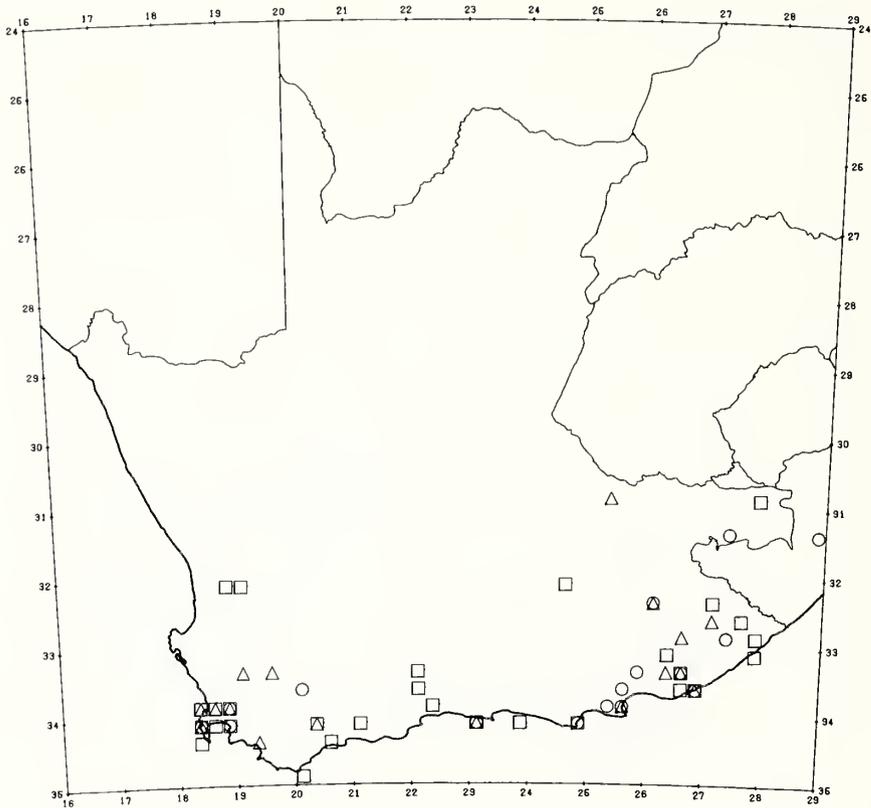


Fig. 66. Distribution of the Redbreasted Sparrowhawk, 1700 – 1969.

Status

A relatively scarce resident species, *A. rufiventris* extended its range into the grassland (treeless areas) of the E. Cape as exotic trees were planted and is now found around homesteads in country where it would not previously have occurred. This range increase is not obvious from a comparison of the maps for the two periods.

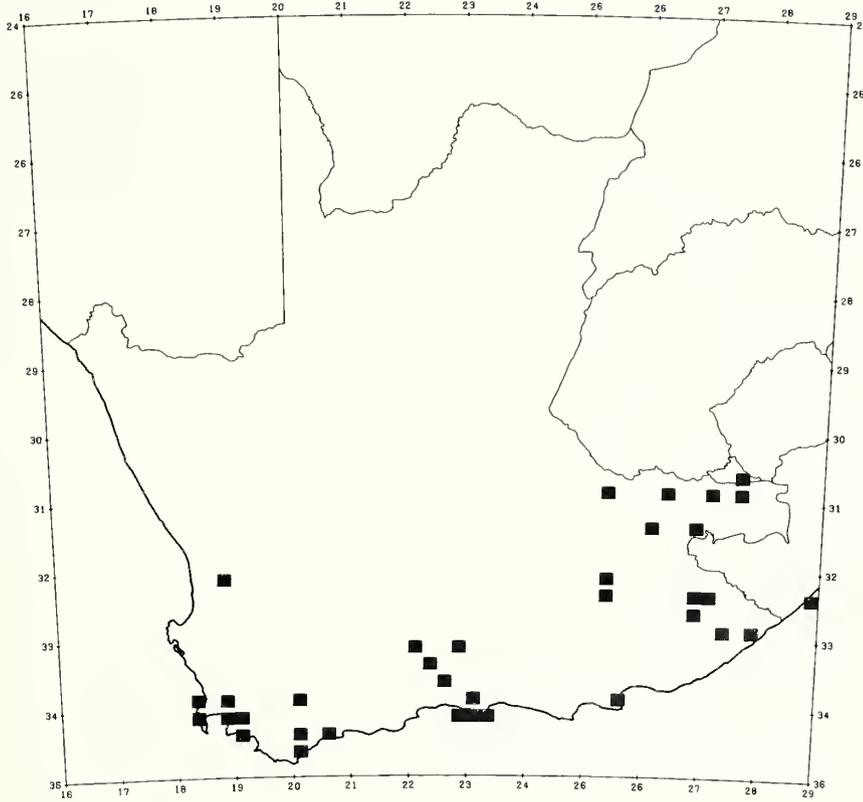


Fig. 67. Distribution of the Redbreasted Sparrowhawk, 1970 – 1979.

Ovambo Sparrowhawk

Accipter ovampensis

Distribution (Figs 68 and 69)

McLachlan & Liversidge (1978) do not record this species from the Cape Province.

Habitat

Bushveld; usually *Acacia* trees along water courses.

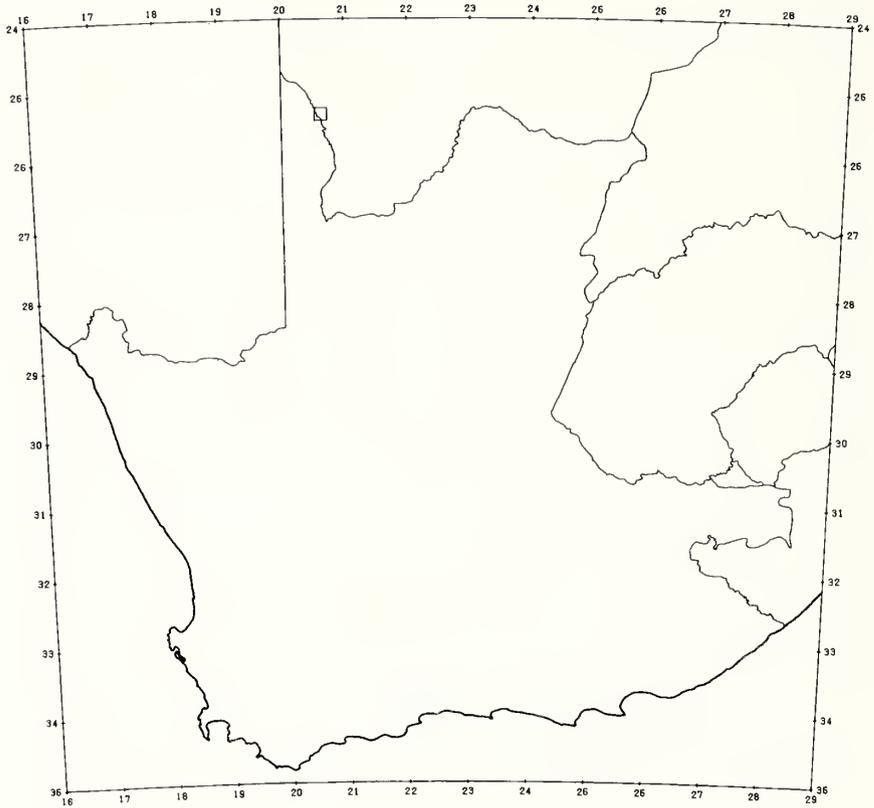


Fig. 68. Distribution of the Ovambo Sparrowhawk, 1700 – 1969.

Status

An extremely rare vagrant to the northern part of the N. Cape; the two records for the Province are far south of the normal range in northern Namibia, northern Botswana, northern Transvaal and Zimbabwe. Siegfried *et al.* (1976) consider that *A. ovampensis* might be included in a revised *South African Red Data Book: Aves*.

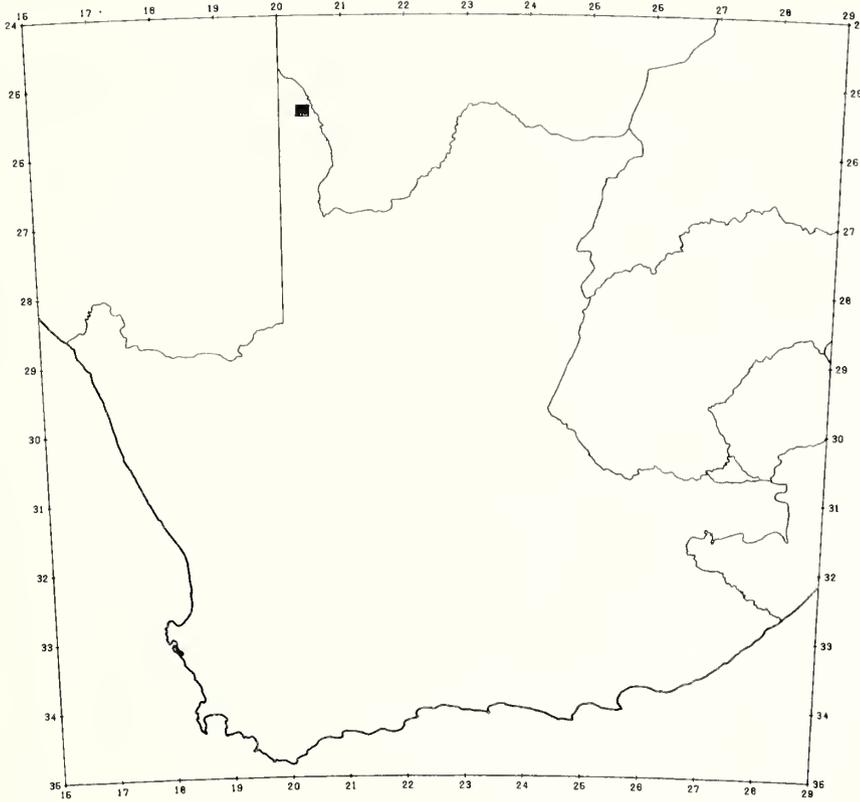


Fig. 69. Distribution of the Ovambo Sparrowhawk, 1970 – 1979.

Little Sparrowhawk

Accipiter minullus

Distribution (Figs 70 and 71)

1700–1969: This distribution accords with that given by Snow (1978).

1970–1979: This distribution accords with that given by McLachlan & Liversidge (1978) except that the species does not extend into the Karoo as shown by these authors.

Habitat

Forest and occasionally groves of exotic trees.

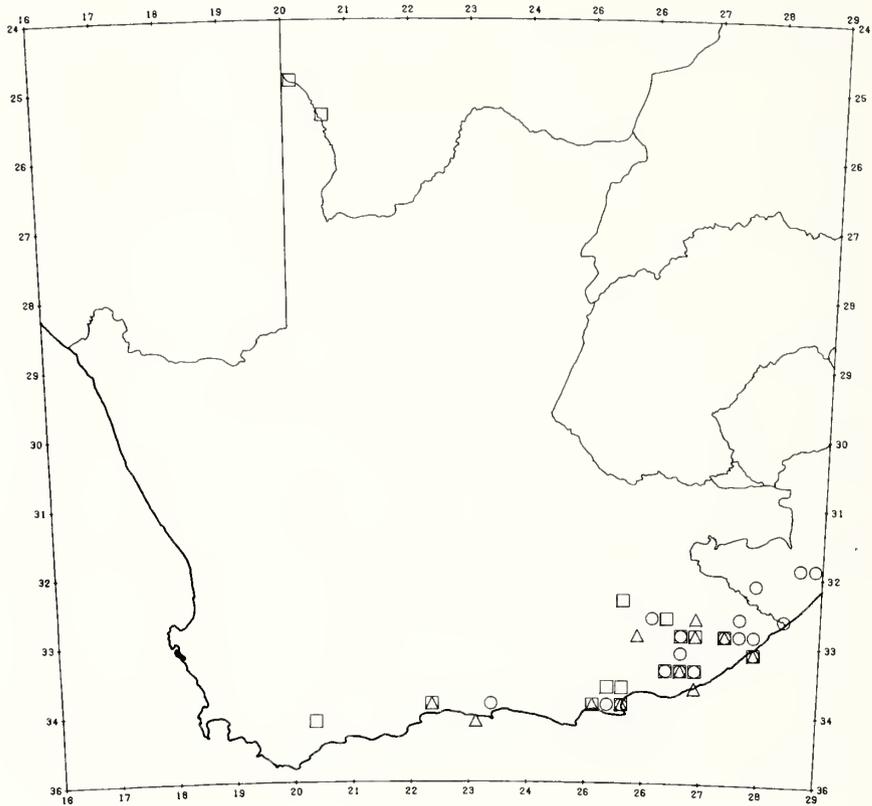


Fig. 70. Distribution of the Little Sparrowhawk, 1700 – 1969.

Status

A scarce resident which shows no change in status in the Province between the two periods.

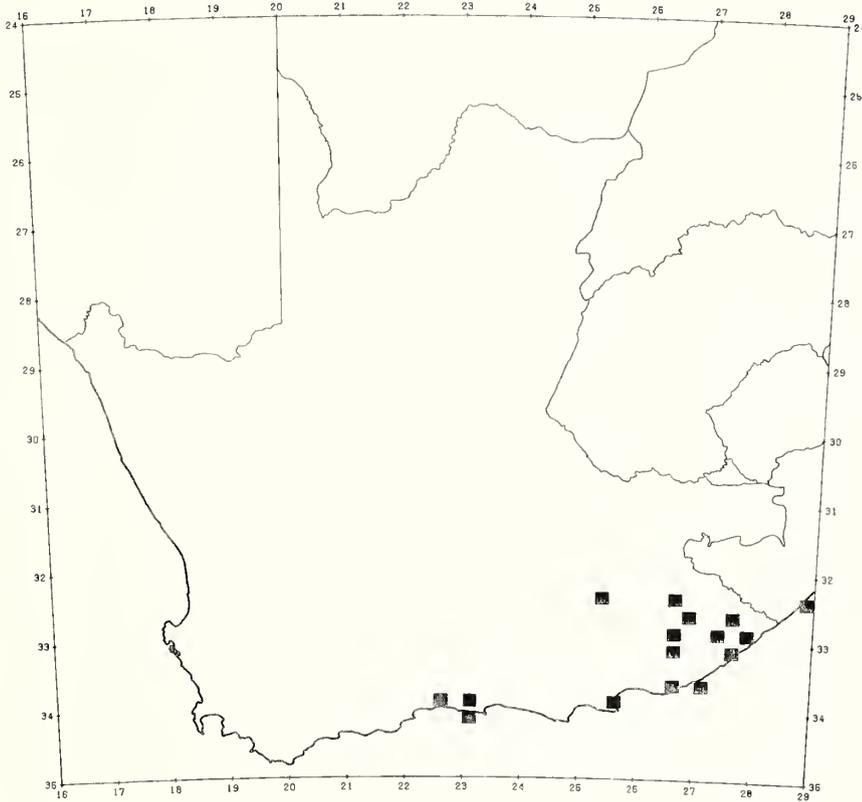


Fig. 71. Distribution of the Little Sparrowhawk, 1970 – 1979.

Black Sparrowhawk

Accipiter melanoleucus

Distribution (Figs 72 and 73)

1700–1969: This distribution coincides with that given by Snow (1978).

1970–1979: The distributions map given by McLachlan & Liversidge (1978) does not record the species in the S.W. Cape and includes the southern part of the Karoo in the range.

Habitat

Forest and plantations.

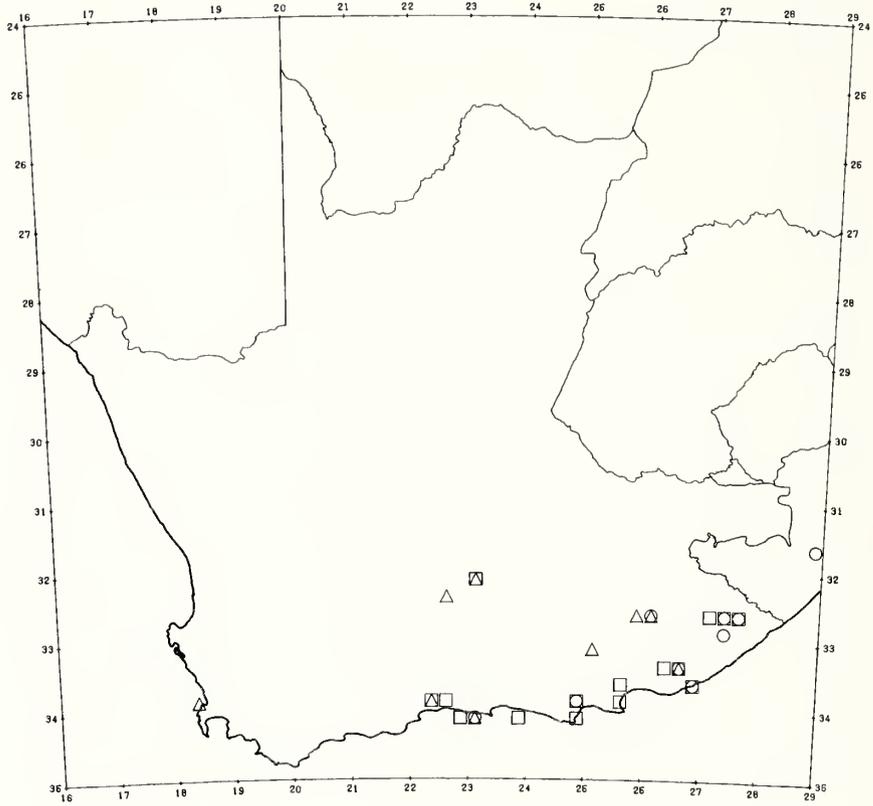


Fig. 72. Distribution of the Black Sparrowhawk, 1700 – 1969.

Status

A scarce resident which because it is unobtrusive may be commoner than thought. There has been no major change in the status of *A. melanoleucus* in the Province between the two periods, except an apparent disappearance from the Karoo. This is no doubt linked to the destruction of wooded kloof habitat. The species is recorded as “threatened at least in part of its range” in South Africa by Siegfried *et al.* (1976).

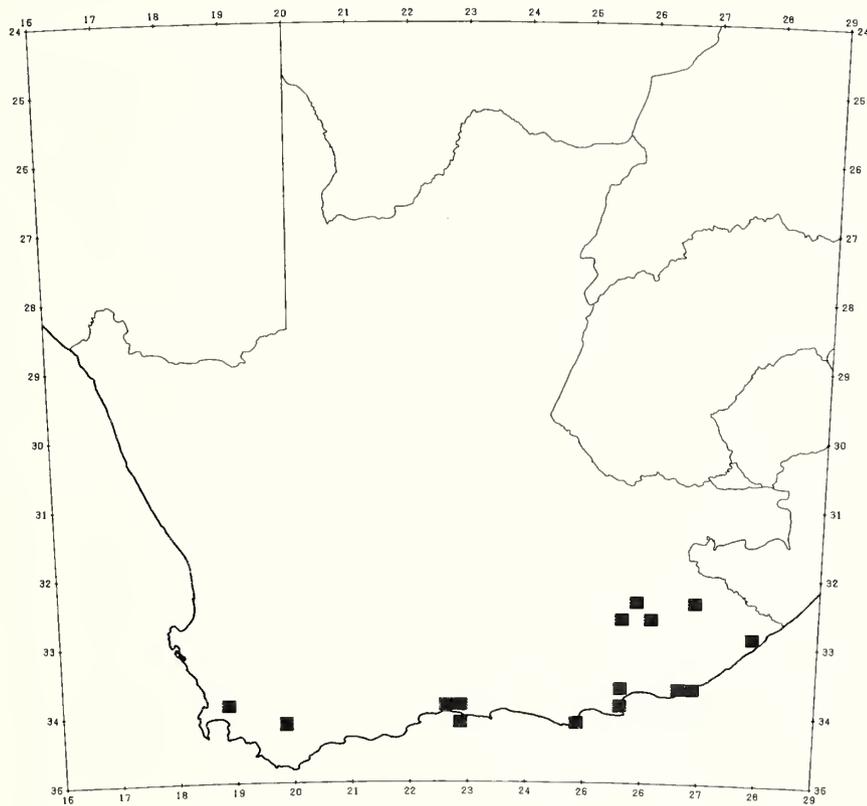


Fig. 73. Distribution of the Black Sparrowhawk, 1970 – 1979.

Little Banded Goshawk*Accipiter badius**Distribution* (Figs 74 and 75)

The distribution for the pre-1970s and 1970s is more restricted than that given by both McLachlan & Liversidge (1978) and Snow (1978). There are reported sightings from the E. Cape (Skead 1967) and Courtenay-Latimer (1964) lists the species as "resident" in the East London area. There are two reported sightings from the E. Cape from the 1970s. However, no specimens of *A. badius* have ever been taken from the E. Cape and the occurrence of the species there needs confirmation.

Habitat

No information from the Cape Province but apparently bushveld. Elsewhere in Africa in savanna woodland.

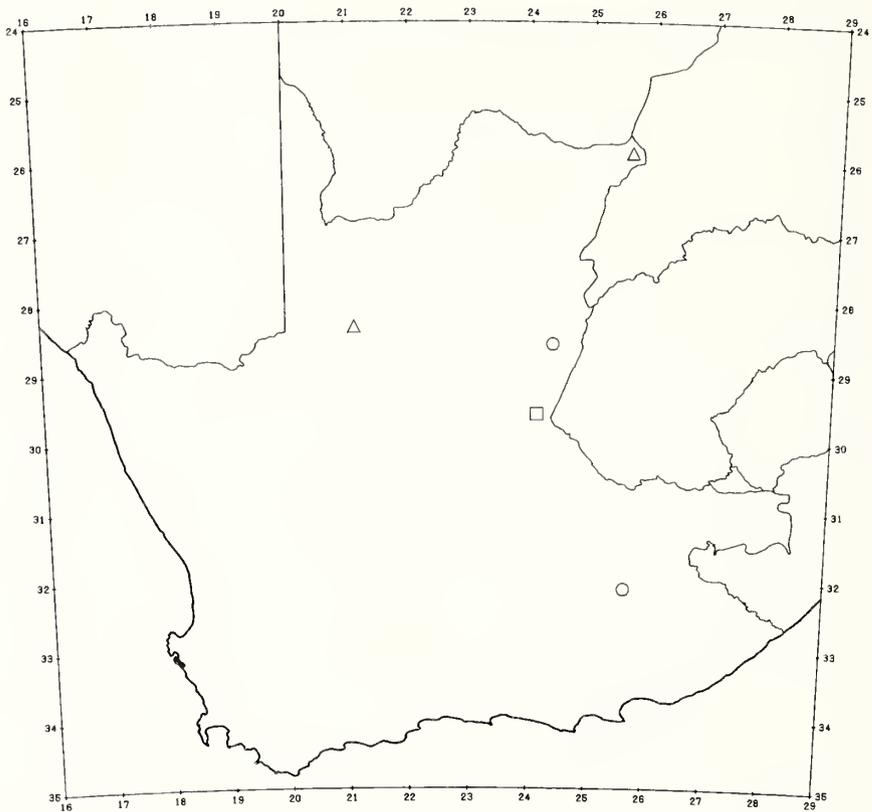


Fig. 74. Distribution of the Little Banded Goshawk, 1700 – 1969.

Status

A rare vagrant in the Province; the species normally occurs in Zululand, Transvaal, Namibia and northwards. There has been no apparent change in status in the Province between the two periods.

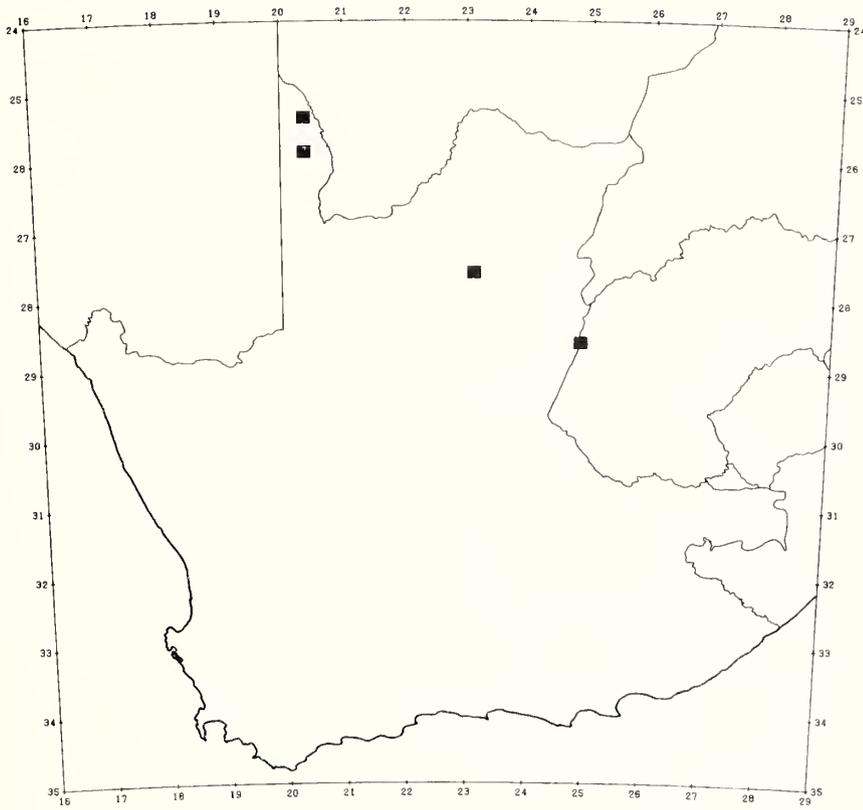


Fig. 75. Distribution of the Little Banded Goshawk, 1970 – 1979.

African Goshawk

Accipiter tachiro

Distribution (Figs 76 and 77)

The distribution for the pre-1970s and 1970s accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

Habitat

Forest and wooded kloofs.

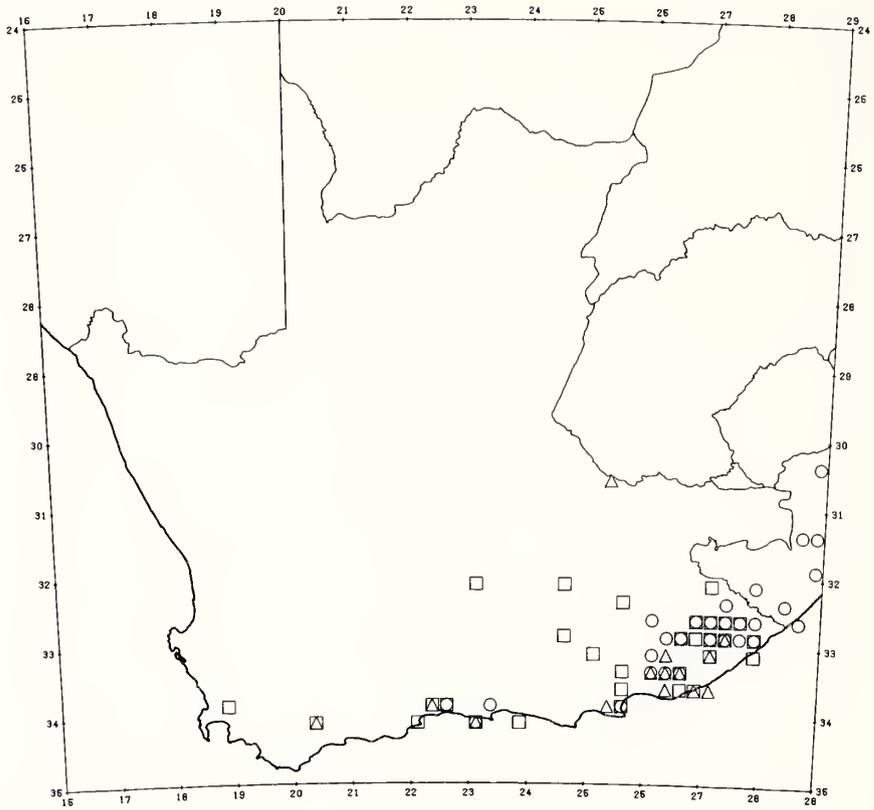


Fig. 76. Distribution of the African Goshawk, 1700 - 1969.

Status

A. tachiro, a resident species, is the commonest accipiter in the E. Cape and S. Cape. However, this species has decreased in the southern and eastern Karoo due to destruction and misutilisation of suitable habitat by man.

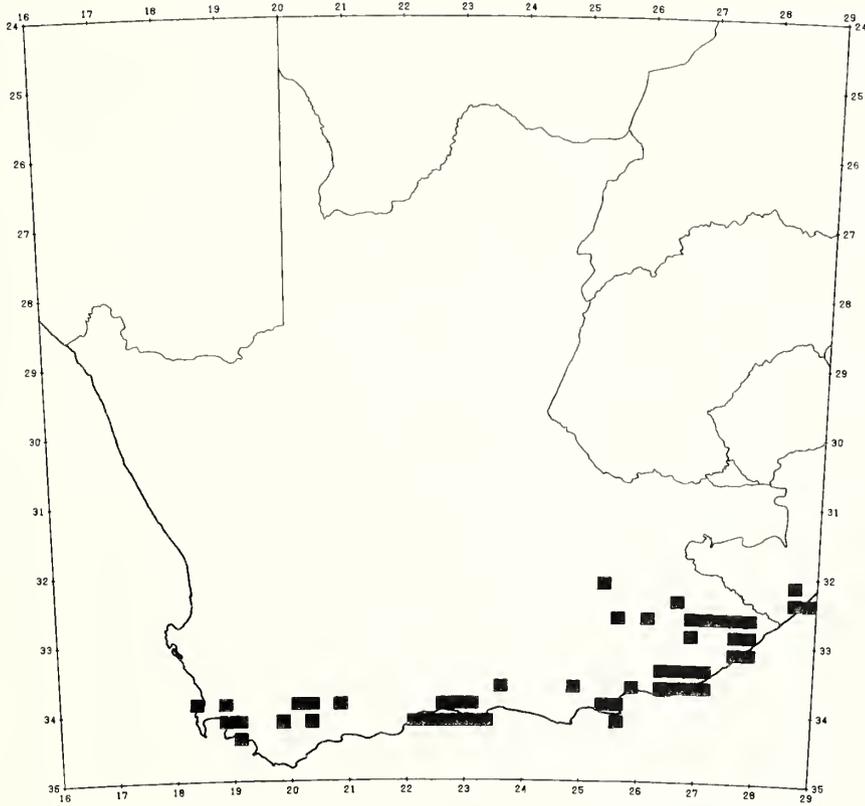


Fig. 77. Distribution of the African Goshawk, 1970 – 1979.

Gabar Goshawk

Micronisus gabar

Distribution (Figs 78 and 79)

The pre-1970s and 1970s distribution differs from that given by McLachlan & Liversidge (1978) and Snow (1978) in that the species is recorded from the S.W. Cape, albeit only one record from the early period.

Habitat

Bushveld and thornveld, more especially *Acacia karroo* trees along watercourses. The species has adapted to thornveld in overgrazed areas and to trees around homesteads in arid areas.

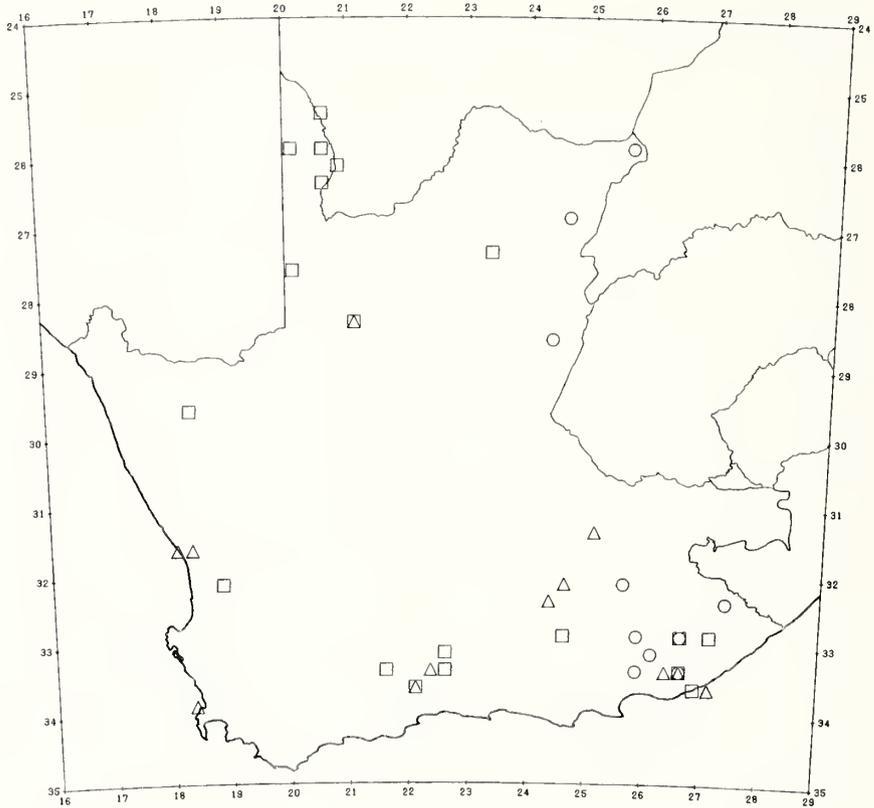


Fig. 78. Distribution of the Gabar Goshawk, 1700 – 1969.

Status

A scarce resident in most of the Province. *M. gabar* is, however, more numerous in the Kalahari Gemsbok National Park. There has been no apparent change in status in the Province between the two periods and the lack of records from the Karoo in the pre-1970s may be due to inadequate sampling.

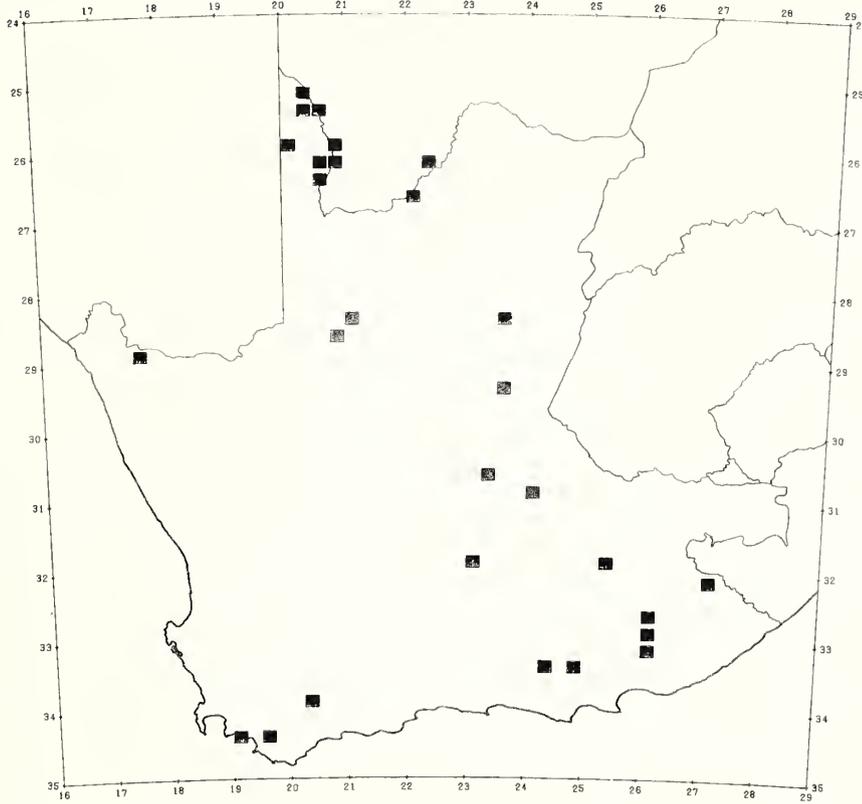


Fig. 79. Distribution of the Gabar Goshawk, 1970 - 1979.

Pale Chanting Goshawk

Melierax canorus

Distribution (Figs 80 and 81)

The distribution for the pre-1970s and 1970s accords with that given by McLachlan & Liversidge (1978) and Snow (1978). Known to occur over most of the N.W. Cape; not considered during a 1977 field survey in this region.

Habitat

Karoo, bushveld, and less frequently macchia, thornveld and grassland.

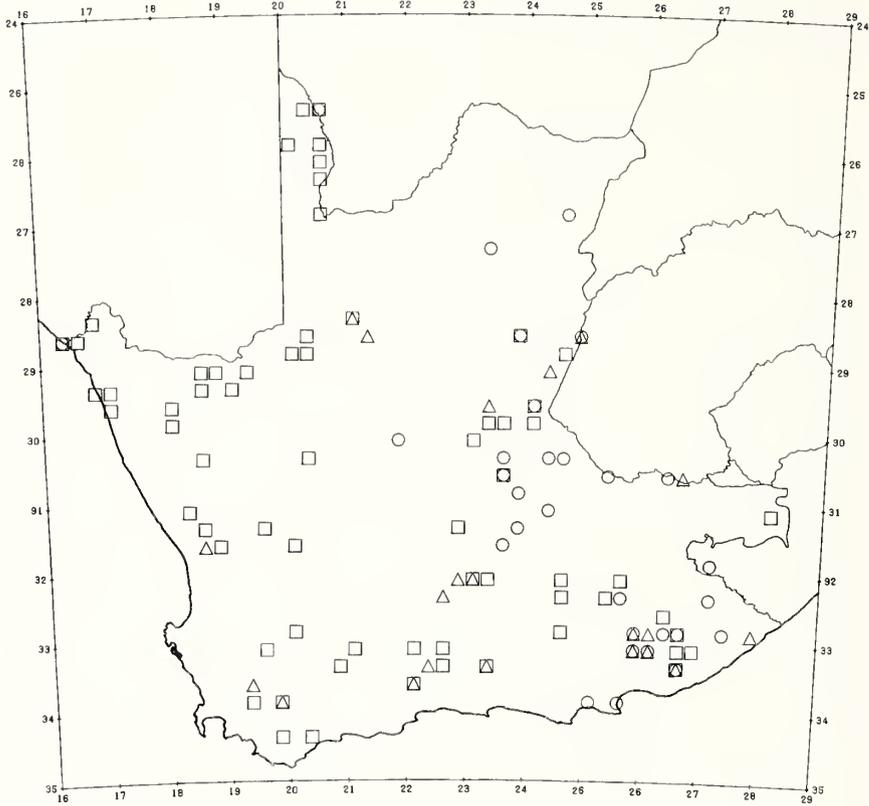


Fig. 80. Distribution of the Pale Chanting Goshawk, 1700 – 1969.

Status

M. canorus is a common resident species in the karoo and bushveld but is subject to local movements and so may not be permanently resident in any locality and may move temporarily into the peripheral macchia, thornveld and grassland. The species shows no change in status in the Province between the two periods.

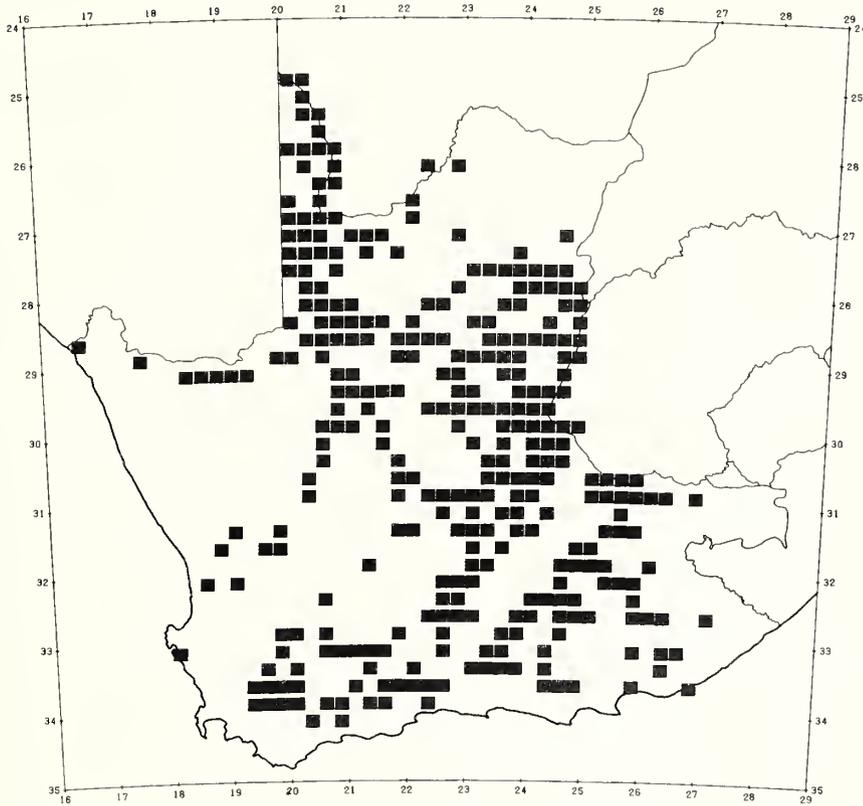


Fig. 81. Distribution of the Pale Chanting Goshawk, 1970 – 1979.

African Marsh Harrier

Circus ranivorus

Distribution (Figs 82 and 83)

1700–1969: This distribution is similar to that given by Snow (1978) except that this author also records the species in the N. Cape.

1970–1979: The increase in records from the N. Cape is due to improved mapping coverage. This distribution is more restricted than that given by McLachlan & Liversidge (1978).

Habitat

Marshy areas along rivers, around dams, lakes and estuaries and vleis.

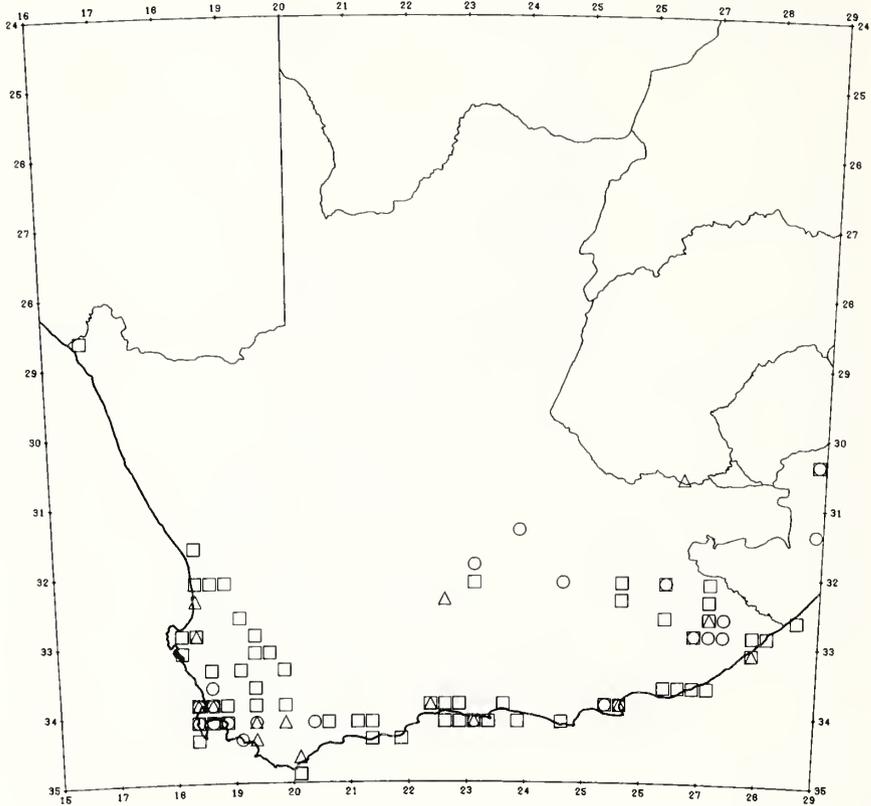


Fig. 82. Distribution of the African Marsh Harrier, 1700 – 1969.

Status

A scarce resident which shows no overall change in range in the Province between the two periods, although there may be some disappearance from the central Karoo. The large number of records from the N. Cape from the 1970s is due to increased sampling in that region. Much habitat has been lost, e.g. in the Karoo, due to modification for agricultural purposes and the overall population has decreased in size. As *C. ranivorus* is vulnerable to extirpation in the Province it should be included in a revised *South African Red Data Book: Aves*.

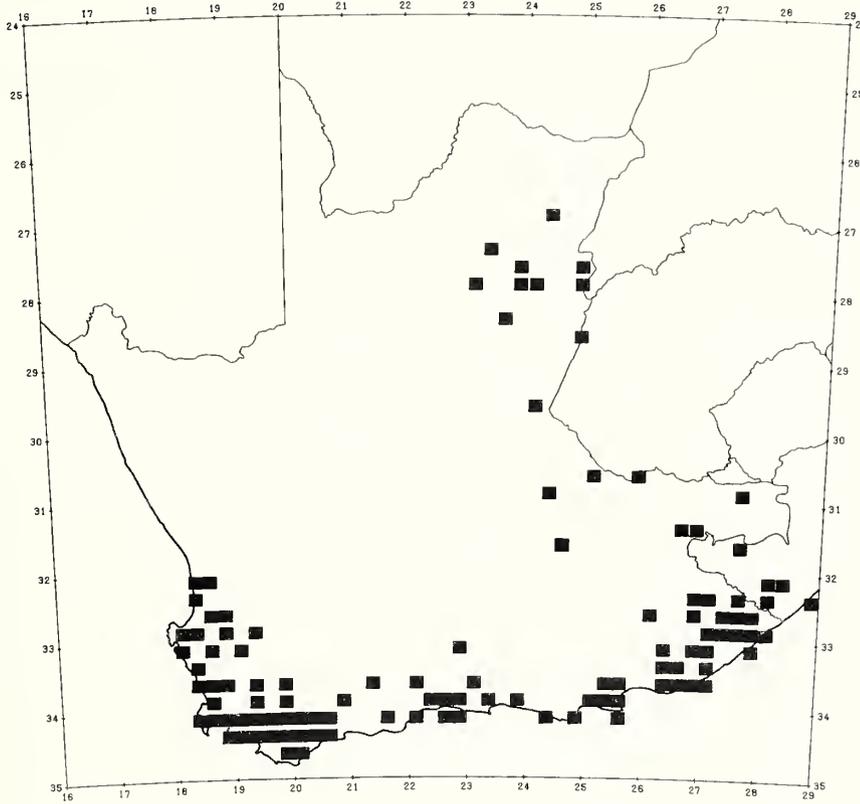


Fig. 83. Distribution of the African Marsh Harrier, 1970 – 1979.

Montagu's Harrier

Circus pygargus

Distribution (Figs 84 and 85)

The 1970s distribution is more restricted than that given by McLachlan & Liversidge (1978).

Habitat

No information for the Cape Province but elsewhere in grassland and open country.

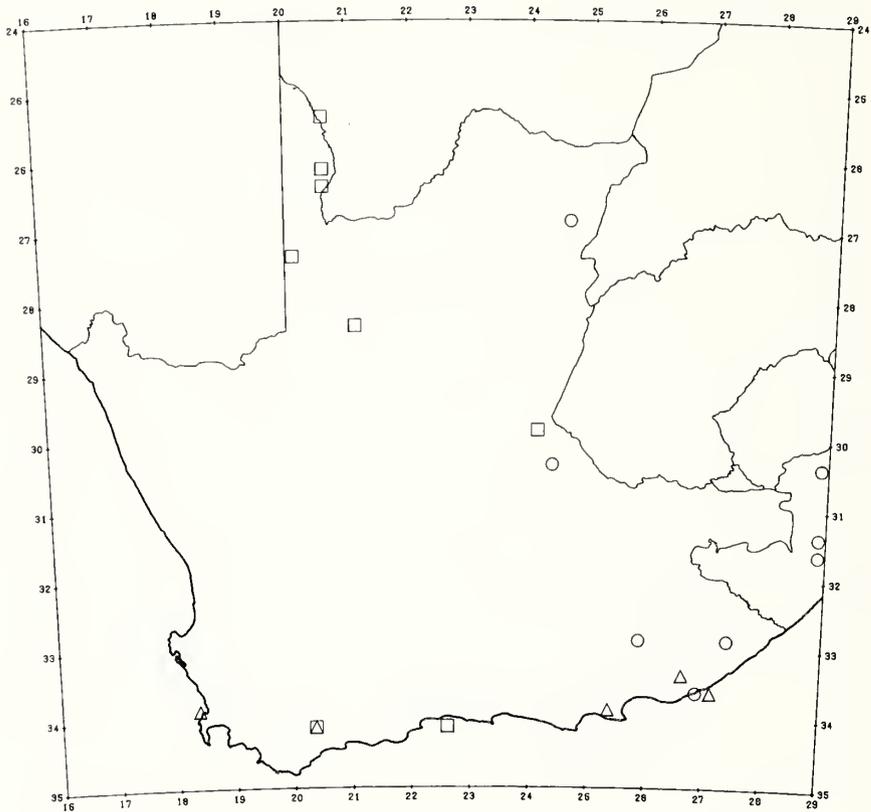


Fig. 84. Distribution of the Montagu's Harrier, 1700 - 1969.

Status

A rare non-breeding Palaearctic migrant which is present during the austral summer. The decrease in records and range in the Province may reflect a decrease in the breeding grounds of this species in the Palaearctic (Cramp & Simmons 1980).

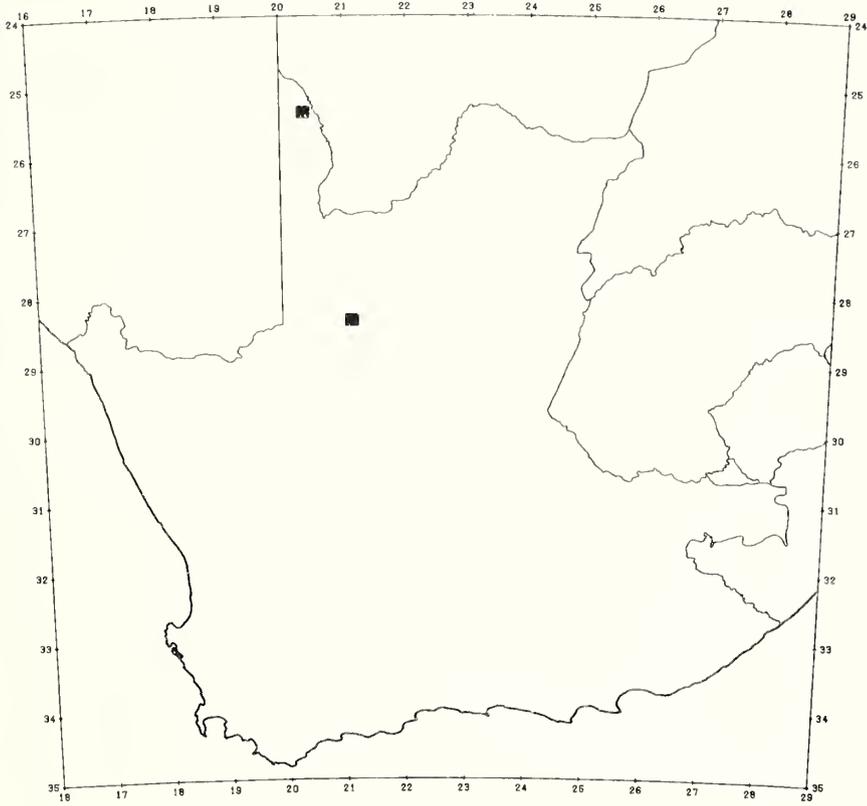


Fig. 85. Distribution of the Montagu's Harrier, 1970 – 1979.

Pallid Harrier

Circus macrourus

Distribution (Figs 86 and 87)

Apart from the S.W. Cape record, the 1970s distribution is similar to that given by McLachlan & Liversidge (1978).

Habitat

No information for the Cape Province but elsewhere in grassland and open country.

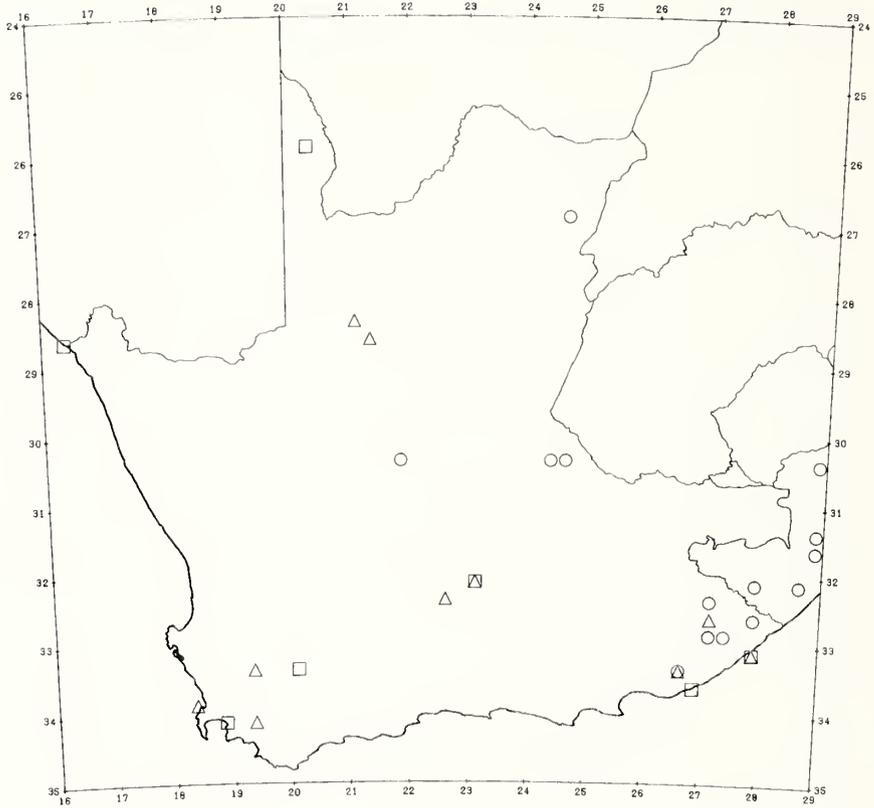


Fig. 86. Distribution of the Pallid Harrier, 1700 – 1969.

Status

A non-breeding Palearctic migrant which is present during the austral summer. The species is, and always has been, rare in the Province. There has been no change in range in the Province between the two periods but infrequently recorded in the 1970s, particularly from the Karoo. This is surprising in view of the population increase in the western Palearctic (Cramp & Simmons 1980).

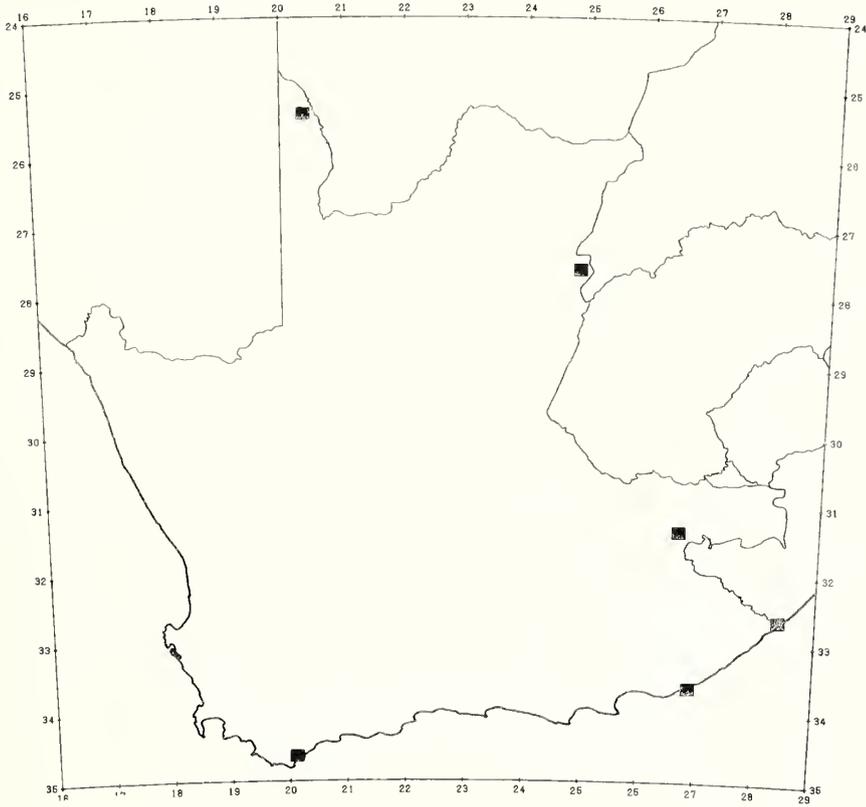


Fig. 87. Distribution of the Pallid Harrier, 1970 – 1979.

Black Harrier

Circus maurus

Distribution (Figs 88 and 89)

1700–1969: This distribution accords with that given by Snow (1978).

1970–1979: This distribution is more restricted than that given by McLachlan & Liversidge (1978).

Habitat

Grassland, karoo and macchia. In open country but not necessarily close to water. The species has adapted to cultivated lands.

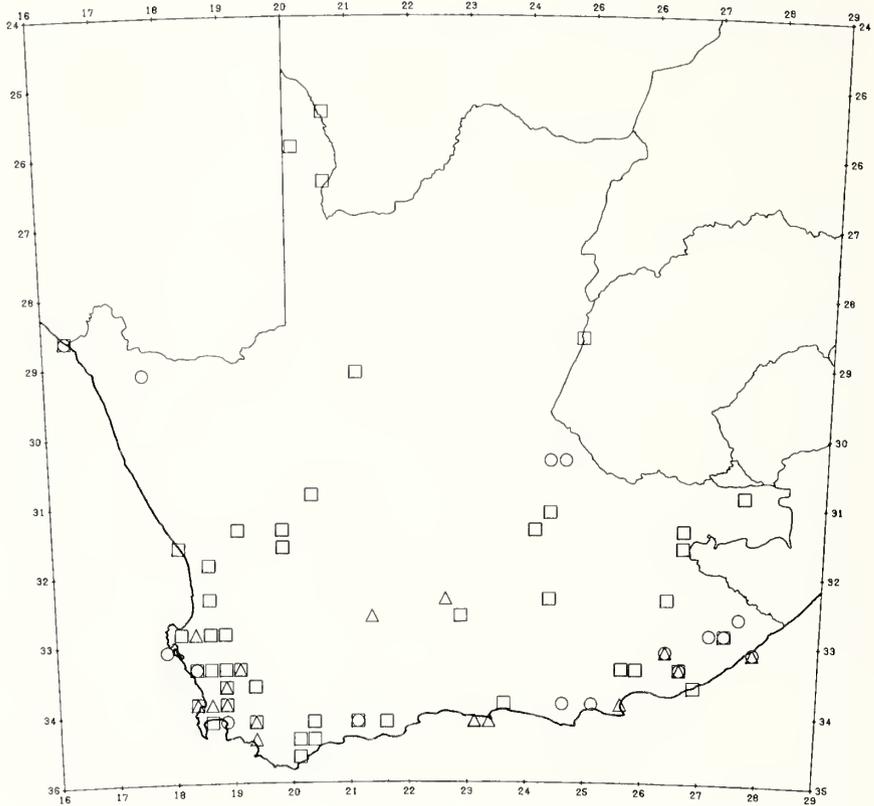


Fig. 88. Distribution of the Black Harrier, 1700 - 1969.

Status

C. maurus is a scarce resident species in the Cape Province. Breeding takes place primarily in late winter and early spring in the Province south of 31° S. The birds undergo a northerly migration during the non-breeding season (mainly June to July) to the northern parts of the Province and adjacent provinces and territories (Van der Merwe 1981). Due to various published statements there is controversy regarding the past and present status of *C. maurus*; the species was considered by some to have decreased to near extinction but subsequently numbers were said to have increased again. Van der Merwe (*op cit.*) has assessed the situation and contends that, on available evidence, the population in South Africa has remained largely unchanged in recent times. *C. maurus* does not warrant inclusion in a revised *South African Red Data Book: Aves*; the species is included in a supplementary list by Siegfried *et al.* (1976).

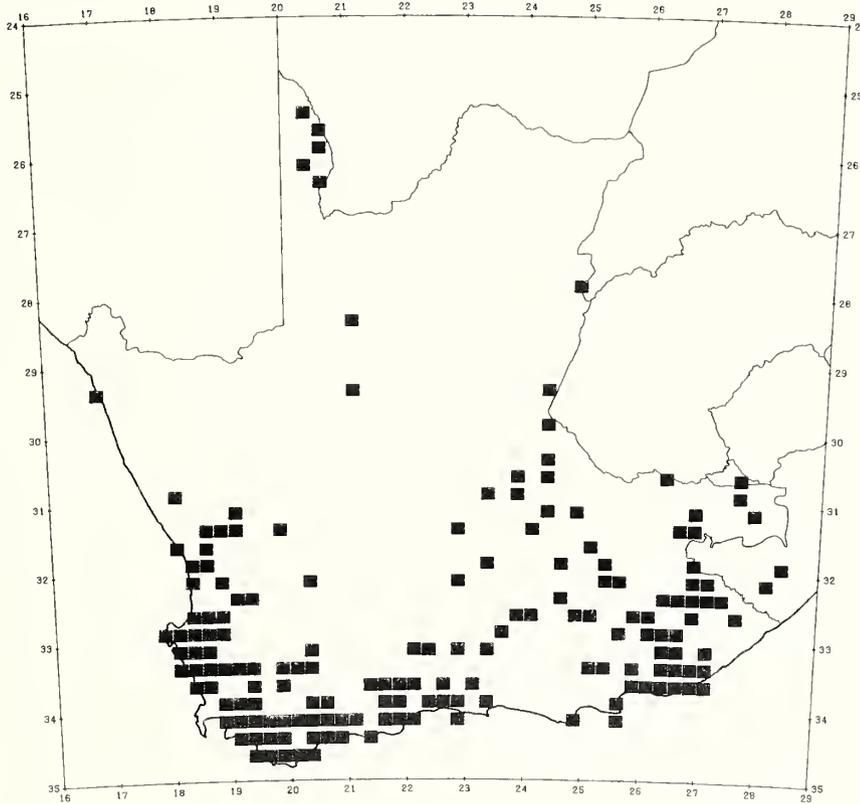


Fig. 89. Distribution of the Black Harrier, 1970 – 1979.

Gymnogene

Polyboroides typus

Distribution (Figs 90 and 91)

1700–1969: This distribution largely accords with that given by Snow (1978).

1970–1979: This distribution is somewhat more restricted than that given by McLachlan & Liversidge (1978).

Habitat

Wooded kloofs and gorges.

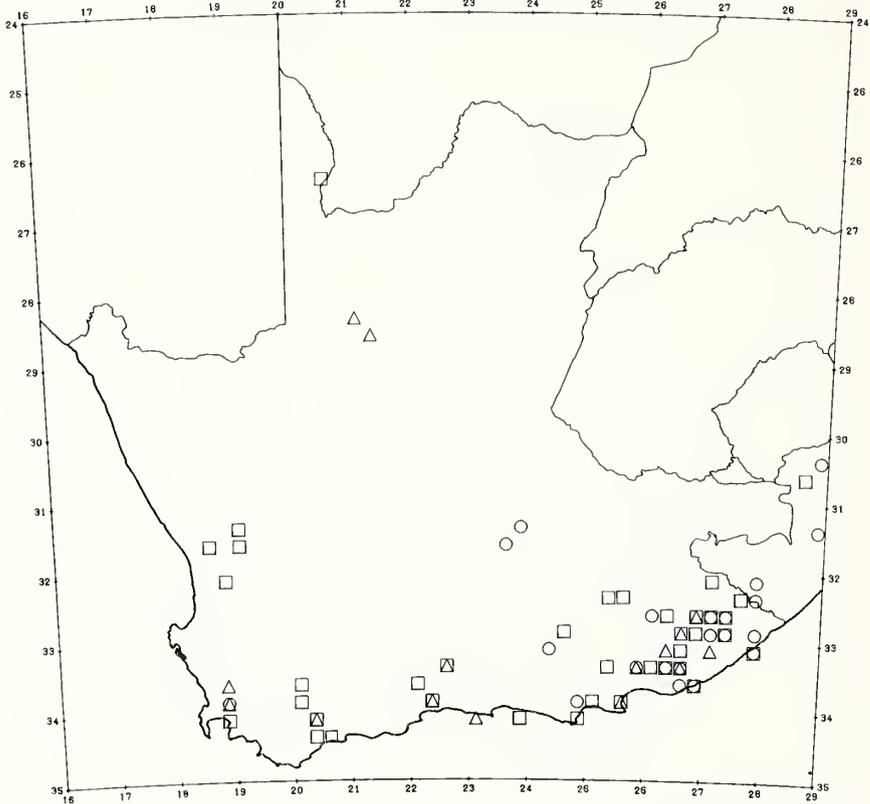


Fig. 90. Distribution of the *Gymnogene*, 1700 – 1969.

Status

A relatively scarce resident. There has been no change in status in the Province between the two periods.

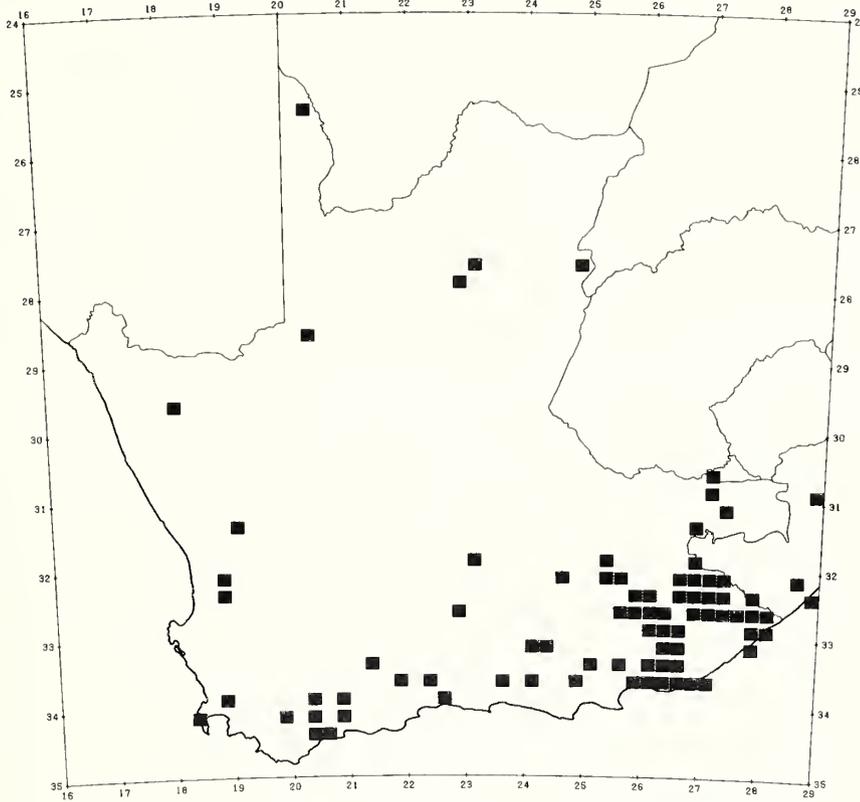


Fig. 91. Distribution of the Gymnogene, 1970 – 1979.

Osprey

Pandion haliaetus

Distribution (Figs 92 and 93)

The 1970s distribution is more restricted than that given by McLachlan & Liversidge (1978). The single record given by Snow (1978) is a breeding record from the S.W. Cape which is now discounted.

Habitat

Mainly estuaries and coastal lakes but also large dams in the interior.

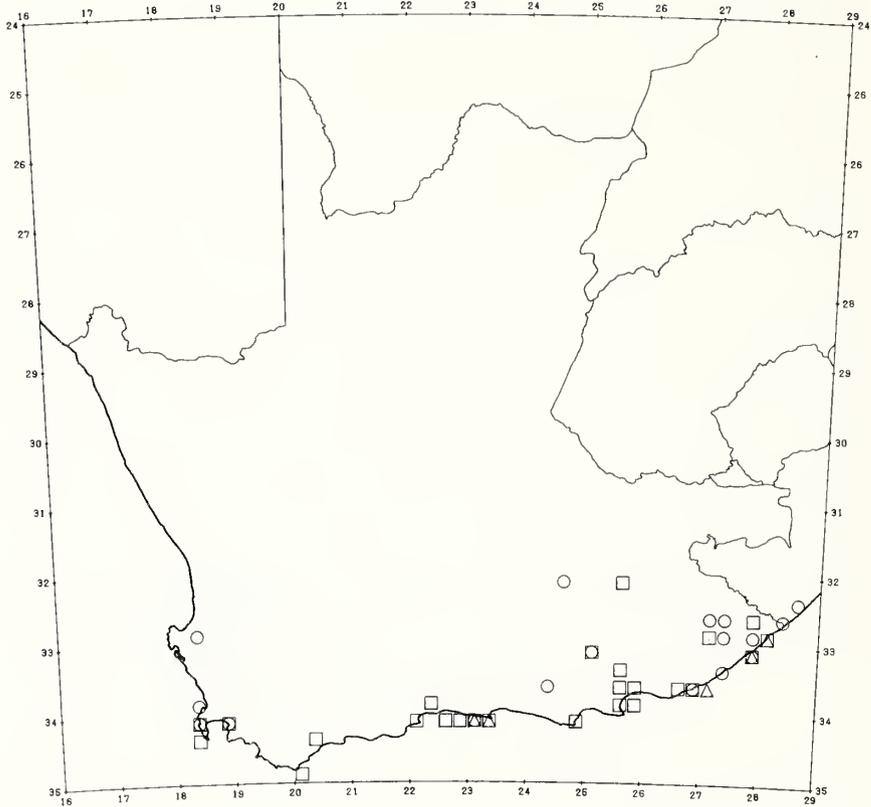


Fig. 92. Distribution of the Osprey, 1700 - 1969.

Status

A rare non-breeding Palaearctic migrant which occurs mainly during the austral summer; a few birds are recorded during the winter (Boshoff & Palmer in prep). There has been no change in status in the Province between the two periods.

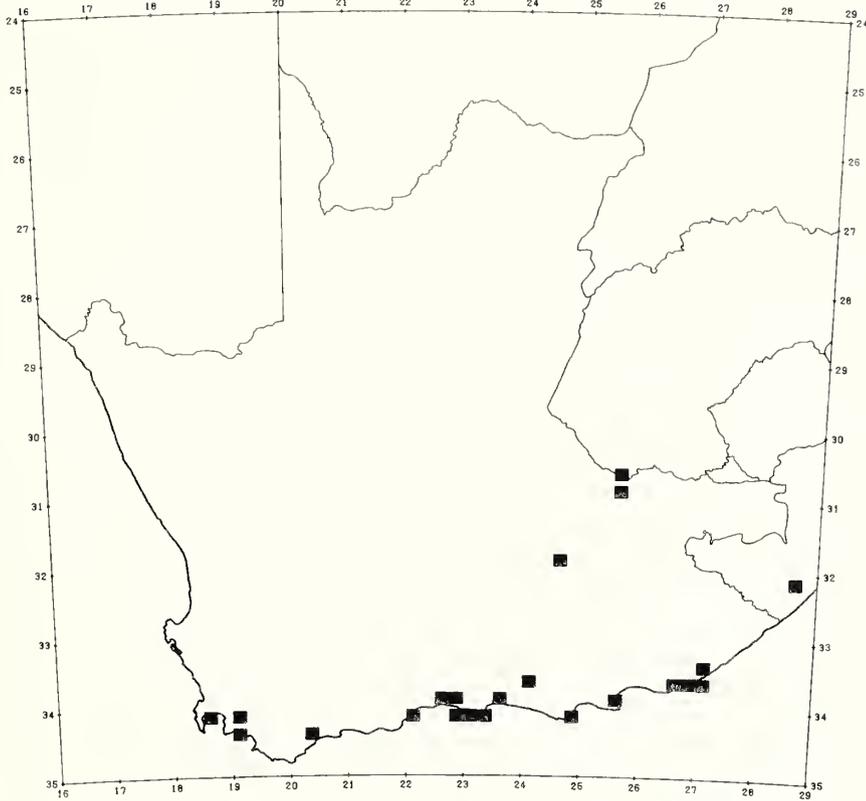


Fig. 93. Distribution of the Osprey, 1970 – 1979.

Peregrine

Falco peregrinus

Distribution (Figs 94 and 95)

The distribution given by McLachlan & Liversidge (1978) is too generalised, whereas the range given by Snow (1978) is limited mainly to the S.W. Cape and E. Cape.

Habitat

Mountainous and broken terrain where there are suitable cliffs for roosting and breeding. The distribution maps suggest that the species may prefer the coastal areas and adjacent interior.

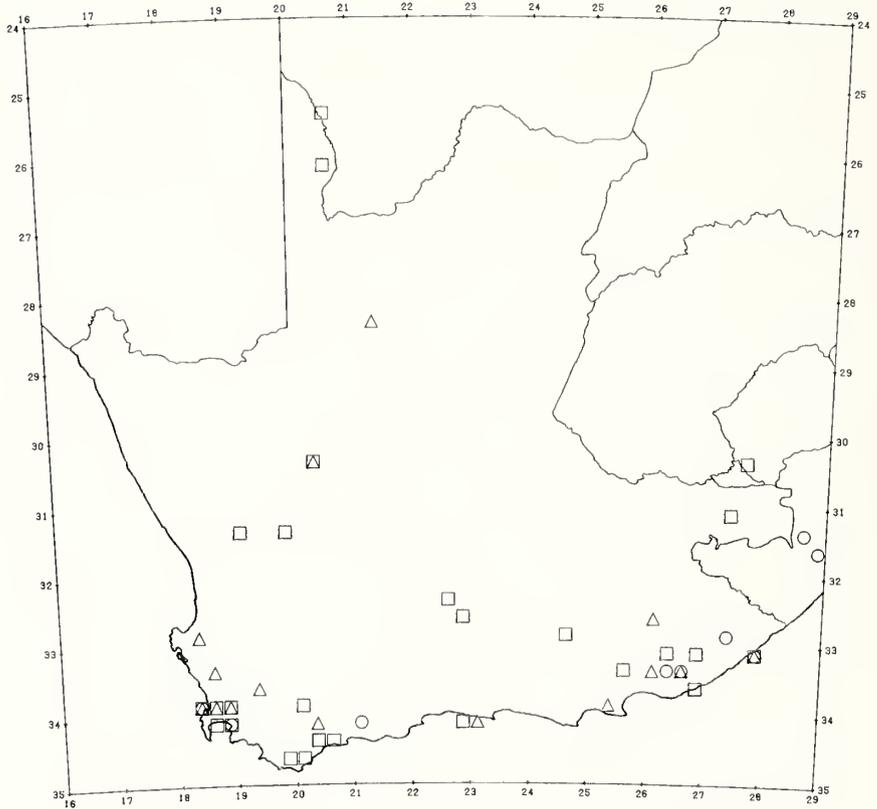


Fig. 94. Distribution of the Peregrine, 1700 – 1969.

Status

Two races of *F. peregrinus* occur in the Cape Province, viz. *F.p. minor*, which is resident, and *F.p. calidus*, which is a non-breeding Palearctic migrant. No distinction between the races is made here. They overlap in range as the migrant race has been collected as far south as Port Elizabeth. It is possible that the Karoo and N. Cape records refer to *F.p. calidus* and that the resident race is confined to the coastal areas. *F. peregrinus* is rare in the Cape Province and apparently has always been rare; there has been no apparent change in status in the Province between the two periods. The species is listed as "possibly threatened" by Siegfried *et al.* (1976).

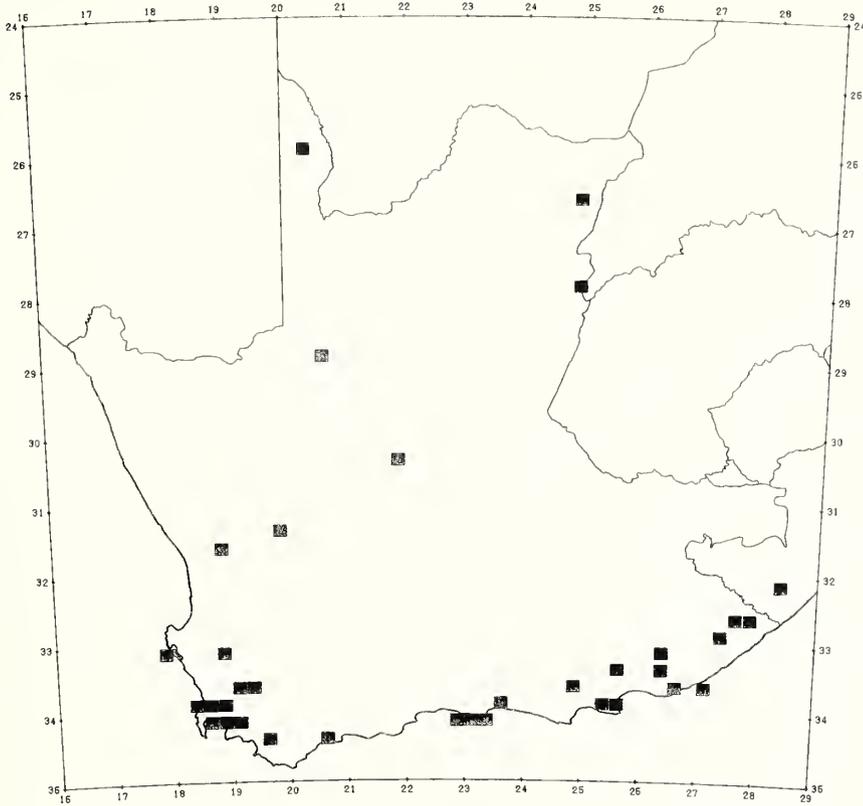


Fig. 95. Distribution of the Peregrine, 1970 – 1979.

Lanner

Falco biarmicus

Distribution (Figs 96 and 97)

The distribution for the pre-1970s and 1970s accords with that given by Snow (1978) and McLachlan & Liversidge (1978).

Habitat

Usually associated with cliffs suitable for breeding but may nest in trees. Birds range widely and can be found in all habitats except forest.

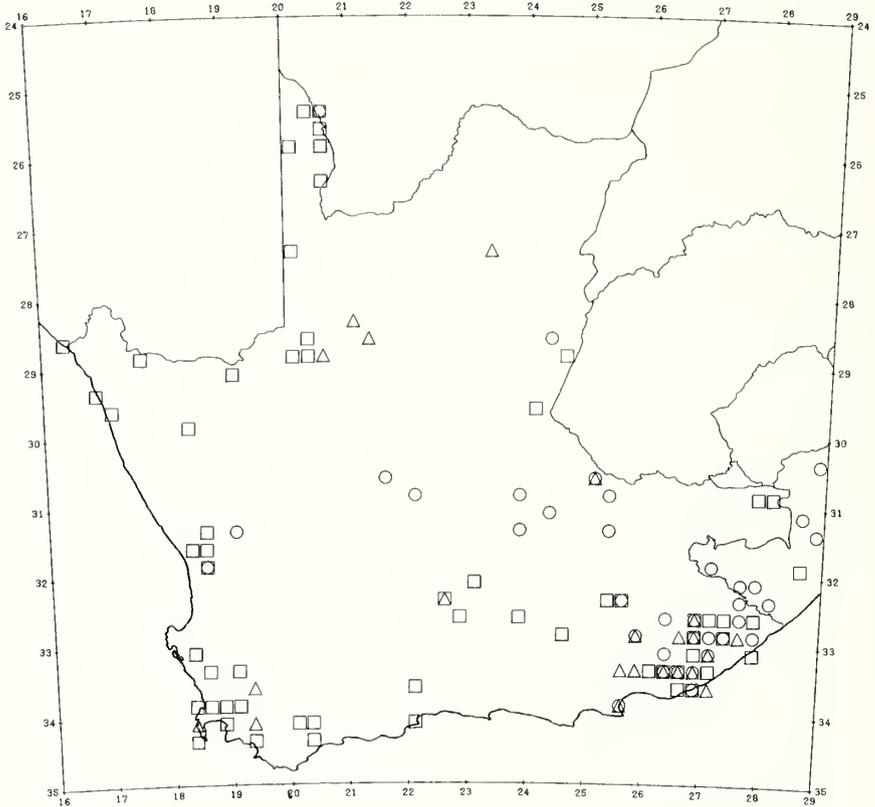


Fig. 96. Distribution of the Lanner, 1700 – 1969.

Status

A relatively scarce resident species. There has been no apparent change in status in the Province between the two periods.

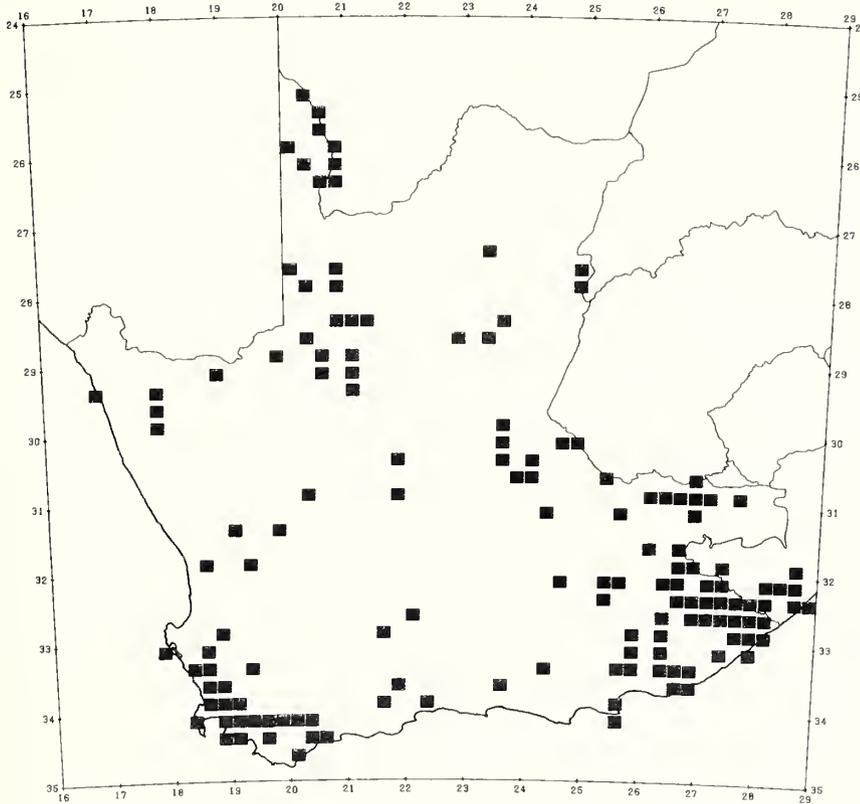


Fig. 97. Distribution of the Lanner, 1970 – 1979.

Hobby

Falco subbuteo

Distribution (Figs 98 and 99)

The 1970s distribution differs markedly from that given by McLachlan & Liversidge (1978).

Habitat

No information for the Cape Province but apparently preferably thornveld and macchia.

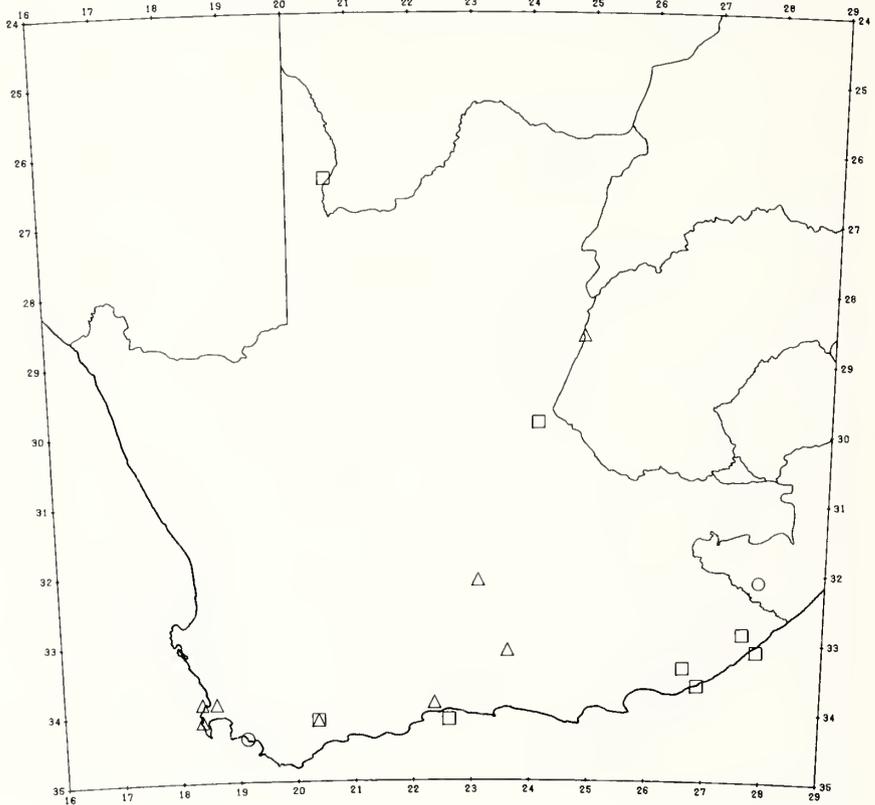


Fig. 98. Distribution of the Hobby, 1700 – 1969.

Status

A rare non-breeding Palaearctic migrant which is present during the austral summer. There has been no apparent change in status in the Province between the two periods, although not recorded from the interior of the Province during the 1970s.

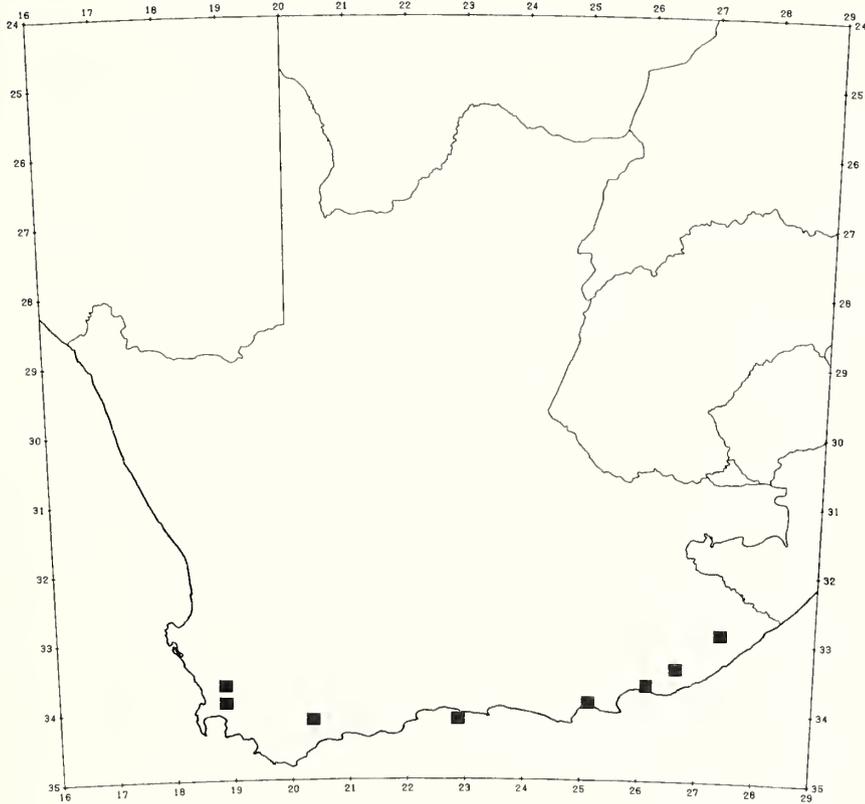


Fig. 99. Distribution of the Hobby, 1970 – 1979.

African Hobby

Falco cuvierii

Distribution (Figs 100 and 101)

1700–1969: This distribution accords with that given by Snow (1978).

1970–1979: This distribution is more restricted than that given by McLachlan & Liversidge (1978).

Habitat

No information from the Cape Province but apparently thornveld.

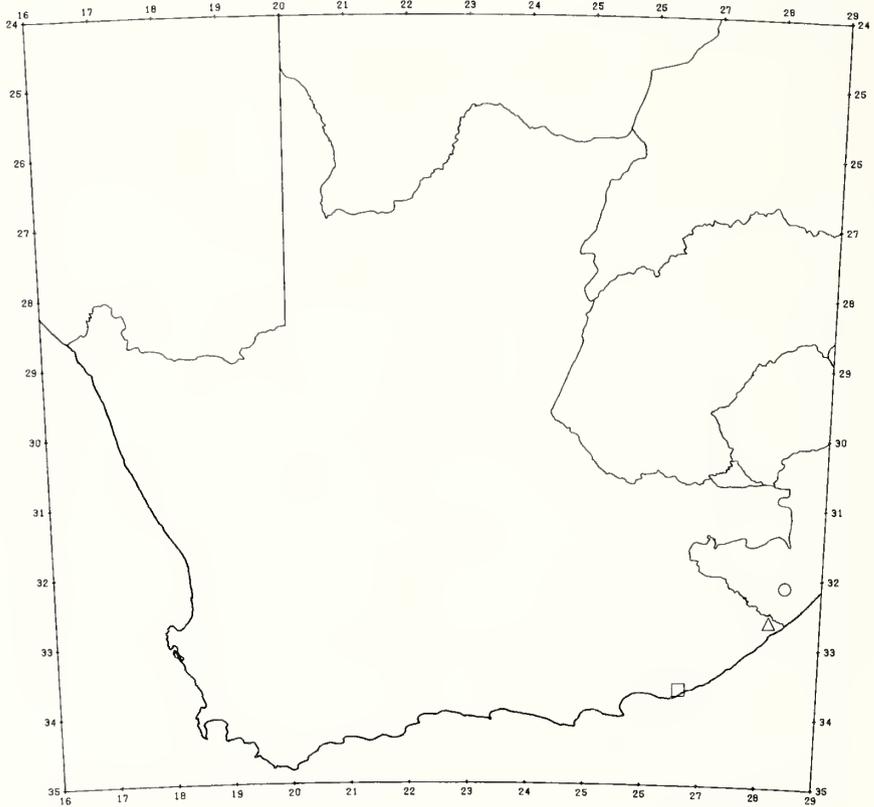


Fig. 100. Distribution of the African Hobby, 1700 – 1969.

Status

There are only five records for the entire 1700 – 1979 period. *F. cuvierii* is considered a rare vagrant in the Province; a breeding record from Idutywa (Transkei) in 1924 is considered equivocal (W. R. J. Dean *in litt.* per A. C. Kemp). There has been no apparent change in status in the Province between the two periods. *F. cuvierii* is listed as “rare and endangered” in South Africa by Siegfried *et al.* (1976).

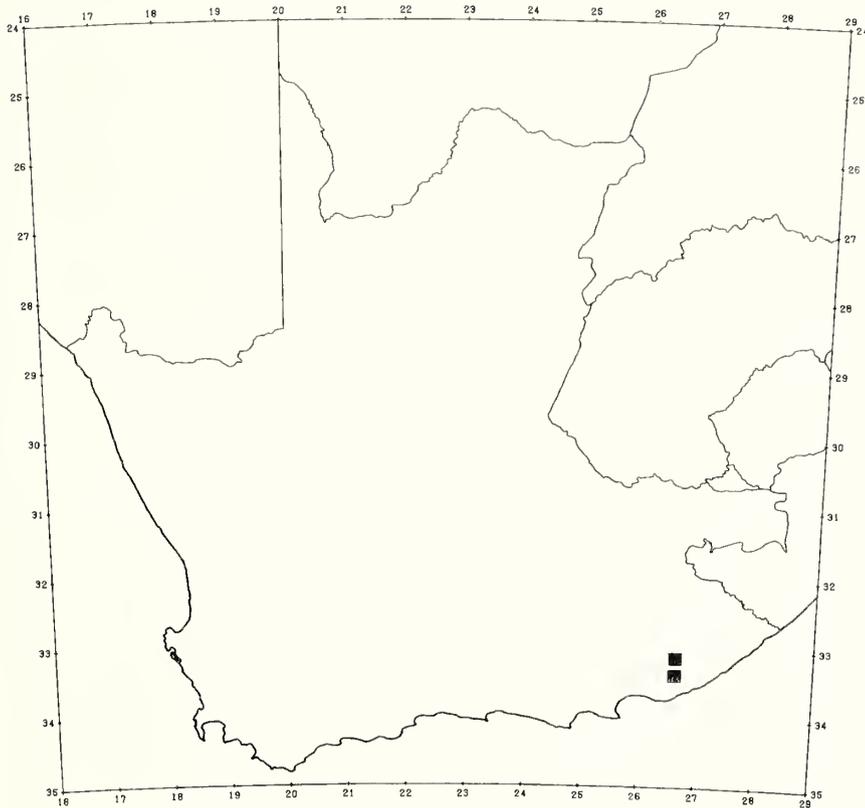


Fig. 101. Distribution of the African Hobby, 1970 – 1979.

Rednecked Falcon

Falco chicquera

Distribution (Figs 102 and 103)

The distribution for the pre-1970s and 1970s largely accords with that given by McLachlan & Liversidge (1978) and Snow (1978).

Habitat

Bushveld. Often associated with *Borassus* palms, e.g. in northern N.W. Cape.

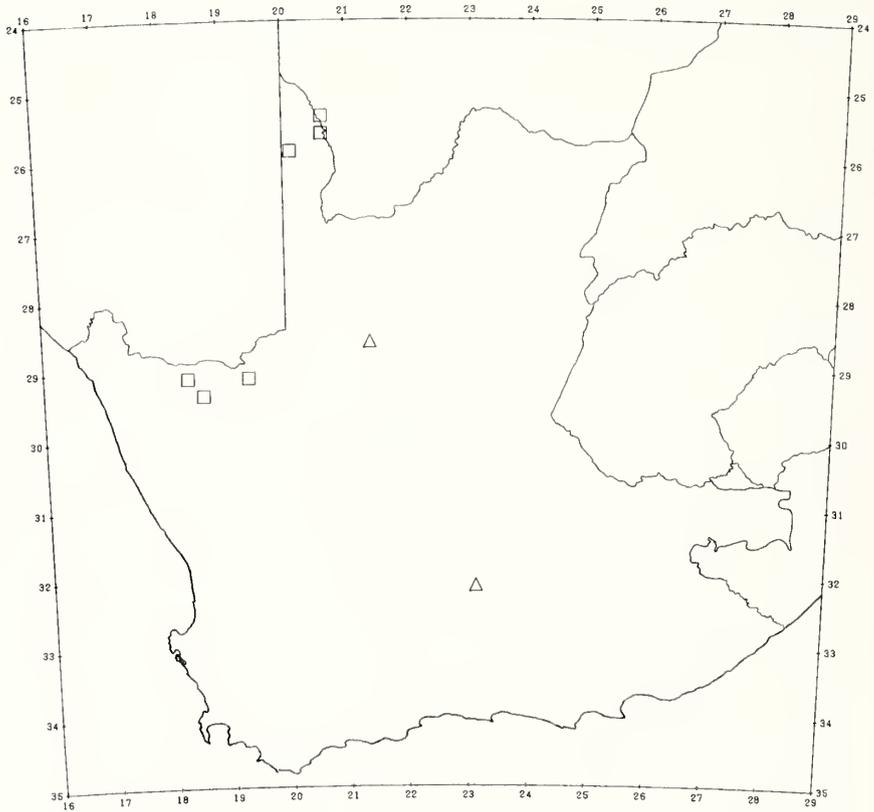


Fig. 102. Distribution of the Rednecked Falcon, 1700 – 1969.

Status

A rare species in the Cape Province, which is on the periphery of its range. Although there are no breeding records from the Province *F. chicquera* may be resident as there is suitable habitat available. There has been no apparent change in status in the Province between the two periods. The species is listed as "vulnerable" in South Africa by Siegfried *et al.* (1976).

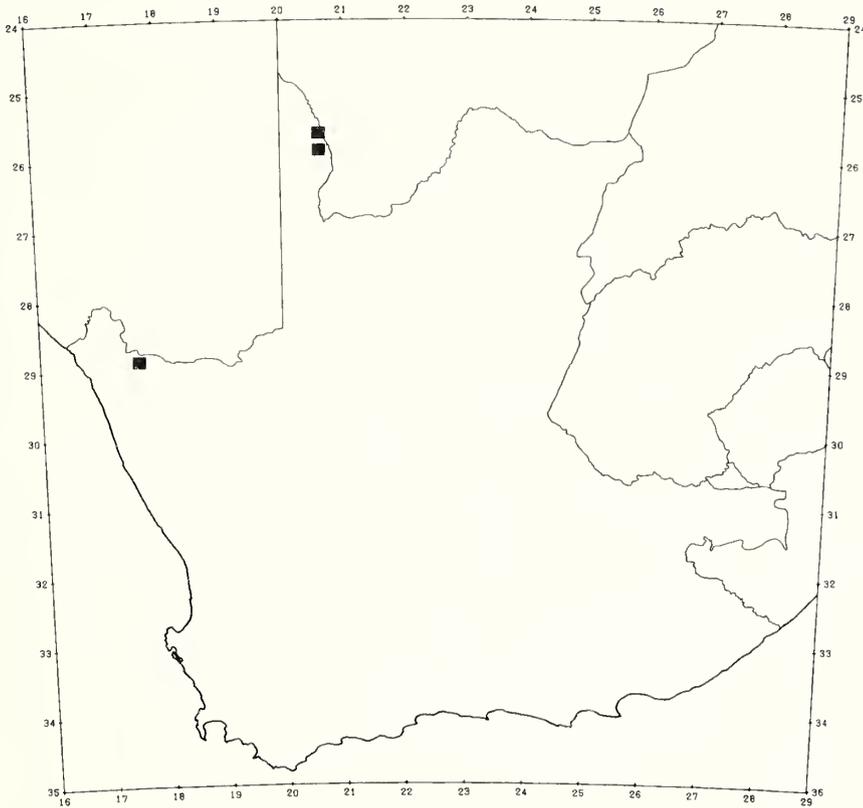


Fig. 103. Distribution of the Rednecked Falcon, 1970 – 1979.

Eastern Redfooted Kestrel

Falco amurensis

Distribution (Figs 104 and 105)

The 1970s distribution is similar to that given by McLachlan & Liversidge (1978).

Habitat

No information from the Cape Province but apparently thornveld and possibly macchia.

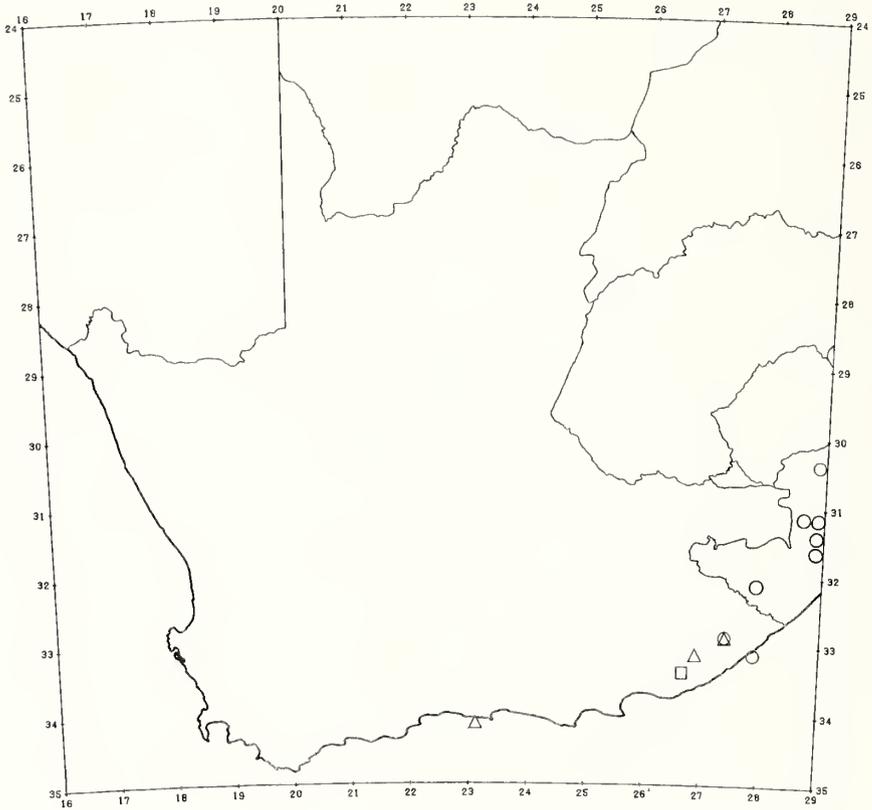


Fig. 104. Distribution of the Eastern Redfooted Kestrel, 1700 – 1969.

Status

A rare non-breeding Palearctic migrant which is present during the austral summer. There has been no change in range in the Province between the two periods.

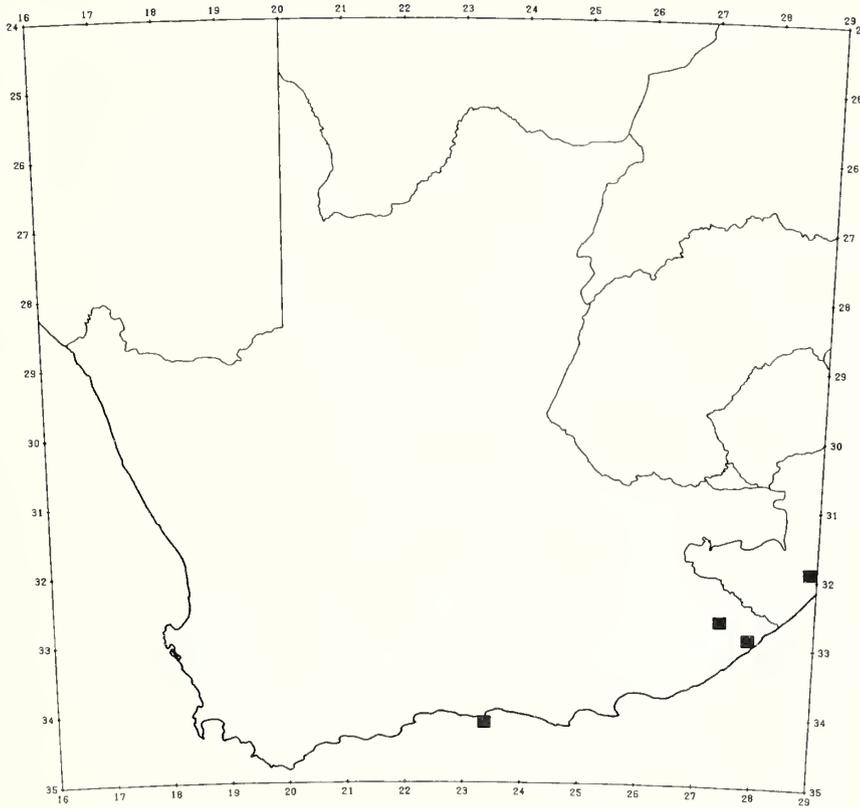


Fig. 105. Distribution of the Eastern Redfooted Kestrel, 1970 – 1979.

Common Kestrel*Falco tinnunculus**Distribution* (Figs 106 and 107)

The distribution for the pre-1970s and 1970s accords with that given by McLachlan & Liversidge (1978) and Snow (1978). Known to occur over most of the N.W. Cape; not considered during a 1977 field survey in that region.

Habitat

All habitats except forest. Breeds mainly on cliffs but is not confined to them and may be found in flat open country.

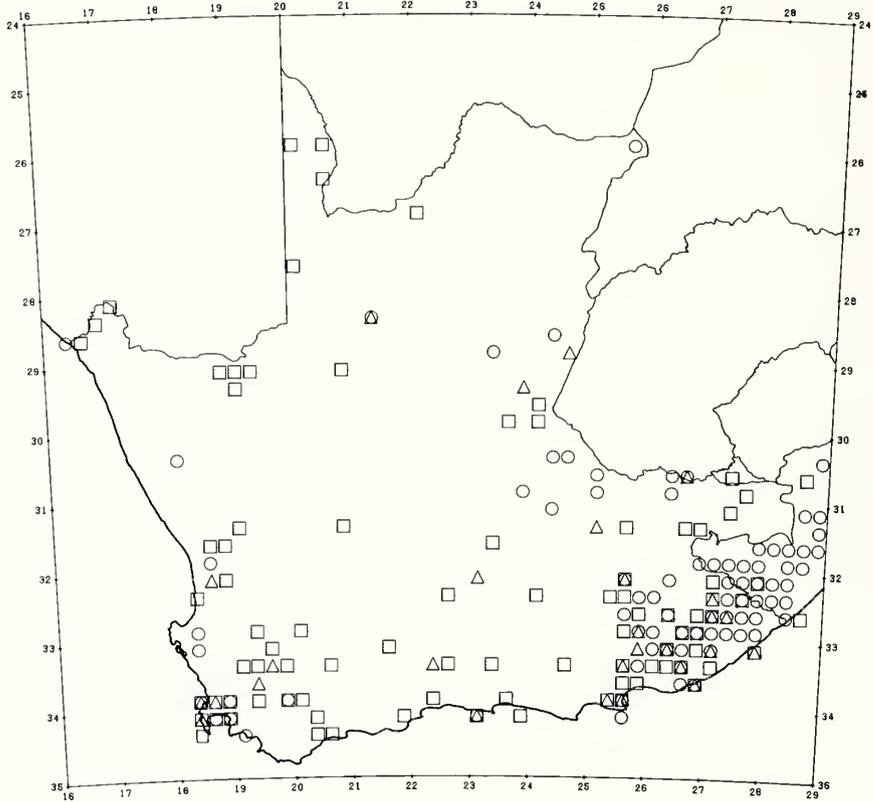


Fig. 106. Distribution of the Common Kestrel, 1700 – 1969.

Status

A resident species which is, and appears to have always been, common i.e. there has been no change in status in the Province between the two periods. *F. tinnunculus* may have benefitted from man's activities as extensive use is made of telephone poles and powerline pylons as hunting perches and nest sites. The species is subject to local movements so that birds may be present in an area at one time and absent in another; these nomads appear to be the non-breeding dispersing segment of the population.

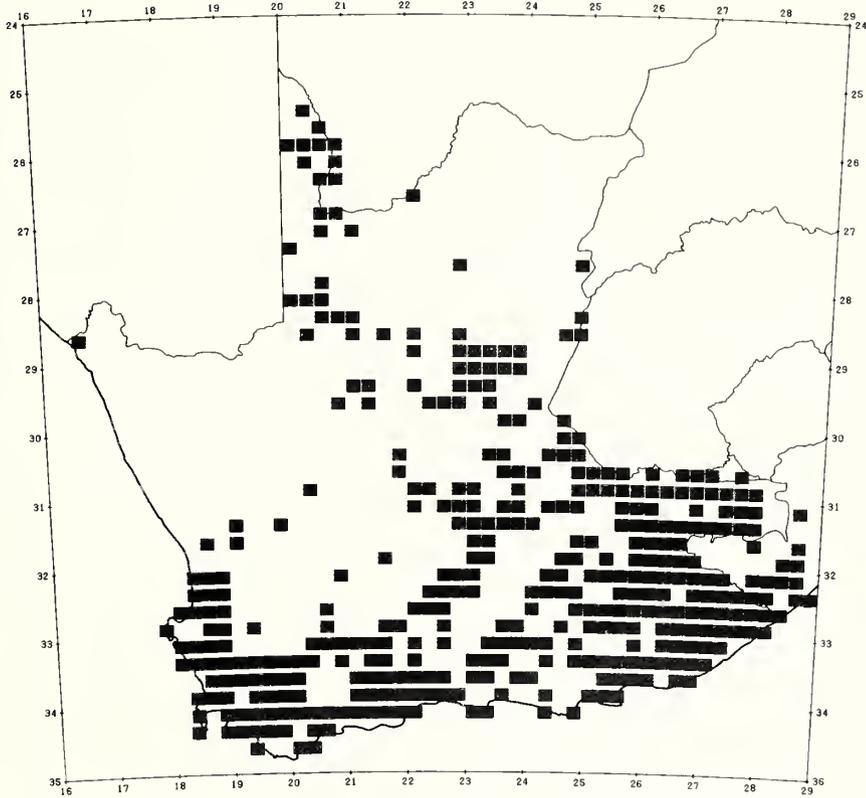


Fig. 107. Distribution of the Common Kestrel, 1970 – 1979.

Greater Kestrel

Falco rupicoloides

Distribution (Figs 108 and 109)

1700–1969: This distribution accords with that given by Snow (1978).

1970–1979: The distribution map given by McLachlan & Liversidge (1978) excludes the S.W. Cape from the species' range but includes all other coastal areas.

Habitat

The arid and semi-arid interior, encompassing the karoo and bushveld and occasionally the grassland, thornveld and macchia.

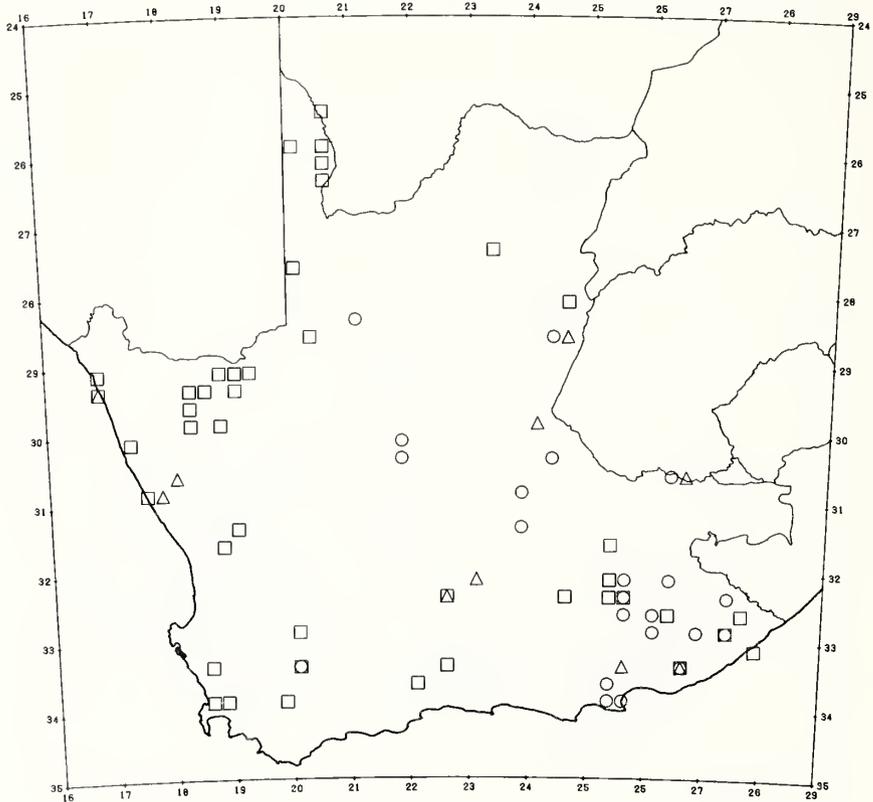


Fig. 108. Distribution of the Greater Kestrel, 1700 – 1969.

Status

A relatively common resident which is subject to nomadic movements so that it may be temporarily absent from the interior and temporarily present in the peripheral areas. This nomadism may be governed by climatic factors, specifically droughts, but the precise mechanisms are not known. Thus the absence of *F. rupicoloides* from the moister coastal areas of the E. Cape, S. Cape and S.W. Cape during the 1970s is probably a natural phenomenon. In the E. Cape the species is considered a rare vagrant with only one breeding record (from the Bedford district). There has been no apparent change in overall status in the Province between the two periods. *F. rupicoloides* makes extensive use of telephone poles and powerline pylons for hunting perches and nest sites.

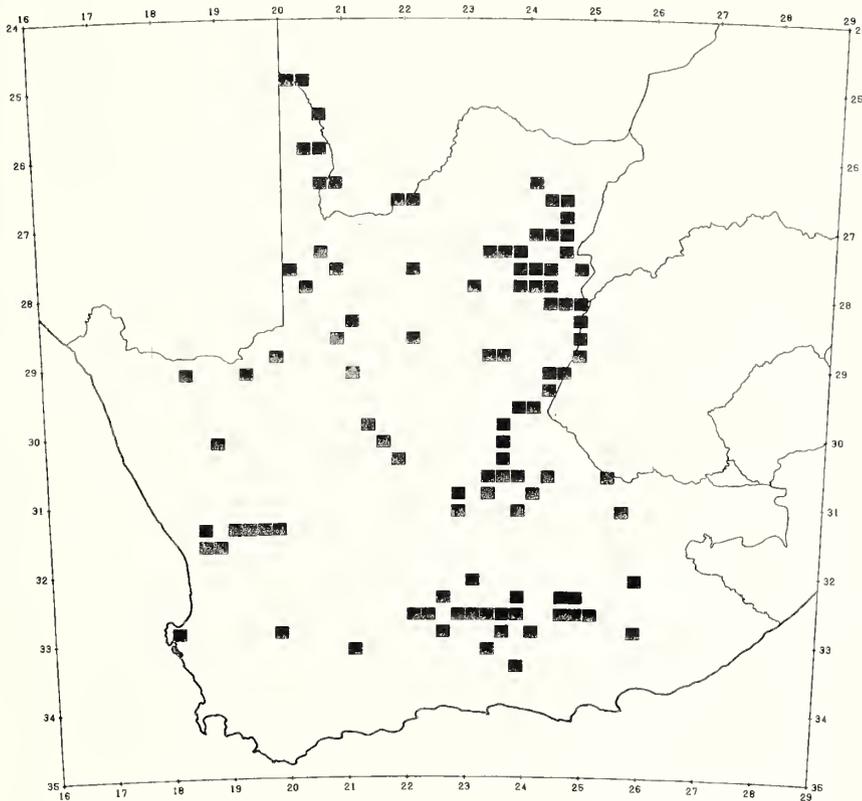


Fig. 109. Distribution of the Greater Kestrel, 1970 – 1979.

Lesser Kestrel

Falco naumanni

Distribution (Figs 110 and 111)

The distribution for the 1970s is more restricted than that given by McLachlan & Liversidge (1978).

Habitat

Grassland primarily and secondarily macchia, karoo and thornveld. The birds forage over open country and roost communally in groves of trees; these groves are often exotic types such as *Eucalyptus* spp. and *Populus* spp. which are planted around farmsteads and in towns.

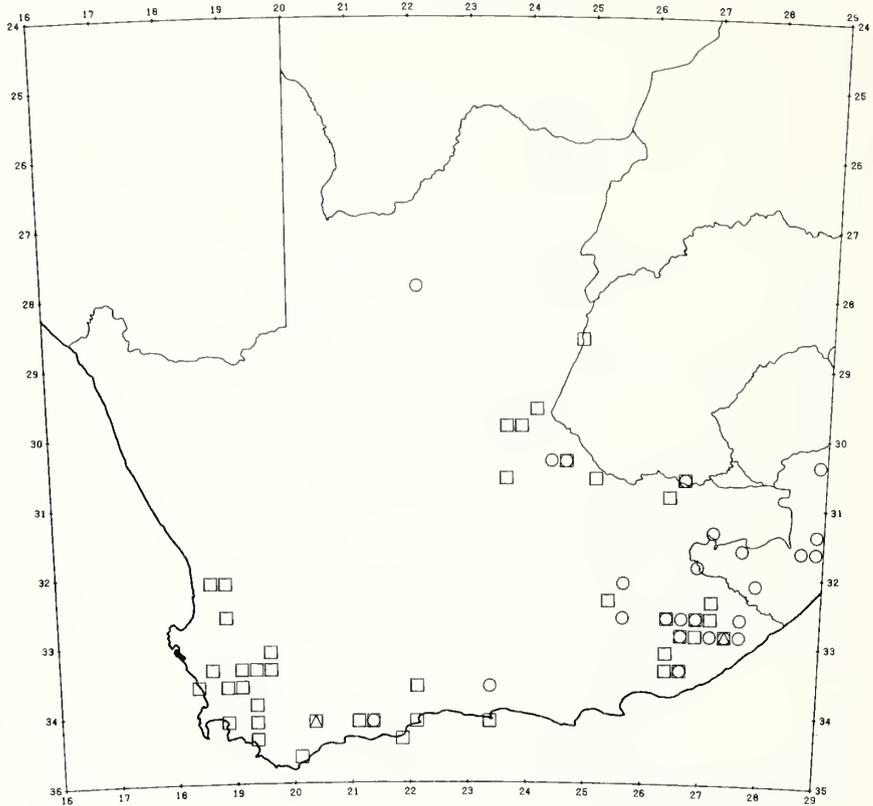


Fig. 110. Distribution of the Lesser Kestrel, 1700 – 1969.

Status

A relatively common non-breeding Palaearctic migrant which is present during the austral summer. The species may have increased its range in the eastern Karoo while undergoing a decrease in the southern regions. The increase may be due to the establishment of groves of exotic trees in the Karoo.

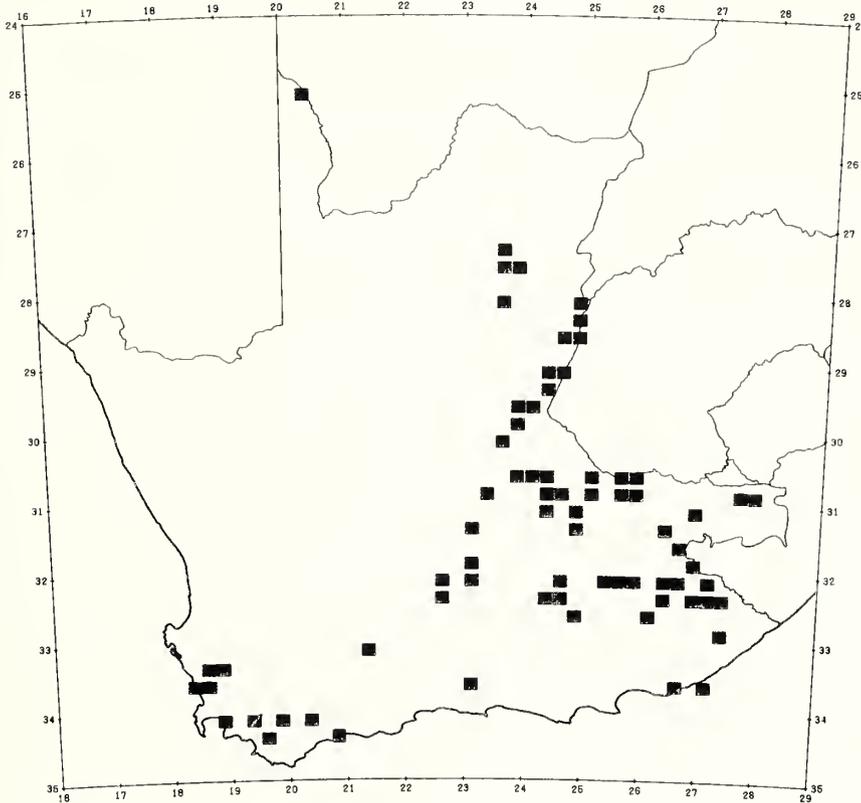


Fig. 111. Distribution of the Lesser Kestrel, 1970 – 1979.

Pygmy Falcon

Polihierax semitorquatus

Distribution (Figs 112 and 113)

The distribution for the pre-1970s accords with that given by Snow (1978) but, as with that for the 1970s, is more restricted than the distribution given by McLachlan & Liversidge (1978).

Habitat

Bushveld, especially where the camelthorn tree *Acacia erioloba* occurs; these trees are used as nest trees by the Social Weaver *Philetarius socius*, a species to which the distribution of *Polihierax semitorquatus* is closely linked since it usually nests in a chamber of a Social Weaver nest.

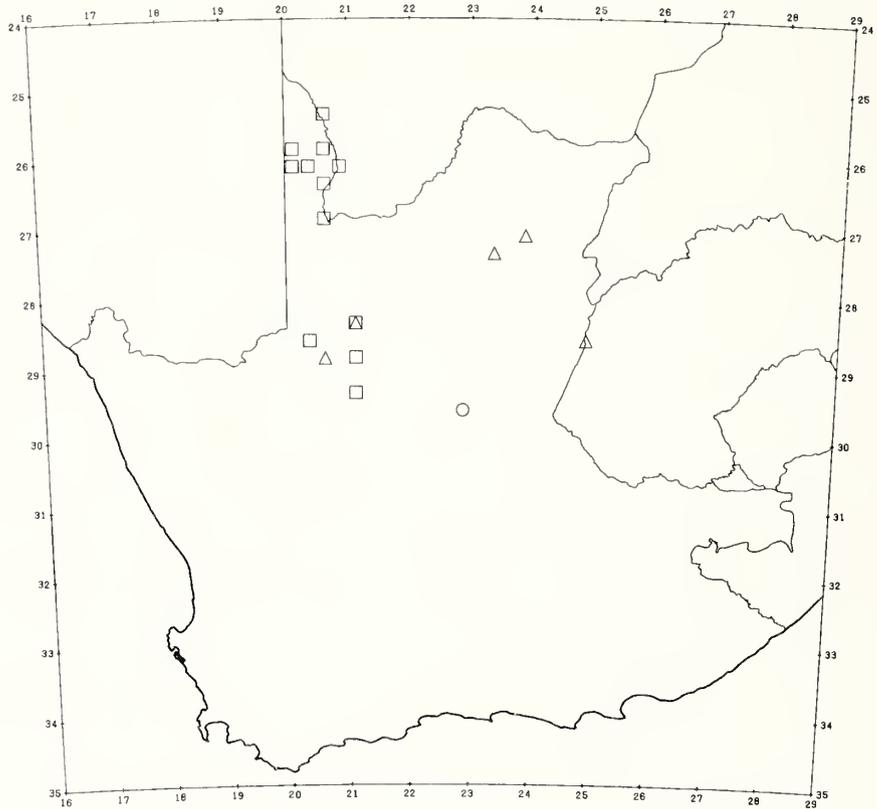


Fig. 112. Distribution of the Pygmy Falcon, 1700 – 1969.

Status

A resident species which is rare outside the Kalahari Gemsbok National Park. There is no evidence of a change in range in the Province between the two periods. However, numbers may have decreased due to a decrease in camelthorn trees, and consequently Social Weaver nests, as a result of overfrequent veld burning by stock farmers. *P. semitorquatus* is listed as "vulnerable" in South Africa by Siegfried *et al.* (1976).

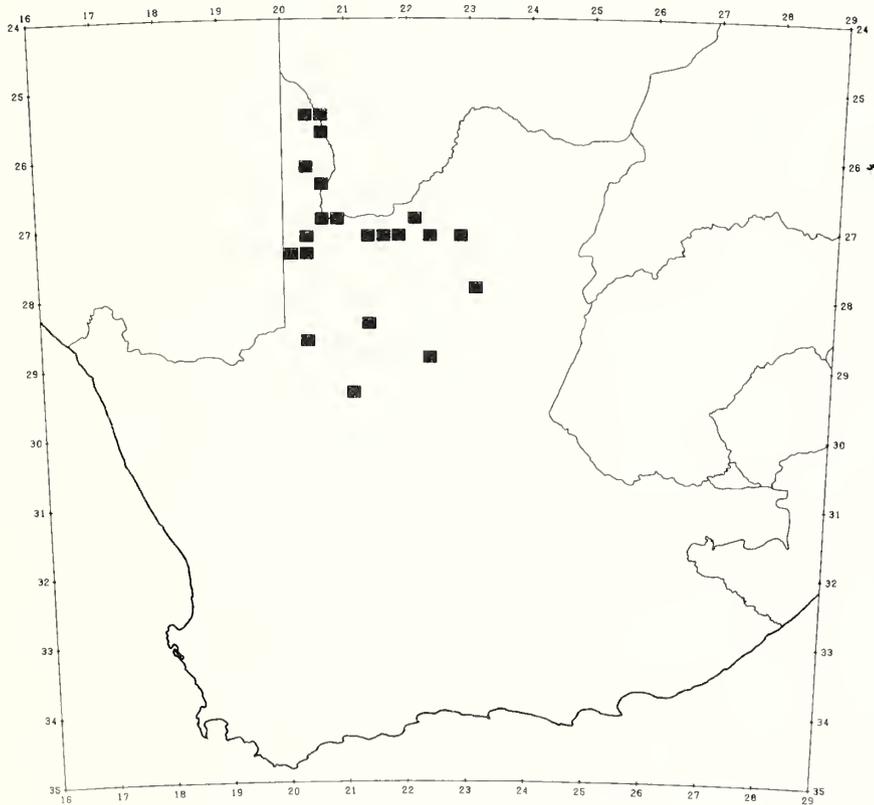


Fig. 113. Distribution of the Pygmy Falcon, 1970 – 1979.

DISCUSSION

The authors contend that the coverage obtained for the 1970s permits a relatively accurate assessment of the distribution of the diurnal raptors of the Cape Province for that decade and also permits a comparison with the pre-1970s period. Of the 55 taxa surveyed the majority (72,6%) show no change in their range. However, almost a quarter (23,6%) of the taxa exhibit a decrease in range of varying degrees. In contrast only two taxa (3,6%) show a small increase. Of the 13 taxa showing a decrease eight are resident in the Province and another formerly bred in the Province.

Many of the distribution maps presented here modify to a greater or lesser extent the maps given for certain taxa by McLachlan & Liversidge (1978) and Snow (1978). Particularly in the case of the latter publication no distinction is made between old and modern records and as a result the maps for certain taxa, e.g. Lappetfaced Vulture, Lammergeyer, Bateleur, are totally inadequate.

It is perhaps relevant that all the taxa, shown by this survey to have decreased their range in the Province, can be classed as "specialists" in that they occupy narrow ecological niches. Such taxa are the first to disappear when habitats are degraded. For example five of the eight taxa of vulture (including the Lammergeyer) recorded in the Province exhibit a decreased range; the removal of the game herds and their replacement by well managed domestic stock has largely contributed to this decrease. Similarly four of the eight true forest taxa have exhibited a decrease, having disappeared from the southern and/or eastern parts of the Karoo. The taxa concerned, *viz.* Longcrested Eagle, Crowned Eagle, Black Sparrowhawk and African Goshawk, used to inhabit thickly wooded kloofs and ravines in that area but man has now virtually totally destroyed the habitat through injudicious burning and use of the trees for building and fencing material. On the other hand the "generalists" are able to persist, usually through adaptation.

The data presented in this paper must be assessed in terms of the constraints imposed upon them. The extraction of data from published sources actually presented less of a problem than those from unpublished sources. This is due to the fact that, although often located in obscure publications, the published data were at least available, whereas there is undoubtedly much material still to be consulted but which is in the form of notes in personal, and thus unpublished, notebooks of many professional and non-professional ornithologists. It is hoped that this paper will stimulate the release of additional unused data. Many valuable data, particularly from the pre-1900 period, were excluded due to the omission of such basic information as date and locality. Furthermore, and this applies mainly to the early records, some of the localities given were so vague as to render the record useless, e.g. "Cape of Good Hope" or "Eastern Province". It was not possible to substantiate all records on the file but for most taxa the incorrect records are in the minority and they are masked by the majority of (correct) records. There is little doubt that more records will come to light in the literature, particularly from obscure sources. For the 1970s, and to a lesser extent the 1950s and 1960s, the authors were able to use many unpublished records, whereas for the preceding period they had to rely almost entirely on published material. The authors consider that 95% of the literature records have been extracted.

There are many variables pertaining to the study of the distribution of raptor populations and the type of data presented here does not lend itself to any form of statistical analysis. Consequently the maps give the data a higher degree of mathematical uniformity than they actually possess. The main factors precluding quantification of trends is the lack of any standardized method of data collection. For example in both the pre-1970s and 1970s, particularly the former period, there are many cases where only interesting or conspicuous taxa were recorded from a locus. Further the "degree of effort" per locus was not controlled, i.e. the time spent and the area covered within a locus shows large variation. Some loci were visited only once

whereas others were visited many times. Many of the records were from roadside counts and the many biases involved in recording raptors from vehicles are well known. Certain taxa, e.g. kestrels, kites and buzzards, are prone to the use of telephone poles or powerline pylons as perches and are thus more conspicuous and therefore readily observed. Other taxa, by virtue of their habitat requirements, are inconspicuous and are therefore rarely observed, e.g. forest and mountain taxa.

Interpretation of the maps is complicated by various factors. An important aspect is that of the number and distribution of observers throughout the entire period covered by the maps. Probably only since 1940, the year in which the first edition of *Birds of South Africa* (Roberts 1940) was published, has there been a marked increase in interest in South African birds. Through time there has also been an increase in the quantity (and quality) of observers. Furthermore, some parts of the Cape Province, e.g. N. Cape and N.W. Cape, are even today very isolated, with poor roads. Accordingly these areas have not been subjected to the same degree of observation as in the case of areas close to or including the cities or more settled parts where active birdwatching clubs may exist. Thus any gaps in distribution, in certain cases, could be attributed to lack of observation rather than the absence of the birds. However, the maps and graphs should be viewed only in terms of general temporal and spatial trends. For certain taxa the two periods selected were adequate to indicate major range fluctuations. However, for others several range fluctuations may have taken place during one or both periods. An example of the latter case is provided by the Cape Vulture population which was widespread and thriving at the time of the rinderpest epidemic in 1896 and the Anglo-Boer War at the turn of the century. The population then decreased in range and numbers during the first part of the present century. This was followed by an increase, particularly during the 1960s, and then another decrease in the 1970s (Boshoff & Vernon 1980a). However, space and the general quality of the data precluded the presentation of one map per decade per taxon.

A relevant criticism of the maps presented here is the fact that no distinction is made between the types of record used, e.g. breeding records, records of regular occurrence and records of vagrants. Mundy (1980) discusses this aspect of distribution surveys in some detail. In the present study it is purely a case of quality and quantity of data which precludes such a breakdown. For virtually all taxa there are too few breeding records available to be able to present a meaningful picture. Further, too little is known of nomadism and local migration to separate the breeding and non-breeding ranges of resident taxa. For most taxa it is generally accepted that the range given includes the breeding range, with the obvious exception of non-breeding Palaearctic migrants. Extralimitals and stragglers can be expected on the periphery of the range of a taxon. In addition there is a security risk attached to the pin-pointing of loci where rare and endangered raptors breed.

A further problem in the interpretation of the survey data is that of the nomadism which several raptor species exhibit, e.g. Blackshouldered Kite, Pale Chanting Goshawk. The authors have little data to aid the understanding of this phenomenon but it appears to be related to changing conditions, which in turn are regulated by climatic events, e.g. an east-west shift of populations according to droughts and floods in the E. Cape and Karoo. To further complicate the issue the natural trend is masked by man's modifications of various habitats. Taxa undergoing local migrations, e.g. Black Harrier, Booted Eagle, present additional interpretation problems.

The scope of this study and the type of data collected do not permit any statements on the dynamic numerical status of the taxa listed. However, it must be emphasized that a static range does not imply a static population in terms of abundance. The following resident taxa which show no range change in the Cape Province are subjectively considered to have undergone a decrease in numbers: Secretary Bird, Whitebacked Vulture, Cuckoo Hawk, Blackbreasted Snake Eagle, African Marsh Harrier, Pygmy Falcon.

The conservation value of this survey is seen mainly as the provision of a set of data which can serve as a baseline for further monitoring of diurnal raptor populations, on a temporal and spatial basis, in the future. In addition the survey has indicated which taxa are most in need of urgent conservation attention, *viz.* the vultures, the large eagles and the forest species.

Button & Clancey (1972), Brooke (1978) and Liversidge *et al.* (1981) have published reports of extremely rare taxa from the Cape Province and Transkei. However, as many of the taxa reported need confirmation and none can be considered as part of the Cape Province raptor avifauna they are not listed by this survey. Similarly there is only one acceptable record for the Western Redfooted Kestrel, *Falco vespertinus*, that of a specimen from the Beaufort West district collected in 1875. *F. vespertinus* is a non-breeding Palaearctic migrant which normally occurs in northern and central Namibia and the single record referred to is probably of a rare vagrant.

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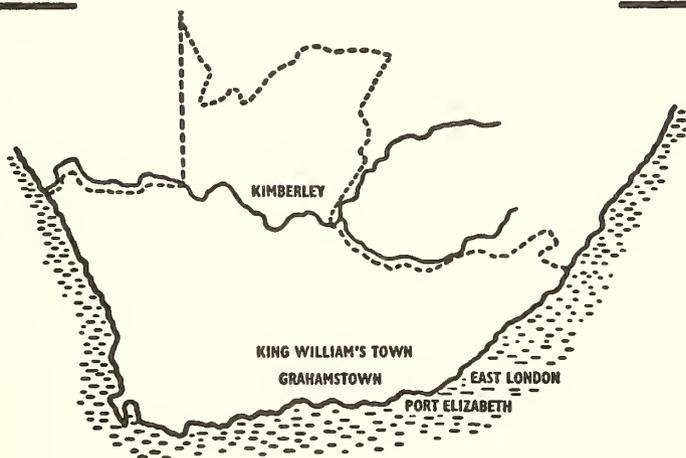
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On the Hydropsychidae (Trichoptera) of Southern Africa with keys to African genera of imagos, larvae and pupae and species lists

by

K. M. F. SCOTT

Albany Museum, Grahamstown, South Africa

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ABSTRACT

The different stages of one species of each of the genera of Hydropsychidae (Trichoptera) found in Southern Africa (south of the Zambezi River), are described, figured and discussed as far as available material allows, the main emphasis being on the immature stages. The genera included are *Hydropsyche*, *Cheumatopsyche*, *Sciadorus*, *Dipletronella*, *Macrostemum*, *Amphipsyche*, *Protomacronema*, *Leptonema*, *Polymorphanisus* and *Aethaloptera*. Of these, *Dipletronella*, from Central Africa, has been included in case it should be found further south and for comparative purposes. Notes on *Hydromanicus*, from the Seychelles, and *Dipletrona*, from North Africa, have been included, and they have also been included in the keys. Illustrated keys to imagos, larvae and pupae of African genera are given ("Africa" here means the Afrotropical Region, including Africa south of the Sahara and the Malagasy Subregion, together with North Africa). In the case of each genus a list of the species recorded from Africa is appended, with references and distribution. *Macrostemum natalense* (Ulmer) is placed in the synonymy of *M. capense* (Walker), and *Sciadorus sinuatus* Marlier transferred to the genus *Dipletronella* as *D. sinuata* (Marlier).

INTRODUCTION

This account of the Hydropsychidae of Southern Africa is based mainly on specimens in the Albany Museum Collection of Freshwater Invertebrates, which derives largely from collections made by the staff of the National Institute for Water Research of the South African Council for Scientific and Industrial Research, during hydrobiological surveys of various river systems throughout South Africa. To these have been added several other collections, and supplementary material has been made available to me by various museums and other workers in the field (see Acknowledgements).

The aim in the present paper has been to describe and illustrate as fully as possible the immature stages of the Southern African genera, including earlier larval instars wherever possible but giving only a very brief description of the adults, together with keys and necessary discussion. References to the literature have been included, and generic diagnoses have been quoted or adapted from it as they are seldom accessible to field workers, yet are invaluable for checking identifications. In each genus the species recorded from Africa have been listed with

comments, noting the known stages, but it has not been possible to check the validity of doubtful species.

The genera fall into three of the four formerly recognized subfamilies of the Hydropsychidae, the Hydropsychinae, Diplectroninae and Macronematinae. The fourth is now usually raised to family status, as the Arctopsychidae, and does not occur in Africa, apparently being confined to the Northern Hemisphere.

The procedure followed is outlined below. The keys, to imagos, mature larvae and pupae, are given first, each couplet being illustrated wherever necessary by reference to the text figures. These keys include all genera recorded from Africa. The term 'Africa' is here used to denote the Afrotropical Region (i.e. Africa south of the Sahara together with South-West Arabia, which formed the old Ethiopian Region, together with the Malagasy Subregion), plus North Africa. (See Crosskey & White, 1977, for the term 'Afrotropical Region.') This seemed desirable for completeness and for use by workers in other parts of Africa.

In point of fact, *Hydromanicus* Brauer, found in the Seychelles, *Diplectrona* Westwood, a Palearctic genus extending into North Africa, and *Diplectronella* Ulmer from Central Africa, are probably the only valid genera included that do not occur in Southern Africa. *Hydropsychodes* Ulmer has been placed in the synonymy of *Cheumatopsyche* Wallengren (Kimmins 1963), *Plesiopsyche* Navás and *Synphitopsyche* Ulmer in that of *Hydropsyche* Pictet (see Ross & Unzicker 1977 and Schmid 1979); the genera *Phanostoma* Brauer and *Amphipsyche* McLachlan have been combined, and *Chloropsyche* McLachlan placed in the synonymy of *Aethaloptera* Brauer (Kimmins 1962a). Excepting in the cases of *Protomacronema* and *Diplectronella*, Southern African specimens have been used in making the drawings.

The keys are followed by a descriptive section, forming the main body of the paper, in which is given as complete a coverage of the developmental stages of each genus as is possible from the material available, together with a brief account of the imagos, the latter mainly for recognition purposes.

In writing these sections, and in building up the keys, reference was, of course, made to the not inconsiderable literature on the subject, and the keys, particularly those to imagos and pupae, owe much to the excellent papers produced by the late Dr Georg Ulmer (1951, 1957), as well as to those of many other workers in the field. Following Ulmer's practice, the couplets have been expanded to enable further points to be checked and identifications made more certain, particularly in cases where parts of a specimen are damaged or missing. Much use has also been made of the late Dr F. C. J. Fischer's invaluable *Trichopteroorum Catalogus* (volumes IV, 1963, and XIII, 1972); his nomenclature has in most cases been followed.

A general treatment of African families of Trichoptera (Marlier's "Généra des Trichoptères de l'Afrique") appeared in 1962, but because this admirable work covers the entire Order, the descriptions are necessarily brief, not very fully illustrated, and include only final instar larvae. It was therefore felt that a much fuller treatment of the family was needed for the use of ecologists in Southern Africa, and for use by workers on any African material. The keys were produced prior to the appearance of Marlier's, being based primarily on the older literature and on specimens in hand. They have, however, been checked against his and others and tested in use for some time.

The genus *Protomacronema*, while mainly Central African, has also been recorded from Zululand (Kwazulu), from the Zambezi River in Mozambique and Rhodesia (now Zimbabwe), and from its upper reaches and tributaries in Angola. Mature larvae were first described by Gibbs (1973), even then tentatively, from Ghanaian material, and the account in this paper is based on specimens generously sent to me by him, and compared with his own description. Statzner (in litt.) has confirmed this correlation. Marlier (1965/66) listed *Protomacronema* larvae as occurring in Angola, basing his identification on their occurrence in the same area as

Protomacronema imagos, together with their notable differences from known Hydropsychid larvae. I borrowed those specimens for study from the Museo do Dundo, but it transpired from Gibbs' work that they were in fact *Leptonema* larvae, probably of *L. normale* Banks, *Leptonema* evidently being a genus showing a wide variation in certain larval characters, notably the procoxae, size of stridulatory files and shape of anal gills.

The genus *Diplectronella*, first described from Ceylon (Ulmer 1928), has only been recorded from Central Africa to date, but may yet be discovered in mountainous regions further south. It has been described from specimens kindly made available by Dr Decelle of the Musée Royale de l'Afrique Centrale at Tervuren, and compared with larvae determined for Dr E. J. Young, collected in Kenya.

Comments on the material studied, particularly the larvae, are given under each genus, only one species being described in each case. Where possible, however, several species have been compared in an endeavour to ensure that characters used in the keys are of generic rather than specific value. Further localities are given from records in the Collection catalogues to supplement the known distribution of certain species. Except where otherwise specified, the specimens studied are in the Albany Museum.

It should be noted that the keys which follow are not necessarily applicable in other parts of the world.

Methods of study have been described by Barnard (1934), Ross (1944), Wiggins (1977) and many others. Terms used in this paper are illustrated in the earlier figures (*cf.* Figs 1-6, 10-12, 17, 19, 24) and occasionally in later ones where required.

Most of the adult specimens studied have been in spirit; in these the setae, particularly of wings, may have been lost, though their bases may still be distinguishable. Pinned (dry) specimens are very fragile, and must be handled most carefully; they tend to lose antennae, legs or wings, rather than setae. Drawings have been made either from spirit material under a stereomicroscope (magnification from $\times 8$ to $\times 216$) or, in the case of genitalia, from material cleared in KOH and drawn in clove oil.

In the case of larvae and pupae all were in spirit. Parts too small for convenient study under the stereomicroscope were mounted in glycerine, gum chloral or Euparal for drawing under a compound microscope (magnification used from $\times 15$ to $\times 600$). An Abbé Drawing Apparatus was used to ensure correct proportions.

SCALES AND ABBREVIATIONS USED

SCALES

Scale lines represent 1,0 mm unless otherwise indicated.

ABBREVIATIONS

Wing notation:

C, costa; Sc, subcosta; RS, Radial sector; R₁, R₂, R₃, R₄, R₅, branches of radius; M₁, M₂, M₃, M₄, branches of media; M, Cu_{1a}, Cu_{1b}, Cu₂, branches of cubitus; 1A, 2A, 3A, anal veins; arc, arculus; dc, discoidal cell; hc, humeral crossvein; mc, median cell; m-cu, crossvein between media and cubitus; pt, pterostigma; r-m, crossvein between radius and media; sdc, subdiscoidal cell; tc, thyridial cell; 1, 2, 3, 4, 5, apical forks; wf, wing fold; wh, wing-coupling hooks. Note corneous points in fork 2 and thyridial cell.

Other abbreviations:

ac, anteclypeus; ava, anterior ventral apotome; ant, antenna; ats, apical tibial spurs; co, coxa; ep, epimeron; fc, frontoclypeus; fca, frontoclypeal apotome; lp, labial palpus; mp, maxillary

palpus; pe, pre-episternum (1st pleural sclerite); p2, second pleural sclerite; psw, posterior setose wart; pt, pterostigma; pts, pre-apical tibial spurs; sf, stridulatory file; st, stipes (plural = stipites); ve, vertex.

KEYS TO GENERA OF AFROTROPICAL HYDROPSYCHIDAE

(a) *IMAGOS*

This key in various forms has been in use for a long time. It owes much to keys and data given by Ulmer (1951), also by Barnard (1934) and Ross (1944); many other authorities have also been consulted, all have been included in the list of references.

1. In hind wing RS first forks at anastomosis (i.e. at level of main cross-veins, cf Figs 91 & 4), from a common base, forming a long subdiscoidal cell; R₁, generally with Sc, joins RS distal to anastomosis (in *Polymorphanisus* by a cross-vein only, Fig. 180); discoidal cell open or absent, strongly curved macrotrichia on costal margin. In forewing discoidal cell closed, open or absent. Antennae 2 to 4 times length of forewing in ♂, longer than forewing in ♀, very slender, threadlike. Maxillary and labial palpi present or absent. Vertex of head generally with anterior setose warts larger than posterior ones (Figs 88, 116); smaller in *Leptonema* (Fig. 158) and ♀ *Protomacronema* (Fig. 144)..... Subfamily MACRONEMATINAE Ulmer 3
- In hind wing RS forks before anastomosis (Figs 4, 46), subdiscoidal cell absent, R₁ and Sc do not join RS apically; discoidal cell closed; strongly curved macrotrichia absent. In forewing discoidal cell closed. Antennae not much longer than forewings, often shorter, slender to fairly stout, not threadlike. Maxillary and labial palpi always present. Vertex with paired posterior warts larger than anterior pair (Figs 1, 20, 43, 66)..... 2
2. In hind wing Sc and R₁ join apically before joining costa. 5th abdominal sternum lacks paired filamentous appendages. Outer leg claws may be concealed by tuft of black setae. African genera with tibial spurs 2.4.4 or 0.4.4. Antennae smooth. ♀ genitalia with sternal plates of VIII partly or completely separated; mid-tibiae and tarsi of ♀ usually dilated. (See Figs 1–6 & 20–25)..... Subfamily HYDROPSYCHINAE Curtis 8
- In hind wing Sc and R₁ remain separate to margin, 5th abdominal sternum with a pair of filamentous lateral appendages, each arising from an internal gland. Outer leg claws not concealed by tuft of setae. African genera with tibial spurs 2.4.4. Antennae appear serratulate owing to setal arrangement and internal dilatation, ♀ genitalia with sternal plates of VIII separated to base, mid-tibiae and tarsi of ♀ not dilated. (See Figs 43–48)..... Subfamily DIPLECTRONINAE Ulmer 10
3. Palpi absent or rudimentary, medium-sized to very large species, wings usually glassy, middle tibiae with 2 or 3 spurs Tribe POLYMORPHANISINI Lestage 4
- Palpi always present, usually well developed, medium-sized species, wings glassy or hairy, middle tibiae with 4 spurs Tribe MACRONEMATINI Lestage 5
4. Tibial spurs 0.2.2 or 0.3.2. Forewing with discoidal cell present or absent, small false discal cell enclosing the corneous spot, median cell very large, quadrangular. Medium-sized (♂ forewing c. 10–18 mm, ♀ smaller) (Figs 192–198)..... *Aethaloptera* Brauer (Syn. *Chloropsyche* McLachlan)
- Tibial spurs 1.3.2, 1.3.3, or 2.3.3. Forewing with discoidal cell closed, median cell subtriangular. Very large (♂ forewing up to 25 mm). Some African species have a pair of conspicuous dark spots on the mesoscutellum. (Figs (Figs 177–180)..... *Polymorphanisus* Walker

5. Forewing with discoidal cell open or absent; palpi large or small. Tibial spurs 0.4.4, 1.4.4, 1.4.3, 1.4.2, 0.4.3, 0.4.2, 0.3.2 or 0.2.2. Wings glassy or hairy, hind wings very wide, triangular, much folded 6
 — Forewing with discoidal cell closed; palpi well developed. Tibial spurs 0.4.4, 1.4.4 or 2.4.4. Wings usually hairy, hind wings normally shaped. 7
6. Palpi present but poorly developed, forewing with false fork 5 between Cu_1 & Cu_2 . Tibial spurs 1.4.4, 1.4.3, 1.4.2, 0.4.3, 0.4.2, 0.3.2 or 0.2.2. No stalked processes on 5th abdominal sternum. Wings glassy, ♂ forewing c. 11–18 mm, ♀ smaller. (Figs 116–121) *Amphipsyche* McLachlan
 — Palpi well developed but slender, often inconspicuous in ♂, shorter in ♀; ♂ forewing with forks, 1, 2, 3, 4 (no false fork 5, Cu_1 , Cu_2 & 1A all ending in an anastomosis), ♀ with forks 1, 2, 3, 4, 5. Tibial spurs 0.4.4. Pair of small knob-like processes, stalked, on 5th abdominal sternum in ♂. Wings hairy, ♂ forewing c. 10–13 mm, ♀ smaller. (Figs 137–144) *Protomacronema* Ulmer
7. Vertex with anterior warts smaller than posterior. Hind wing with fork 5 longer than fork 2. 2nd segment of maxillary palp longer than third. 5th sternum in both sexes with pair of fenestrae. Spurs 2.4.4 or 1.4.4. Wings usually hairy, a few species with clear wings. ♂ forewing c. 10–17 mm. ♀ usually larger. (Figs 158–163)
 *Leptonema* Guérin-Ménéville
 — Vertex with anterior warts larger than posterior. Forewing with Sc joining R_1 before reaching wing margin; hind wing with fork 5 shorter than fork 2. 2nd segment of maxillary palp shorter than 3rd. 5th sternum in ♂ (not in ♀) without fenestrae but with a pair of lateral processes. Spurs 2.4.4 or 1.4.4. Wings usually glassy, sometimes hairy, often brightly patterned, ♂ forewing c. 10–20 mm, ♀ smaller. (Figs 88–93) *Macrostemum* Kolenati
8. Hind wing with fork 1 present (may be small), median cell closed or open; tibial spurs 2.4.4 9
 — Hind wing usually with fork 1 absent (if present compare with couplet 9), median cell open, veins M & Cu_1 usually well separated, cross-vein large. Spurs 2.4.4, rarely 0.4.4. ♂ copulatory organ without long forked ventral process. ♀ with sternal plates of VIII separated to base of segment; mid-tibiae and tarsi of ♀ dilated. ♂ forewing 6–8 mm long, ♀ slightly larger. (Figs 20–25)
 *Cheumatopsyche* Wallengren (Syn. *Hydropsychodes* Ulmer)
9. Median cell in hind wing closed, veins M & Cu_1 usually very close together, cross-vein short. ♂ copulatory organ with forked ventral process longer than the organ itself (Afrotropical species & certain N. American species). ♀ with sternal plates of VIII separated for only 2/3 distance to base of segment, mid-tibiae and tarsi strongly widened. ♂ forewing 9–11 mm, ♀ slightly larger. (Figs 1–6)
 *Hydropsyche* Pictet (Synonyms *Plesiopsyche* Navás & *Symphitopsyche* Ulmer)
 — Median cell in hind wing open, veins M & Cu_1 well separated, crossvein clear. ♂ copulatory organ without long forked ventral process, in this species terminal segment of ♂ claspers apically concave, blackened, with thick inner covering of black setae. ♂ mid-leg not widened. ♂ forewing 7–8 mm, ♀ 8–10 mm. (See Ulmer 1910a: 47–49, figs 11–14 for wings & ♂ genitalia)
 *Hydromanicus seychellensis* Ulmer (Seychelles)
10. Fork 1 in hind wing present, obvious; hind wing with Sc & R_1 sinuous, strongly bent upwards to meet costa apically. Vertex of head with two pairs large warts. ♂ with 2 pairs large, rounded reticulated internal organs in abdomen (number depends on species, 2 pairs being most usual); processes on sternum of V very long. ♂ forewing 7–9 mm (in *D. felix* McLachlan, the only known African species). (For figures see

- Mosely 1939, figs 411–415) *Diplectrona* Westwood (North Africa only)
 — Fork 1 in hind wing absent (if present then minute), other characters various 11
11. Eyes rather small, sparsely pubescent; hind wing with Sc & R₁ not strongly bent upwards to meet costa, wing not deeply rounded posteriorly, fork 1 absent (occasionally present but minute). Vertex of head with narrow anterolateral warts, posterior warts very large. ♂ abdomen with 2 pairs large, rounded reticulate internal organs, processes on abdomen V (♂, ♀) short, not extending beyond segment V. ♂ forewing 5–9 mm. (Figs 43–48) *Sciadorus* Barnard
- Eyes fairly large, strongly pubescent; hind wing with Sc & R₁ sinuous, bowed towards costa basally & strongly bent up to meet costa apically; wing deeply rounded posteriorly, fork 1 always absent. Vertex of head with sinuous beanshaped anterolateral warts, posterior warts fairly large (compare Figs 66 & 43). ♂ abdomen without such large internal organs, processes on abdomen V very long, reaching end of abdomen in ♂, in ♀ to mid-VI or longer. ♂ forewing 7–11. (Figs 66–72)
 *Diplectronella* Ulmer

(b) LARVAE

All Hydropsychid larvae are campodeiform, having long, two-jointed anal prolegs projecting beyond and free from the membranous lobes of the tenth abdominal segment; all three thoracic terga are sclerotised, and tufted tracheal gills are present on the ventral surface of thorax and abdomen in all instars except the first and, in some Macronematine genera, the second. In counting gills it must be borne in mind that, as the abdomen enlarges in later instars, the double stems of certain gills may become quite widely separated. The larval head is oval to oblong, with eyes (grouped ocelli) placed below several cuticular lenses; antennae minute, situated close to the bases of the large mandibles; maxillary palpi stout, sometimes very long, labial palpi very small, not easily seen. The ventral side of the head usually bears stridulatory files (except in the Polymorphanisini), the scrapers being situated on the forelegs. When present these organs are presumably used by a larva as a warning to other larvae trespassing on its “territory”, i.e. too close to its net (see Johnstone 1964), or actually invading it (Jansson & Vuoristo 1979), when stridulation often accompanied by fighting between the larvae has been observed. Abdominal terga I–VIII are without dorsal sclerites, though there may be one on IX; setose sternal plates may be present on VIII & IX, or IX only or absent. The larvae lack transportable cases but construct shelters and spin complex catching nets in which to trap food. These structures differ according to genus, and sometimes within a genus. Most genera may also sally forth at times to capture prey or, being very pugnacious, to repel invaders, or to escape unfavourable conditions (see Sattler 1963, Kaiser 1965, Edington 1965, Wallace 1975 and others).

The larvae live on and under rocks or stones or amongst roots of aquatic macrophytes in running water or on wave-washed shores of large lakes. They often abound where food supplies are plentiful and flow is rapid, as may be the case below impoundments. Biological notes are given under each genus.

In this family there appear to be either five or six larval instars, the Macronematinae having six, the other subfamilies five. **The key which follows applies to mature larvae** and cannot be used for first or second instar larvae in which neither gills nor pre-episterna (fore trochantin of Wiggins 1977) nor limb claws are as yet sufficiently developed. It must be used with caution in the case of third instar larvae. Fourth and fifth instars (the latter where there are six) are sufficiently like the mature larva for reasonably easy recognition, though the colour pattern may not as yet be fully developed. Early instars can, however, sometimes be recognized from characters mentioned in the text, particularly when collected together with later instars of the same species.

Synonymy, given in the key to imagos under the genera concerned, is not repeated in the keys to larvae and pupae. Synonyms can, of course, also be found, with references, in the sections on the genera which follow the keys.

1. Pre-episternum at base of foreleg forked (all African genera in this group) (Fig. 17); apex of submentum with deep median incision (Figs 12, 32); dorsal surface of head without carina, ventral surface with stridulatory files (Figs 12, 32); anteclypeus not sclerotised; left mandible with inner brush of setae (Fig. 14); branched tracheal gills on abdominal segments II–VI in four rows, small conical dorsolateral gills (“Zipfelkiemen” of Ulmer) present; setose ventral sclerites on VIII & IX HYDROPSYCHINAE Curtis 3
- Pre-episternum at base of foreleg not forked but simple (Figs 61, 105a, 132); apex of submentum entire (Figs 58, 131); dorsal surface of head with or without carina (Figs 100, 102, 57); stridulatory files present or absent, anteclypeus with or without sclerites; left mandible with or without inner brush; branched tracheal gills on abdominal segments II–VI in two, four, six or eight rows, “Zipfelkiemen” present or absent 2
2. Meso- and metanotal shields with transverse sutures along which they break at ecdysis (Fig. 59); head without carina; frontoclypeal apotome very broad, with deep indentations opposite eyes, behind which it is strongly expanded (Fig. 57); anterior and posterior ventral apotomes large (Figs 58, 81), stridulatory files present; left mandible with inner brush; tracheal gills in four or six rows, “Zipfelkiemen” present; setose ventral sclerites on segments VIII & IX DIPLECTRONINAE Ulmer 5
- Meso- and metanotal shields without transverse sutures, remaining whole at ecdysis (Figs 111, 207); head with or without carina, frontoclypeal apotome not widely expanded behind eyes (Fig. 100); anterior ventral apotome small, posterior ventral apotome minute or absent, stridulatory files present or absent; left mandible with or without inner brush; tracheal gills in two, six or eight rows, “Zipfelkiemen” absent; setose ventral sclerites on IX only (except in *Leptonema*) or absent MACRONEMATINAE Ulmer 7
3. Naked dorsal branch of pre-episternum about 1½ times length of bristly branch and as wide basally; head and thorax with small, weak setae, mainly tapered, a few blunt or scale-like, glabrous in appearance; 3 metasternal gills, larvae up to 15 mm long. (Marlier 1978c, Figs 12–13.) *Hydromanicus* Brauer (Seychelles)
- Naked dorsal branch of pre-episternum as long as or shorter than the bristly branch, basally narrower (Fig. 17); head and thorax strongly setose, rough in appearance 4
4. Most setae on head short, blunt, peglike; right mandible without setulae on upper apical tooth; anterior margin of frontoclypeal apotome smooth; large paired oval sclerites present on intersegmental fold posterior to prosternal shield; 2 pairs metasternal gills, four anal gills. Larva up to c. 15 mm long. (Figs 11–19, Table I) *Hydropsyche* Pictet
- Setae on head tapered; right mandible with small tuft of setulae on upper apical tooth; anterior margin of frontoclypeal apotome often notched or crenulate; sclerites on intersegmental fold small, sometimes concealed or absent; 3 metasternal gills, four or five anal gills. Larvae up to c. 8 mm in length. (Figs 30–40, Table III) *Cheumatopsyche* Wallengren
5. Frontoclypeal apotome widest in centre, anterior and posterior ventral apotomes very large, together much longer than mid-ventral ecdysial line; no line of setulae on upper surface of mandibles; head & thoracic nota with many small sharply pointed setae 6

- Frontoclypeal apotome at least as broad anteriorly as in middle or broader, anterior and posterior ventral apotomes fairly large, but together shorter than mid-ventral ecdysial line; a line of setulae on upper surface of each mandible; head and thoracic nota with many large setae, some of which are blunt much as in *Hydropsyche*; basal seta on foreclaw slender, fairly long, on other claws stumpy; branched tracheal gills in four rows, no fan on anal prolegs. Length of larva c. 15–18 mm. (Figs 79–87, Table VII).....*Diplectronella* Ulmer
- 6. Foreclaw and basal seta slender, pointed; branched tracheal gills in four rows; few apical setae on anal prolegs (see Wiggins 1977, fig. 6.4)*Diplectrona* Westwood (N. Africa)
- Basal seta of foreclaw short, stumpy, spinelike, as is claw; branched tracheal gills in six rows; large fans on anal prolegs. Length of larva 13–14 mm. (Figs 56–65, Table V).....*Sciadorus* Barnard
- 7. Stridulatory files absent; mandibles without lines of setulae or inner brush; pre-episternum large, sharply pointed, either collarlike (Fig. 188) or dagger-shaped (Fig. 208); body glabrous, gills on abdominal segments II–VI in eight rows. (Early instars of both genera have the frontoclypeal apotome with characteristic triangular margin.) Tribe POLYMORPHANISINI Lestage 8
- Stridulatory files present; mandibles with or without lines of setulae and inner brush; pre-episternum small, conical (Fig. 132); body glabrous or rough, gills on abdominal segments II–VI in two, six or eight rows Tribe MACRONEMATINI Lestage 9
- 8. Pre-episternum collar-like with sharp anterior points; head and thorax long, narrow, smooth, shining, much narrower than abdomen; frontoclypeal apotome narrow, labrum large, almost circular, lacking strong lateral brushes, maxillary palpi very long, slender, retractile; forelegs without brushes; setose plates on sterna of VIII, IX, absent. Larvae large, up to 40 mm in length or more. (Figs 185–191, Table XVI).....*Polymorphanisus* Walker
- Pre-episternum narrow, dagger-shaped, as long as coxa; head relatively short & broad; thoracic segments broader than long, not strikingly narrower than abdomen; frontoclypeal apotome broadly triangular, broad labrum with strong lateral brushes, maxillary palpi small; forelegs with weak brushes on tibia and tarsus; setose plates present on sternum of IX. Larva medium-sized, 14–15 mm long. (Figs 203–213, Table XVIII)*Aethaloptera* Brauer
- 9. Head with U- or horseshoe-shaped carina on dorsal surface, enclosing a broad, partly sunken area (Figs 100–102); mandibles without inner bristles or lines of setulae; foreleg with or without brush, fore femur with thumblike basal process (Fig. 132a); tracheal gills on abdominal segments II–VI in six or eight rows, body smooth 10
- Head without carina; inner brush on left mandible, line of setulae along upper tooth in both mandibles; forelegs without brushes, anterior femur without basal process but with stridulatory protuberance, fore coxae variously armed according to species; tracheal gills on abdominal segments II–VI in two rows, body rough, bristly (thickly clad with small scalelike setae). (Figs 168–176, Table XIV).....*Leptonema* Guérin-Méneville
- 10. Carina cuts off a triangular piece from apex of frontoclypeal apotome, head (known species) bright chestnut or orange-brown, smooth, with fringe of long, stiff setae bordering carina; anteclypeus with two sclerotized plates; prosternal plate with median sulcus; brushes on forelegs very strong; gills on abdominal segments II & III in eight rows, on IV–VI in six rows. (Figs 99–109, Table IX) *Macrostemum* Kolenati
- Carina does not cut off a triangular piece from apex of frontoclypeal apotome, head (known species) dark brown or yellow with orange-brown or yellowish patterning;

- anteclypeus with four sclerotized plates; prosternal plate without median sulcus; brushes on forelegs weak; gills on abdominal segments II–VI in either six or eight rows 11
11. Carina runs through apex of frontoclypeal apotome exactly through point, head brown or yellow, usually with two conspicuous pale marks on frontoclypeal apotome and many setulae, no long curled setae on head; abdominal segments II–VI with gills in eight rows. (Figs 127–136, Table XI) *Amphipsyche* McLachlan
- Carina runs along apex of frontoclypeal apotome outlining a triangle, head in only known species brown patterned with orange-brown, long curling secondary setae on frontoclypeal apotome and within border of carina; gills on abdominal segments II–VI in six rows. (Figs 148–157, Table XIII) *Protomacronema* Ulmer (correlated by Gibbs (1973), confirmed by Statzner, in litt. (6.ix.1980) & paper (1981))

(c) PUPAE

Hydropsychid pupae are easily recognizable by their branched, tufted abdominal gills and typical anal processes (Figs 7, 8, 49, 52 etc.). The ventral gills are very similar to those of the larvae, however, the lateral gills may have enlarged pouch-like bases or resemble conical pockets, several often being superimposed (Figs 49, 122). The paired anal processes are situated at the end of the abdomen and may be wide or narrow, usually terminating in finger-like, plate-like or bifurcated apices (Figs 95, 125, 75). In the male there are paired ventral pockets containing the genitalia. Presegmental hook-bearing plates occur on abdominal terga II/III to VI/VII/VIII, varying according to genus, and postsegmental hook-bearing plates on terga III, III and IV or III, IV and V, at any rate in African species (Figs 7, 7a). The abdomen does not bear a long fringe of lateral setae, though the venter may be hairy and the dorsum may show lines or patches of setae or patches of shagreening (cuticular thickenings resembling those on sharkskin).

The mid-legs, particularly of the female, are generally flattened, widened and fringed with setae to form oars. The final instar larva constructs a stout case of sand grains or rock fragments, sometimes with an admixture of vegetable matter, in which to pupate. Within this case, which is anchored to the rock or stone adjacent to it, is a silken cocoon enclosing the pupa. The pupal case almost invariably has sieve plates at each end to allow free passage of water. At the anterior end is a cap of sand grains which, on emergence, is removed by the pupa (pharate imago) using its mandibles (Figs 27–29). The discarded larval sclerites are generally retained within the case, tucked into the posterior end. When still present they can be used to assist in identification of the species and in the correlation of larva, pupa and imago in the case of a mature male pupa with undamaged genitalia. The pupa is exarate, leaving the case as a pharate adult, able to swim to the surface of the water and climb up any projecting object on which eclosion takes place and from which the perfect insect flies away.

1. Antennae short, stout, not more than $1\frac{3}{4}$ times body length at most in ♂, usually little longer than body, often shorter, in ♀. Anal appendages with apices deeply forked (Figs 53, 75) or ending in two points with a concavity between them (Figs 8, 26a), or truncate (Seychelles genus only); mandibles and palpi always present; lateral gills conical, tracheal gills branched 2
- Antennae very long, filiform, 2–4 times body length, coiled round or dorsal to posterior end of body in ♂, in ♀ shorter, not coiled but recurved; anal appendages not apically forked or cup-shaped, but apices bluntly or sharply pointed (see Figs 95, 124, 145, 165, 184, 201); mandibles present or absent, if present with well-developed apical & lateral teeth (Fig. 97), palpi present or absent; presegmental dorsal plates

- on segments II/III–VI/VII/VIII, postsegmental on III or III & IV; lateral gills not conical but may have expanded pouch-like bases; tibial spurs various 7
 MACRONEMATINAE Ulmer
2. Anal appendages straight, narrow, apices deeply forked (Figs 53, 75); antennae as long as or shorter than body; sternum of V with pair of ventrolateral filiform processes; gills on segments II–VII, (Figs 49–79); presegmental dorsal plates on II–VII/VIII, postsegmental on III & IV or III, IV, V; tibial spurs 2.4.4 3
 DIPLECTRONINAE Ulmer
- Anal appendages curved dorsad, apices truncate or ending in two points with a concavity between them (Figs 8, 26a); antennae not more than $1\frac{3}{4}$ times body length, usually less, in ♀ shorter than body; sternum of V without filiform processes; gills on segments II–IV/VII; presegmental dorsal plates on II/III–VIII, postsegmental on III & IV; tibial spurs 2.4.4 or 0.4.4 5
 HYDROPSYCHINAE Curtis
3. Anal appendages with both branches of apical forks very long, dagger-shaped; inner surface of mandibles proximal to teeth smooth; presegmental dorsal plates on segments II–VII, postsegmental on III & IV. (For figs see Ulmer 1957 pl. 30 figs 607–610) *Diplectrona* Westwood (North Africa)
- Anal appendages with branches of apical fork shorter, not dagger-shaped (Figs 53, 75) 4
4. Anal appendages with both terminal points of apical fork subtriangular, pointed, strongly denticulate, particularly within fork; inner surface of mandibles proximal to teeth smooth; presegmental dorsal plates on segments II–VIII, postsegmental on III, IV and V. (Figs 49–53, Table VI) *Sciadorus* Barnard
- Anal appendages with terminal points of apical fork broad, blunt; inner surface of mandibles proximal to teeth denticulate; presegmental dorsal plates on II–VII, postsegmental on III and IV. (Figs 73–77, Table VIII) *Diplectronella* Ulmer
5. Anal appendages with wide, blunt apices, finely crenate or serrated apically but not concave; presegmental plates on III–VIII; mandibles with large apical teeth; ventral and lateral gills on segments II–VII; mid-legs of ♂ & ♀ not widened but tarsi fringed; antennae (♂) wound once round apex of abdomen; pupal exuviae 13 mm long. (See Marlier 1978b figs 24–26) *Hydromanicus* Brauer (Seychelles)
- Anal appendages with apices clearly concave between lateral points; antennae (♂) shorter, not wound round apex of abdomen but recurved (Fig. 7); mid-legs ♂, ♀, widened, flattened, with swimming fringe 6
6. Presegmental plates on III–VIII (II–VIII in a few species), postsegmental plates on III forming, long narrow strips, on IV smaller, inconspicuous; mandibles with fairly large terminal teeth, inner margin smooth, anal appendages with concave apices, long fine setae within these; pupae 8–14 mm long. (Figs 7–9, Table II) *Hydropsyche* Pictet
- Presegmental plates on II–VIII, postsegmental plates on III widely oval, on IV clearly visible; mandibles with small terminal and lateral teeth, separated by lateral serrations; anal appendages with concave apices studded with papillae and setate tubercles, no long fine setae within them. Pupa 5–7 mm long. (Figs 26–28, Table IV) *Cheumatopsyche* Wallengren
7. Mid-leg with two or three tibial spurs; maxillary and labial palpi absent or rudimentary, mandibles present or absent; postsegmental plates on segments III or III and IV 8
- Mid-leg with four tibial spurs; maxillary and labial palpi clearly present, mandibles present, large; postsegmental plates on segment III only except in *Protomacronema* 9

8. Medium-sized pupa (length c. 10 mm); anal appendages widened at base, apices rounded; mandibles present, small, with inflated bases and large teeth; presegmental plates present on II–VIII, prominent, only two denticles each, postsegmental plates narrow strips of minute denticles on segment III only; tibial spurs 0.2.2 or 0.3.3. (Figs 199–202, Table XIX) *Aethaloptera* Brauer
- Pupa much larger (length c. 22 mm); anal appendages with widened apices ending in several large blunt points; mandibles absent; presegmental dorsal plates on III–VII, two to five denticles on each, postsegmental plates on III or III and IV, oval with many points on III, also a narrow strip with a few minute points on IV according to Marlier, but not evident on our material; tibial spurs 1.3.3 or 2.3.3. (Figs 183, 184, Table XVII) *Polymorphanus* Walker
9. Tibial spurs 0.4.4; each anal appendage ends in a sharp sclerotized point (Figs 145, 146); presegmental plates on V–VIII (only part of exuviae available, probably II or III–VIII), there appear to be two sets of postsegmental plates (3 plates on torn part of exuviae), probably from III and IV; no gills present on exuviae. (Figs 145–147) *Protomacronema* Ulmer
- Tibial spurs not 0.4.4 (may be 2.4.4, 1.4.4, 1.4.3, 1.4.2, 0.4.3, 0.4.2, 0.3.2 or 0.2.2); anal appendages do not end in such sclerotized points; presegmental plates on II/III–VIII 10
10. Anal appendages short, broad, contracted at ends to form terminal plates fringed with setulae; presegmental plates on II–VIII, tufted gills on II–VII/VIII, most lateral gills with pouchlike bases; palpi present but small, mandibles short, with inflated bases and four to five large serrated teeth; tibial spurs 1.4.4, 1.4.3, 1.4.2, 0.4.3, 0.4.2, 0.3.2 or 0.2.2. (Figs 122–125, Table XII) *Amphipsyche* Wallengren
- Anal appendages long, terminating in finger-like processes; presegmental plates on II/III–VIII; branchial gills on II–VII, some lateral gills either pouchlike or with pouchlike bases; palpi large, well-developed, bases of mandibles not inflated though they may be wide, apical teeth very large, several smaller teeth as well, margins serrulate; tibial spurs 2.4.4, 1.4.4 or 0.4.4 11
11. Anal appendages large with “bare” dorsal apical finger (is minutely spinose, appearing bare except under high magnification), otherwise thickly fringed ventrally with very long setae; presegmental plates on III–VIII; tufted gills in six rows on II & III, four rows on IV–VII; a pair of small processes on fifth sternum (♂ only), shagreening on dorsal side strong, obvious. (Figs 94–98, Table X) . . . *Macrostemum* Kolenati
- Anal appendages long, cylindrical, contracted apically into a fingerlike process covered with minute setiferous papillae and spinules, ventrally a shorter projection outlined by long setae; presegmental plates on II–VIII; ventral tufted gills in two rows on II–VII, conical lateral gills in two rows on III–VII. No processes on fifth sternum, but traces of paired fenestrae (present in imago); shagreening on dorsal side scarcely visible. (Figs 164–167, Table XV) *Leptonema* Guérin-Méneville

DESCRIPTIONS, DISCUSSION, BIOLOGY AND SPECIES LISTS

Subfamily HYDROPSYCHINAE Curtis 1835

Genus *HYDROPSYCHE* Pictet 1834

Hydropsyche Pictet 1834: 23, 199 (for entire family plus others)

Type species *cinerea* Pictet, synonym of *instabilis* (Curtis) (subsequent selection of Ross 1944). Switzerland.

Hydropsyche Pictet; Ulmer 1907a: 169, pl. 23 figs 208b–e. ♂ ♀.

(Key, generic diagnosis, list of known species, including the African *H. propinqua*.)

Hydropsyche Pictet; Barnard 1934: 395 (diagnosis for imago).

Hydropsyche Pictet; Lepneva 1964 (1970 translation): 547 (diagnosis of larval and pupal stages).

Hydropsyche Pictet; Wiggins 1977: 106, 107, figs 6.6A–G (larva).

Hydropsyche Pictet; Fischer 1963: 6–8; 1972: 99–100.

Generic diagnosis (derived from Ulmer 1907a, Barnard 1934, Mosely and Kimmins 1953 and other sources):

Imago: tibial spurs of ♂, ♀, 2.4.4; anterior tarsus of ♂ with one claw normal, the other concealed by a tuft of dark setae. Maxillary palpi with first segment short, second longer, third subtriangular, third and fourth subequal, fifth as long as rest together, articulated. Labial palpi with first and second segments short, subtriangular, third slightly longer than others together, articulated. Mandibles sclerotized, probably functional, meeting beneath labrum (Crichton 1957: 75, 76, fig. 43). Head: vertex with two large, oval posterior warts, anterior warts smaller; antennae moderately slender, in ♂ slightly longer than forewings, in ♀ shorter, with fine dark ridge winding spirally round the joints, becoming indistinct apically. Eyes (oculi) of ♂ in some species larger than in ♀. Forewings with apical forks 1, 2, 3, 4, 5 present, discoidal cell short, broad, crossveins m-cu and cu well separated; hind wings with forks 1, 2, 3, 5 present, discoidal cell always closed, median cell present, usually closed, M and Cu₁ close together and crossvein very short. Mid-tibiae and tarsi of ♀ flattened, dilated. Fifth abdominal sterna lack filamentous processes or internal vesicles (though there may be small tufts on pleura of some abdominal segments). ♂ genitalia with a strong sclerotized prolongation of 9th and 10th terga and a pair of slender, two-jointed claspers; prominent copulatory organ (phallosome plus endotheca, the aedeagus and parameres having been lost by specialization, see Schmid 1968), which in Afrotropical species (and one group of North American species) has a long apically forked ventral endothecal lobe. ♀ genitalia with sternal plates of 8th segment separated for two-thirds distance to base of segment; distal margin of XI with a pair of cerci between two pairs of small lobes.

The genus is the largest in the family and is almost cosmopolitan, being found in all regions with the exception of the Neotropical.

Hydropsyche longifurca Kimmins

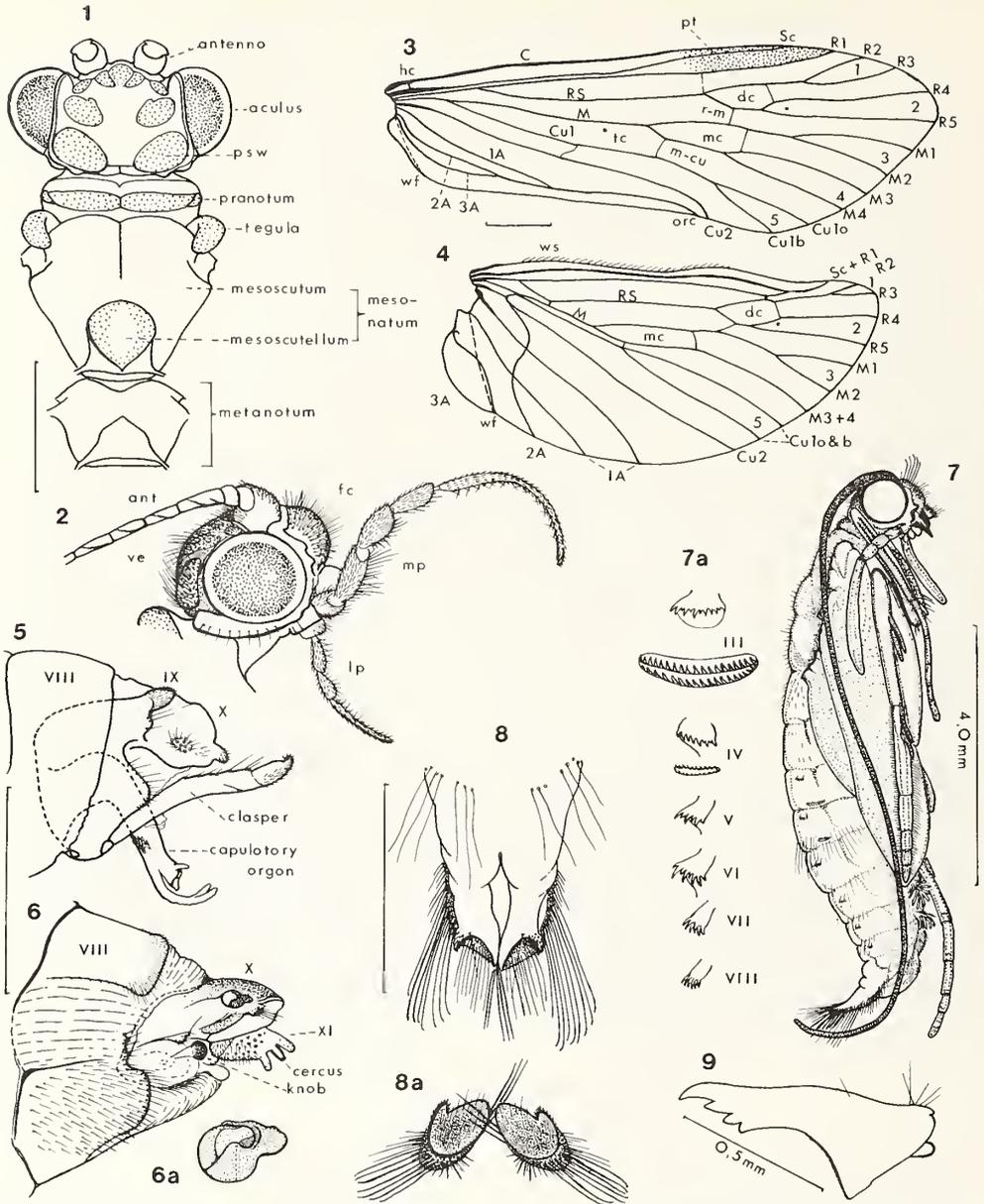
(Figs 1–19, Tables I, II)

Hydropsyche longifurca Kimmins, 1957a: 40, 41, figs 11–13 (♂ genitalia).

Portuguese East Africa, Chirinda, Busi River. ♂.

Holotype ♂ in British Museum (Nat. Hist.), 4 paratypes in B.M. (Nat. Hist.) and Coryndon Museum, Nairobi, Kenya.

Distribution: Mozambique (Portuguese East Africa); South Africa: Natal, Eastern Transvaal; Zimbabwe (formerly Rhodesia), at Victoria Falls.



Figs 1-9. HYDROPSYCHINAE: *Hydropsyche longifurca*, ♂, ♀ pupa and probable ♀. 1. ♂: dorsal view of head & thoracic nota, 2. ♂: lateral view of head & palpi, 3, 4. ♂: fore & hind wings (right), 5. ♂: lateral view of genitalia, 6. probable ♀: lateral view of genitalia, 6a, same, clasper receptacle further enlarged, 7. ♂ pupa: habitus, right appendages only shown, 7a, same, dorsal plates of pupa further enlarged (right), 8. ♂ pupa: anal appendages, dorsal, 8a, same, terminal view of anal appendages, 9. ♂ pupa: right mandible, dorsal.

DESCRIPTION OF IMAGOS (Figs 1-6)

Male imago (in spirit): a medium-sized species, forewings *c.* 9 mm long, pale fuscous, with thin pubescence, hind wings pale yellowish; head and thorax brown with paler warts, palpi and legs yellowish. Antennae slender, scape short, rounded, basal part of flagellum with dark spiral ridge which fades out after about six segments. Eyes large, black. Vertex with large pair of posterior warts, two pairs of smaller anterolateral warts, and three still smaller anterior warts near antennal bases. Face with wide lozenge-shaped median wart. Setae on head short, curled, golden brown. Pronotum with pair of long, tapered median warts, very small outer pair. Mesoscutum without warts, mesoscutellum with subtriangular wart with lateral bands of setae. Abdomen purplish brown with usual shrunken tufts on pleura. Genitalia as in fig. 5 (see also Kimmins 1957a figs 11-13).

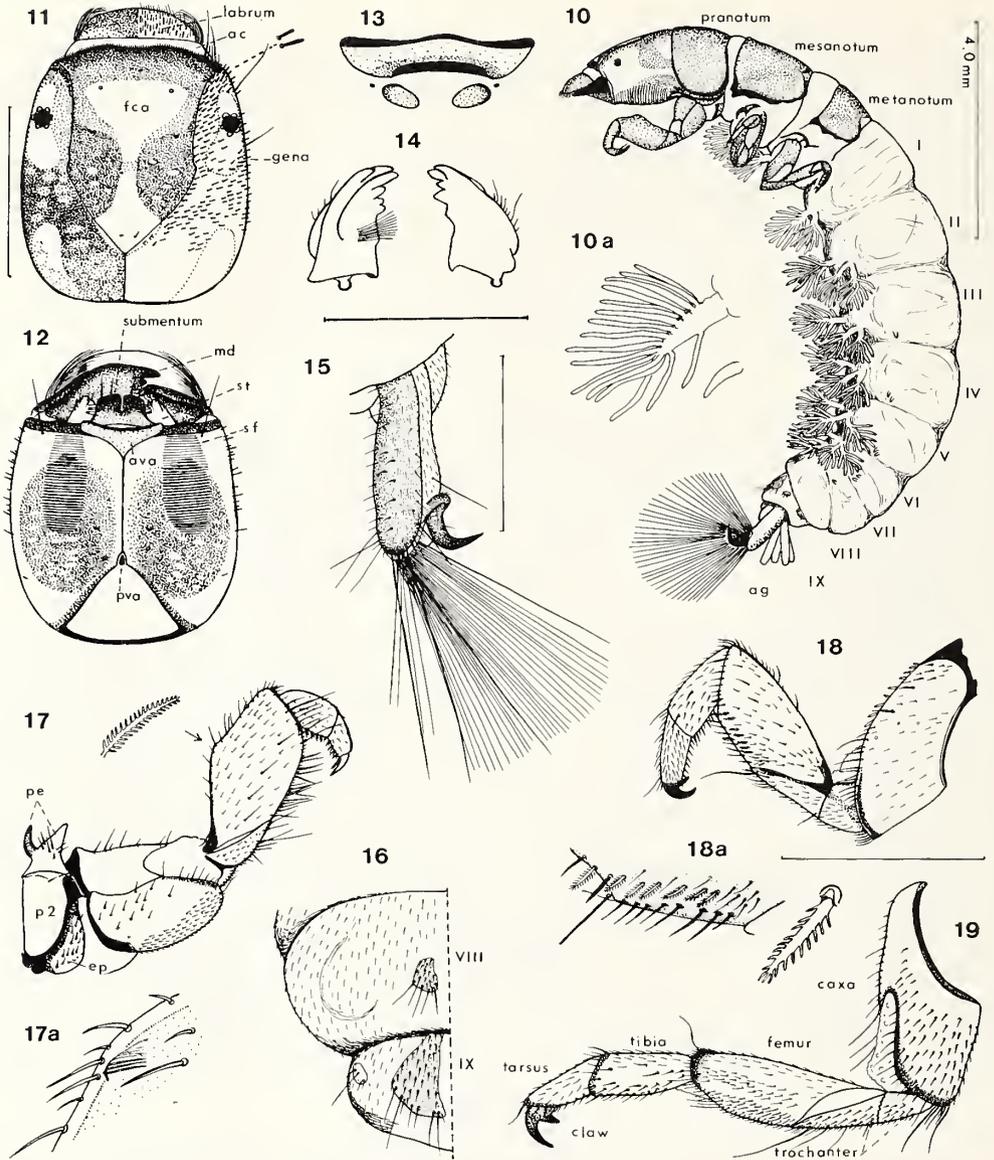
Kimmins (1957a) described the pinned ♂ as: "General appearance ochraceous, abdomen fuscous. Forewing pale fuscous, with numerous ochraceous irrorations. Venation as in *H. namwa* Mosely."

Probable female imago (in spirit, Figs 6, 6a): three females available. Very similar to ♂, somewhat larger, with similar large eyes; length of forewings 12 mm. Sternal plates of VIII subquadrangular in shape, with short setae, longer setae along distal margins, only partially separated ventrally. 8th tergites finely pubescent, with setose posterolateral angles; X hood-like, clasper receptacles rounded (Fig. 6a), clasper grooves unclear, sclerotized knob present on each side near genital atrium, ventral plate mainly membranous. I do not know what the knobs may be; Barnard described the ♀ of his *H. ulmeri* as having such "chitinous knobs", and figures them (1934: 359, fig. 36), so both these species, *ulmeri* and ? *longifurca*, would appear to possess them.

Material of *H. longifurca* in the Albany Museum comprises 6 males, 3 probable females and over 100 larvae, also 3 pupae, including a mature male and a fairly mature female, together with pupal cases and some larval sclerites. These would be sufficient to establish the relationship between the different stages of this species, were there proof as to whether the sclerites pertained to the male or the female (both were in the same container, with remains of pupal cases and a few larval sclerites). The larvae have a definite and very characteristic colour pattern on their heads, which renders recognition even of larval sclerites easy. The fact that both adult females and female pupae were found in association with males, male pupa and larvae renders it very likely that all belong to the same species (the only one so far found in these areas), but there is still the possibility that larva and/or female could be those of *ulmeri*, whose females appear very similar from Barnard's figures, though the ventral plates of the latter differ somewhat in shape, as *ulmeri* has been recorded from the same general area (Zululand, Transvaal, Orange Free State and probably Rhodesia). All males in the Albany Museum collections are, however, *H. longifurca* (identified by both D. E. Kimmins and myself), and I have as yet seen no *ulmeri*. *H. ulmeri* and *H. longifurca* are the only species recorded from Southern Africa to date, though we do have what appears to be the female of another species collected from the Orange River in the Warrenton area; this has subtriangular sternal plates and lacks the lateral sclerotized knobs.

DESCRIPTION OF PROBABLE LARVA (Figs 11-19; Table I)

Mature larva (in spirit; Figs 11-19): length 12-15 mm. Larvae considerably larger than those of the other Hydropsychine genus found in Southern Africa (*Cheumatopsyche*), and with one characteristic feature which facilitates recognition, even in early instars. This is the distinctive shape of the great majority of the setae on head and thoracic nota, which are short and blunt-ended, either truncated or shaped like an Indian club (Fig. 11). These short, blunt setae are very numerous in later instars, giving the head (apart from the frontoclypeal apotome) and thoracic nota a bristly unshaven appearance. This feature greatly facilitates separation from



Figs 10-19. HYDROPSYCHINAE: *Hydropsyche longifurca*, probable larva (mature). 10. habitus of mature larva, 10a, same, mesocoxal gill & conical lateral gill further enlarged, 11, 12. dorsal & ventral views of head, colour pattern shown on left gena & frontoelypeal apotome, setae on right; blunt setae further enlarged, 13. prosternal plate & intersegmental sclerites, 14. left & right mandibles, 15. right anal proleg & claw, 16. ventral view of right half of abdominal segments VIII & IX, showing setose sclerites, 17. right foreleg, showing pleural sclerites at base, arrow indicates position of scraper of stridulator; plumose seta enlarged, 17a, same, margin of femur further enlarged to show scraper, 18. mid-leg, anterior view, 18a, margin of femur & single plumose seta further enlarged, 19. hind leg, anterior view.

Cheumatopsyche larvae even in the early instars. Diplectronine larvae also have some club-shaped or scale-like setae, but are easily separable from the Hydropsychinae on other characters (see key).

Head (Figs 11, 12): subquadrate, dorsally flattened but without carina, with strongly marked dark chestnut brown and yellow pattern; dorsal and lateral surfaces of genae thickly studded with short, dark, blunt setae, very few such setae on frontoclypeal apotome except along the anterior margin; none on posterior part of head which can be withdrawn inside the pronotum. The colour pattern as illustrated is that most commonly seen, and at first I thought that a dark variant might be another species, but several samples show a clear gradation from the usual pattern by a progressive darkening, in which the light hour-glass shape on the frontoclypeal apotome gradually closes until only two light patches remain; the rest of the head darkens similarly. Eyes black, as usual set in paler areas, each below six small cuticular lenses. Stridulatory files large, elongate oval in shape, colour pattern continued across them. Anterior ventral apotome widely subtriangular, light brownish yellow, with sutures on both sides; posterior ventral apotome minute, black.

Mouthparts (Figs 11, 12, 14): labrum brown, retractile, setose, with small, pale brushes on ventral side; anteclypeus pale, unsclerotized; mandibles strong, dark brown, left mandible with inner brush of setae and five apical and subapical teeth, the proximal one having two cusps; right mandible with four teeth, no inner brush; neither mandible bears setulae on upper apical tooth; mandibles triangular in section, outer face set with strong setae between flanges. Maxillary palpi short, stout, five-segmented; labium short, thick, palpi not visible; only mandibles seen when mouthparts retracted, as is often the case in preserved specimens. Submentum brown, darkening to a blackish apex with deep median incision. Stipites light brownish yellow, conspicuous.

Thorax (Fig. 10): pro-, meso- and metanota brown, pronotum darkest, all thickly studded with short, blunt setae interspersed with small, fine setae; nota fringed anteriorly with blunt setae and finer setae; meso- and metanota with darker brown diagonal stripes, the former with median crescent-shaped black mark at posterior margin, the latter with a smaller similar black mark there; all three nota with wide black lateral borders. Pre-episternum bifid, dorsal branch smooth, blackish, ventral branch bearing several setae (Fig. 17). Prosternal plate (Fig. 13) a transverse bar with heavily sclerotized anterior and posterior margins; posterior to this a pair of oval sclerites on the intersegmental fold, often partly or completely covered by a fold of the epidermis. One pair of branched tracheal gills on mesosternum, two pairs on metasternum. Thoracic pleura and sterna covered with small, fine setae interspersed with many larger, blunt brown ones, giving a rough, hairy appearance to the larva.

Legs (Figs 17-19): stout, foreleg with tarsal claw bearing a single long basal seta, scraper of stridulator on anterior angle of femur (see Fig. 17a), a few large plumose setae on posterior margin of trochanter and femur, many smaller ones on coxa, a clump of stout setae on inner side of femur. Mid- and hind legs with tarsal claws bearing a single thick basal spine, femora with a row of feathered setae near posterior margin, coxae with a few small plumose setae on outer side; fewer plumose setae on mid- than on hind legs.

Abdomen (Figs 10, 15, 16): this, like thoracic pleura and sterna, is rough and hairy in appearance. Densely tufted tracheal gills present in two rows on segments I and VII, four rows on segments II-VI (see Table I). There are also minute conical lateral gills, "Zipfelkiemen" of Ulmer, on segments III-VII. Sterna of segments VIII and IX each bear a pair of subtriangular sclerotized plates set with stout, mainly short, spinelike setae, the plates on IX being much larger than those of VIII. Segment IX has in addition a pair of small, pale ventrolateral sclerites and a pair of larger dorsolateral sclerites, often partially concealed beneath VIII. Anal prolegs long, well developed, each bearing an apical tuft of very long dark bristle-like setae; anal claws strong, right-angled, plain. Four anal gills.

Earlier instars: there are five larval instars in the Hydropsychinae, not six as found in those Macronematinae for which we have adequate material. All five appear to be represented in our collection, though not in sufficient numbers to give adequate ranges of head width or adequate separation of instars on a histogram.

First instar: no tracheal gills: pre-episternum minute, as yet unbranched, very few setae but those present are comparatively long; blunt setae on head and thorax (8 on head, 6 on prothorax, 9 each on meso- and metanota); only head and pronotum moderately well sclerotized (latter showing dark margin); head with very faint indication of pattern, stridulatory files absent, two small "teeth" on anterior margin of head (egg bursters); meso- and metanota very pale, scarcely distinguishable. All tarsal claws with three basal spines (*cf.* Fig. 41), a few small plumose setae on legs. Recognizable as *Hydropsyche* by presence of blunt setae, which in this instar are very long. Four anal gills.

Second instar: simple, unbranched gills present on meso- and metasterna and abdominal segments I–VII, arranged as in final instar but none with two main stems as yet. Pre-episternum with future dorsal branch visible as a point on ventral branch. More blunt setae present, but still scanty. Head pattern still faint but recognizable; stridulatory files present but uncoloured, scrapers just visible on fore femora. Thoracic nota all well sclerotized, with dark margins. All tarsal claws with one basal seta or spine only (as in subsequent instars); a few plumose setae on trochanters and femora of fore and hind legs, none seen on mid-legs.

Third instar: ventral gills with 1–2 branches, anterior ventro-lateral gills with 2–4 branches, posterior ventro-lateral gills with one only; gills on I and VII have developed two main stems. Pre-episternum clearly bifid, but dorsal branch not yet fully developed. Several feathered setae on trochanter and femur of foreleg (as in subsequent instars) and a few on hind femur. Head pattern clear. More blunt setae on thorax, a few on abdomen.

Fourth instar: all ventrolateral gills have two main stems; ventrolateral and ventral gills have 4–12 branches. Pre-episternum with both processes fully developed. Many blunt setae present on head, thoracic nota and abdomen. Stridulatory files coloured and clearly visible, head pattern fully developed.

Fifth instar: this is the mature larva described above. Ventral and ventrolateral gills with many branches (*c.* 12–25); minute conical lateral gills present on segments III–VI. Larvae strongly setose, but in older larvae whose abdomen has become much enlarged many abdominal setae may have been lost.

DESCRIPTION OF PUPA (Figs 7–9, Table II)

There are only two mature pupae in the collection, one male and one probable female, both in fairly good condition, with cases and some larval sclerites (see above for comments). The ♂ pupa was identified by Mr D. E. Kimmins as well as by myself. There is also one immature female pupa.

Male pupa (pharate adult) (in spirit, Figs 7–9): length 8.0 mm. Fully mature, light yellowish to golden brown in colour. Antennae moderately slender, slightly longer than body; imago clearly visible through pupal pelt, head warts as imago, setae on them long, silky, pressed forwards; short brown setae scattered on pupal skin covering vertex, also on thoracic terga and, more thickly, on face. Labrum rounded, with a pair of rounded setose protuberances on anterior margin, a smaller lateral pair. Mandibles smooth, dark red-brown, with four (right mandible) or five (left mandible) large teeth along inner edge at apex. No smaller teeth or serrations. Bases are minutely pubescent along inner margin. Palpi long, as in imago. Legs much as in imago, with tibial spurs 2.4.4, mid-leg widened, flattened and with swimming fringe. Fore-legs reach to end of II, mid-legs to VI and hind legs well beyond genitalia. Wing cases brownish, forewing reaching to middle of VI, hind wing to base of V. Abdomen mottled, mainly purplish brown; segments II–VII with large flattened ventral tracheal gill tufts, small conical

TABLE I:

Number and position of tracheal gills and other characters 1st to 5th larval instars of
Hydropsyche? longifurca

Segment no.	1st instar		2nd instar		3rd instar		4th instar		5th instar	
Mesosternal gills	—		1 pair		1 pair		1 pair		1 pair	
Metasternal gills	—		2 pairs		2 pairs		2 pairs		2 pairs	
Abdominal gills	VL	V	VL	V	VL	V	VL	V	VL	V
I	—	—	—	1	—	2*	—	2	—	2
II	—	—	1	1	1	1	2	1	2	1
III	—	—	1	1	1	1	2	1	2	1
IV	—	—	1	1	1	1	2	1	2	1
V	—	—	1	1	1	1	2	1	2	1
VI	—	—	1	1	1	1	2	1	2	1
VII	—	—	1	—	2	—	2	—	2	—
Tarsal claws	3 basal spines absent		1 basal spine simple (unbranched)		1 1-4 branches		1 c. 4-12 branches		1 c. 12-25 branches	
Gills	c. 0,2mm		c. 0,33mm		c. 0,45-0,67 mm		c. 0,78-0,98 mm		c. 1,25-1,40 mm	
Head width at eyes	simple, minute		2nd point just visible		bifid but unequal		bifid, fully developed		bifid, fully developed	
Pre-episternum										

* The figure 2 denotes that the abdominal gill in question has two main stems.

Head widths are from specimens available, but numbers are insufficient to give a good indication, hence the addition of c. = circa.

VL = ventrolateral gills.

V = ventral gills.

N.B. There are also very small conical lateral gills on segments III-VII, mature larva.

pocket-like lateral gills on III-VI. The ventral tufted gills on II are separate, but on III-VI have paired stems and numerous filaments. Paired dorsal plates on III-VIII (see Table II for gill and dorsal plate arrangement); presegmental plates on III-VIII, teeth small to very small, postsegmental plates on III and IV, the former being elongated double strips of minute forward-projecting denticles, the latter smaller and in this specimen largely concealed beneath an epidermal fold. Shagreening practically invisible (some on anal appendages but only seen at $\times 400$); Transverse belts of long setae on IV and V (dorsal), venter hairy, particularly posterior to gills. Anal appendages of medium length, stout, strongly curved dorsad ending in wide cup-like sclerotized apices which appear shortly bifid in dorsal view, mitt-shaped in terminal view (Fig. 8a); there are long, fine setae within the concavity. Each anal appendage bears a thick belt of long, stout lateral setae and two or three very stout, shorter setae projecting downwards from near the "toe". Male genitalia in pockets as usual.

Pupa of probable female: very like that of male but lacking pockets for genitalia. Female genitalia not fully mature, but appear to be the same as those of the female imago described above. Anal appendages similar to those of the male. Length of ♀ pupa 9.0 mm.

Pupal cases much damaged, but remains indicate that they were firmly built of stone fragments joined with silk, with the ends capped with stones between which two or three curved slits allowed for the passage of water. Some larval sclerites within cases, but many evidently lost during collection. The pupa lies within a silken cocoon in the case. These two cases had evidently been attached to one another as well as to a rock or stone, the side adpressed to the stone being closed by a silken membrane.

TABLE II:

Tracheal gills, dorsal plates etc. of ♂ pupa of *Hydropsyche longifurca* Kimmins

Abdominal segment no.	Tracheal gills (right side)		Dorsal plates	Setae etc.
	L	V		
I	—	—	—	
II	1	1	—	
III	(1)	2*	Presegmental pair Postsegmental pair	
IV	(2)	2	Presegmental pair Postsegmental pair	Thick fringe of setae near posterior margin
V	(3)	2	Presegmental pair	thin fringe of setae near posterior margin
VI	(2)	2	Presegmental pair	
VII	—	1	Presegmental pair	
VIII	—	—	Presegmental pair	
IX	—	—	—	

* The figure 2 denotes that the gill in question has 2 main stems

(1) Brackets indicate that the gill in question is unbranched and pocket-like, with one, two or three pockets superimposed on one another.

L = lateral gills (pocket-like)

V = ventral gills—flattened, thickly tufted branchial gills.

REMARKS

Hydropsyche being an almost cosmopolitan genus rich in species (less so in Africa than in the Northern Hemisphere), there is much literature on it.

African species of *Hydropsyche* include 16 species from the Afrotropical mainland, of which only two have been recorded from Southern Africa, and nine or ten from the Malagasy Subregion. In addition there are about ten North African species, which form part of the Palearctic fauna. Several of the Afrotropical species may be invalid because they were described from females only, which, when finally correlated, may prove to belong to species at present known from the male sex only. Such lack of correlation between males and females in many species is a clear warning against description of new species based on females.

Navás's genus *Plesiopsyche* has been placed in synonymy with *Hydropsyche* by Ross & Unzicker (1977), who state that the ♀ concerned is a typical member of the *H. propinqua* group.

The genus *Symphitopsyche* was originally created by Ulmer (1907b) for *Hydropsyche mauritiana* McLachlan, but has been generally regarded as a probable synonym of *Hydropsyche*. Ross & Unzicker (1977), however, resurrected the genus and applied it to many American species of *Hydropsyche* as well as to all the Afrotropical species (the "*propinqua* group"). Schmid (1979) pointed out that Ross & Unzicker's "new genera" (including *Symphitopsyche*) were merely species groups of *Hydropsyche*. The name *Symphitopsyche* thus falls into the synonymy of *Hydropsyche*. This is borne out by the fact that I found the "*Symphitopsyche*" larvae from the U.S.A. (very kindly sent to me by Dr G. A. Schuster) were virtually indistinguishable from our *Hydropsyche* larvae, such minor differences as are present certainly being no more than distinctions between groups of species. Thus *Symphitopsyche mauritiana* reverts to *Hydropsyche*. *S. plutonis* Banks, however, is not a *Hydropsyche* and has been transferred to the genus *Cheumatopsyche* (Mosely 1939b).

Larval and pupal stages of *Hydropsyche* have been described, often in great detail, from other parts of the world, notably by Siltala (1907, two species) and Lepneva (1964, 1970 translation, several species). As far as Afrotropical species are concerned, Marlier (1962b) gave a general description of larva and pupa; he also briefly described the pupa of *H. bwambana* Mosely (Marlier 1943b).

The larvae and pupae ascribed tentatively to *H. longifurca* Kimmins and described above, almost undoubtedly pertain to that species, the only doubt being the recorded presence of *H. ulmeri* Barnard in at least part of the same area. All the males in the Albany Museum collections are, however, *longifurca*. In addition to the *longifurca*-type larvae and pupae, there is material of a different species from the Inyanga Highlands of Rhodesia (Zimbabwe) which includes larvae and immature male pupae, unfortunately too immature for identification to species. These show definite differences from the ones described above. The larvae are very dark brown in colour, younger instars uniformly so, as are some mature larvae, other mature larvae show one or two small pale patches on the frontoclypeal apotome. There are also a few plain brown larvae from other areas in Southern Africa, including places from which we have many more of the patterned *longifurca*-type larvae. The Inyanga pupae, while clearly a species of *Hydropsyche*, do show minor differences from those of *longifurca*, particularly in gill arrangement, the ventral gills on the seventh abdominal segment having paired stems, and there being lateral gills on it as well. Abdominal sterna II-VI each have a pair of round blackish spots, placed towards the sides, not seen in *longifurca*. It is possible that these larvae and pupae are of *ulmeri*, the only other species so far recorded from Southern Africa.

BIOLOGY

Young larvae are often found amongst vegetation or under stones, and feed on microplankton (Kaiser 1965). Older larvae are predacious. They build themselves shelters of bits of stone and vegetable matter fastened together with silk, within which they live. In front of these, facing into the current, they weave coarse-meshed catching nets of silk to trap their prey, small planktonic or benthic animals, and inevitably also scraps of plant material, algae and detritus, most being eaten but unwanted matter thrown out. The nets are usually held open by small sticks and silken guy ropes as well as by the pressure of the current. There is an exit hole at the posterior end of the shelter. Where stones or sand are scarce, *Hydropsyche* larvae utilize crevices in which the shelter may be made of silk only, without the usual reinforcement.

The larvae remain in their retreats, holding on by means of their anal claws, though they may scramble half out to forage (Fremling 1960). Under unfavourable conditions (slow flow or still water, as in the laboratory), larvae may leave their retreats, fail to build nets and fight one another (Philipson 1969). Malicky (1973) mentions that larvae do not weave nets in very cold northern winters, but in the less severe African climate nets always appear to be present in suitable situations. *Hydropsyche* larvae may be found in fast-flowing, clean, cool, clear, silt-free streams and rivers. They also occur in large lakes along stony wave-washed shores where the water is well aerated.

The Inyanga (Zimbabwe, formerly Rhodesia) specimens (not *longifurca* but another species) were collected from a small cascade just above the Pungwe Falls, from rock surfaces in fairly deep water, flowing fast and strongly. At this site shelters and pupal cases were common and conspicuous, being made of white quartz chips. At the upstream end of each shelter was a wide net, bellied out by the current. In living larvae the head, thorax and legs were dark brown, the abdomen bright green. The net was supported by bundles of twiglets bound together with silk and arranged round the opening of the shelter and also around the edge of the net. Water temperature at the time of collection was 12–14° C, and pH was 6.8–6.9. Turnbull-Kemp (1970) commented that the *Hydropsyche* and *Cheumatopsyche* species at Inyanga form an important source of food for trout. They are known to be among the Hydropsychid predators of *Simulium* larvae in Uganda (Hynes & Williams 1962), and the same may well apply here.

Hydropsyche species are, on the whole, poorly represented in Africa. In Central Africa there are some 13 species. In South Africa only two have been recorded to date and these may well be restricted to Natal and parts of the Transvaal and Orange Free State. The Albany Museum collections include larvae from the Orange River at Prieska and a single female from the Storms River (South Cape), but no other specimens from the Cape Province.

Prior to pupation the larva constructs a strong dome-shaped shelter of large sand grains, sometimes with scraps of vegetation, either by altering the larval shelter (Fremling 1960) or by construction of a new one (Sattler 1958 and others). Inside this it enters the prepupal stage, subsequently pupating within a silken cocoon. At each end of the case there are slits to permit a current of water to flow through. At the anterior end these are situated in a cap or lid of stones which can be cut loose by means of the pupal mandibles when eclosion takes place. Should the current speed or water level drop and the oxygen supply diminish, the pupa maintains rhythmic undulatory movements of the abdomen which keep the water circulating through the case and round the gills. At eclosion the pupa, by now a pharate adult, cuts open cocoon and top of case, swims to the surface by means of its oar-like mid-legs, climbs out onto a stone or stick and there ecdyses, freeing itself from the pupal exuviae and flying away.

Fremling (1960) gave an interesting and detailed account of the life cycle of *H. orris* in the Mississippi River below the dam at Keokuk, Iowa, where this species abounded (together with other Trichoptera) during the summer months, creating an acute nuisance problem in the adjacent town where adults were attracted to the town lights in vast numbers. At dusk and shortly before dawn adult males formed dense swarms, to which females were attracted, in the air near the river banks. Mating couples dropped to the ground. Mating also occurred on lighted windows and elsewhere without prior swarming. Females appeared to have scent glands along the sides of the abdomen which attracted the males. On heavily overcast days they might still swarm during daylight hours but on bright sunny ones sheltered under vegetation. The *H. orris* females not having fully mature eggs on emergence laid them some time later. They were able to survive for up to ten days if provided with water, longer if sugar solution was available. A day or two after mating the females walked or swam down to a depth of as much as 12 ft (c. 360 cm) to oviposit on submerged objects or floats, evidently preferring these to floats at the surface, oviposition being most concentrated at depths of 3–4 ft (c. 90–120 cm). They then

emerged from the water but might re-enter it before dying. Larvae were found in large numbers in the river at depths of up to 40 ft (c. 1 200 cm) on buoy anchoring chains and in turbine chambers, and appeared to pass through five larval stadia. Fremling considered that the species was bivoltine, adults emerging throughout the warmer months, with peaks in early and late summer. Recent work (Mackay 1978) shows that *Hydropsyche* species may be either univoltine or bivoltine and that this may vary in different areas.

Fremling found that the *H. orris* larvae occurred in faster current than the other Hydropsychidae present, forming 100% of samples at a speed of 5 ft/sec. (c. 150 cm/sec.) and 90% at 3 ft/sec. (c. 90 cm/sec.) whereas *Cheumatopsyche campyla* larvae only formed 2% of samples at the latter speed. He found that *H. orris* eggs took 8–11 days to hatch in the laboratory and that the first instar larvae were able to swim well. Later instars were not observed swimming.

D. Scott (1958), in his study of the River Dean, observed that at surface current speeds of over 40 cm/sec. *Hydropsyche* larvae occurred under stones, preying on the rich concentration of smaller insects sheltering there. Chutter (1970) noted that in Natal *Hydropsyche* larvae were found in stony runs in the eroding zone of rivers at all seasons of the year.

AFRICAN SPECIES OF *HYDROPSYCHE*

- H. abyssinica* Kimmins, 1963:140–142, figs 54–59 (wings, ♂, ♀ genitalia). ♂ ♀.
Distribution: Ethiopia.
- H. alluaudina* (Navás), 1931a: 127, fig. 64 (♀ wing), as *Plesiopsyche*. ♀.
Ross & Unzicker 1977: 304–305, synonymize *Plesiopsyche* with *Hydropsyche*. In any case the species may not be a valid one, having been described from the ♀ only.
Distribution: Ruwenzori.
- H. atlanta* Botosaneanu, 1975: 272, 273, fig. 1 (♂ genitalia). ♂.
Synonym of *H. obscura* Navás (Botosaneanu 1980).
Distribution: Grand Atlas, North Africa.
- H. angulata* (Navás), 1934c: 73, fig. 14 (wing), as *Symphitopsyche*. Sex not stated, identity unclear.
Distribution: Madagascar.
- H. bwambana* Mosely, 1939b: 24–25, figs 72–74 (intromittent organ). ♂ ♀.
Marlier 1934b: 20, 21, fig. 27 (pupal mandibles and appendages). Description of ♂ pupa.
Distribution: Ruwenzori; Belgian Congo.
- H. contubernalis* McLachlan, 1865: 129–130, pl. 13, fig. 12. ♂. Europe.
Botosaneanu (1967, Limnofauna Europaea) lists this from Morocco.
Fischer, 1963: 41, places *contubernalis* in the synonymy of *H. guttata* Pictet.
Dakki, 1978: 113, refers the specimens concerned to *H. resmineda* Malicky.
Distribution: remains Europe only, Morocco is incorrect.
- H. diminuta* Walker, 1852, now placed in *Cheumatopsyche*.
- H. fasciolata* Navás, 1926: 109, 110, fig. 43 (♂ genitalia). ♂.
Distribution: Belgian Congo.
- H. fezana* Navás, 1932b: 111–112, fig. 4 (♀ forewing). ♀. (Also given as *fezana*.)
Dakki, 1978: 116, figs 4, 5, 6, describes Navás' ♀ from the Inst. Sci. Mus. Rabat. He considers that material described as *H. instabilis* from North Africa is in fact *H. fezana*, thus also extending the distribution to Algeria.
H. ouedorum Botosaneanu 1975 is a synonym of *H. fezana* (Dakki 1978).
Distribution: Morocco, Algeria.
- H. fulvipes* (Curtis), 1834: 213, as *Philopotamus*. ♀.
Tobias, 1972: 262–264, figs 126–129, redescription of ♂, ♀.
Dakki, 1978: 113; Navás' specimens identified as *fulvipes* are in fact a ♂ *pellucidula* and a

- ♀ *maroccana*; the North African distribution thus falls away.
 Distribution: Europe (Morocco incorrect).
- H. furcata* Jacquemart, 1963b: 1–2, fig. 1 (♂ genitalia). ♂.
 Distribution: Mauritius.
- H. guttata* Pictet, 1834: 203–204, pl. 17f, figs 3a–d (also metam.) ♂ ♀.
 Mosely 1939c: 186, 189, figs 397–399 (♂ genitalia). ♂.
 Tobias 1972: 248–249, figs 79–84 (♂, ♀ genitalia). ♂ ♀.
 Dakki 1978: doubts presence of this species in North Africa.
 Distribution: Europe, ? Algeria.
- H. hirta* Jacquemart, S. & Statzner, B., 1981: 13, pls VI figs 10–13 & XV fig. 8 (♂ gen., wing).
 ♂.
 Distribution: Zaïre.
- H. inflata* Navás, 1917: 118, 119, fig. 1a–d (wing tips, ♂ genitalia). ♂.
 Dakki 1978: 113; type appears to have been lost, but he thinks that Navás' material was probably of *H. lobata*, whose larvae have been found in this area.
 Distribution: ? Morocco, Algeria.
- H. instabilis* (Curtis), 1834: 213, as *Philopotamus*. ♀.
 Hildrew & Morgan, 1975: 217–219, figs 3, 7 (♂ genitalia), discuss this species, pointing out that it has frequently been misidentified, the caddisfly in question being in fact *siltalai* (*Ibid.*, figs 1, 5). It is therefore uncertain whether the North African specimens are *instabilis* or *siltalai*. Hildrew & Morgan gave a key to adult ♂♂ and notes on larvae.
 Dakki, 1978; considers North African material to be *H. fezana* Navás.
 Distribution: Europe and possibly North Africa (Morocco, Algeria).
- H. jeanneli* Mosely, 1939a: 299–300, figs 16–19 (♂ genitalia). ♂. (♀ collected but not described.) (Note that Moseley's figures have been reversed and the captions attached to the wrong ones; figs 16–19 labelled *H. jeanneli* are to be found on p. 301 over the captions for *Chimarra elga*.)
 Distribution: Mount Elgon (Kenya).
- H. lobata* McLachlan, 1884: 43, pl. 5, figs 1–4. ♂.
 Dakki, 1978; attributes Navás' *H. inflata* specimens to *H. lobata*, describes the ♀ and has collected larvae from Morocco.
 Distribution: Europe, Morocco.
- H. longifurca* Kimmins, 1957a: 40–41, figs 11–13 (♂ genitalia). ♂.
 Jacquemart 1963a: 370, fig. 26a–d (wings, ♂ genitalia).
 Distribution: Portuguese East Africa; South Africa (Natal, Eastern Transvaal); Zimbabwe.
- H. longipalpis* Banks, 1920: 357, pl. 2, fig. 22. ♂.
 Distribution: Madagascar.
- H. maniemensis* Marlier, 1961: 159, 189–191, fig. 18 (wings, ♂ genitalia). ♂ ♀.
 Distribution: Kivu.
- H. marlieri* Jacquemart, S. & Statzner, B., 1981: 13, pls VI figs 7–9 & XV fig. 7 (♂ gen., wing).
 ♂.
 Distribution: Zaïre.
- H. maroccana* Navás, 1936b: 95, 96, fig. 16 (♂ genitalia). ♂.
 Dakki, 1978: 113, 114, places *H. timha* Mosely in synonymy and illustrates ♀ genitalia.
 Distribution: Morocco, Canary Islands.
- H. maura* Navás, 1932b: 110, 111, fig. 3 (♀ hind wing). (Also as *mauri*). ♀.
 Probably a doubtful species as ♀ only and whereabouts of type unknown.
 Distribution: Morocco.

- H. mauritiana* McLachlan, 1871: 133, pl. 4, fig. 17 (♂ genitalia). ♂.
 Ulmer, 1907b: 32, 33, fig. 48 (wings), places it in the genus *Symphitopsyche*, as did subsequent authors until Schmid (1979) indicated that its place is in the genus *Hydropsyche*. (See under Remarks below.)
 Distribution: Mauritius, Madagascar.
- H. mokaensis* Jacquemart, 1960: 3, fig. 2a–d (wings, ♂ genitalia). ♂.
 Distribution: Mauritius.
- H. moselyi* Jacquemart, S. & Statzner, B., 1981: 12, 13, pls VI figs 4–6 & XV fig. 6 (♂ gen., wing). ♂, 1, p.
 Distribution: Zaïre.
- H. namwa* Mosely, 1939b: 23, 24, figs 67–71 (wings genitalia, ♂). ♂ ♀.
 Distribution: Ruwenzori.
- H. nubila* Gauthier, 1928. *A nomen nudum* never later substantiated.
- H. obscura* Navás, 1928a: 189–190, fig. 4 (wingtip, ♂ genitalia). ♂.
 Botosaneanu, 1980: 191, places *H. atlanta* Botosaneanu in synonymy with it.
 Distribution: Algeria, Morocco.
- H. ornatula* McLachlan, 1878: 363–364, pl. 39, figs 1–3 (♂ genitalia). ♂ ♀.
 Mosely, 1939a: 186, 188–189, figs 394–396 (wings, ♂ genitalia).
 Dakki, 1978: 113, considers that the Moroccan specimens were in fact *H. resmineda* McLachlan.
 Distribution: Europe, Morocco and Algeria falling away.
- H. ouedorum* Botosaneanu, 1975: 272–275, fig. 2 (♂ genitalia). ♂.
 Dakki, 1978; places it in synonymy with *H. fezana*.
 Distribution: Morocco.
- H. palpalis* Navás, 1936a: 108, 109, fig. 41 (wing). ♂.
 Distribution: Madagascar.
- H. pellucidula* (Curtis), 1834: 213, as *Philopotamus*. ♀.
 Mosely, 1939a: 186–187, figs 388–391 (♂, ♀ genitalia). ♂ ♀.
 Dakki, 1978: 113, ♂ identified by Navás (1935) as *fulvipes* was *pellucidula*, and the species is widely distributed in Morocco.
 Distribution: Europe, Morocco, Algeria.
- H. plesia* Navás, 1934a: 372, fig. 3 (hind wing). ♀.
 Distribution: Kenya.
- H. propinqua* Ulmer, 1907b: 21–23, figs 32, 33 (♂ genitalia). ♂.
 Distribution: Cameroons; Togo; Tanganyika; Ethiopia; Congo; Ruanda; Madagascar.
 South African material transferred to *H. ulmeri* n. sp. by K. H. Barnard (1934).
- H. sexfasciata* Ulmer, 1904b; now placed in *Cheumatopsyche*.
- H. resmineda* Malicky, 1977: 6, 7, pl. 3 (♂ genitalia). ♂. Morocco.
 Dakki, 1978: 112, 113, 118, fig. 2 (♀ genitalia), describes ♀ & attributes the *H. ornatula* McLachlan from Morocco to this species.
 Distribution: Morocco.
- H. striolata* Navás, 1934b: 88, 89, fig. 54 (♀ wing). ♀.
 Distribution: Cameroons.
- H. timha* Mosely, 1938: 272–274, 277, figs 1–3 (♂ genitalia). ♂. (♀ not described although material available).
 Dakki, 1978: 114, places *timha* in synonymy with *H. maroccana* Navás.
 Distribution: Morocco; Canary Islands.
- H. ulmeri* Barnard, 1934: 359, 360, fig. 36a–c (♂ genitalia). ♂ ♀. Barnard here described the Zululand material placed by Ulmer (1907b) in *H. propinqua* as a new species.
 Distribution: South Africa (Zululand, Transvaal).

- H. vulpina* Navás, 1934b: 89–90, fig. 55 (♀ hind wing). ♀.
 Distribution: North Africa (Cyrenaica).
H. wamba Mosely, 1939b: 25–26, figs 75–79 (♂ genitalia). ♂, ♀.
 Distribution: Ruwenzori.
H. wittei Marlier, 1943a: 8–9, fig. 5 (♂ genitalia). ♂.
 Distribution: Belgian Congo.

Genus CHEUMATOPSYCHE Wallengren 1891

Cheumatopsyche Wallengren 1891: 138, 142.

Type species *Hydropsyche lepida* Pictet.

Cheumatopsyche Wallengren; Kimmins 1960a: 255–267, 76 figs, review of African species.

Cheumatopsyche Wallengren; Kimmins 1963: 130, 131, synonymy of *Hydropsychodes* Ulmer with *Cheumatopsyche* and new diagnosis.

Cheumatopsyche Wallengren; Lepneva 1964 (1970 translation): 581–590 (larval and pupal stages).

Cheumatopsyche Wallengren; Wiggins 1977: 100, 101, Figs 6.3A–F (larva).

Cheumatopsyche Wallengren; Fischer 1963: 106; 1972: 133.

Generic diagnosis (derived from Kimmins 1963, Mosely and Kimmins 1953 and other sources): Imago: tibial spurs 2.4.4, sometimes 0.4.4 in male, forelegs with both tarsal claws clearly visible. Maxillary palpi with first segment short, second usually cylindrical, sometimes triangularly dilated, third and fourth subequal, fifth about as long as first three together, articulated. Labial palpi small, slender, three segmented, third articulated. Antennae may or may not have diagonal dark markings on basal segments. Head with large posterior warts, smaller anterior ones. In forewing discoidal cell closed, forks 1, 2, 3, 4, 5 present, crossveins m-cu and cu situated fairly close together. In hind wing forks 2, 3, 5 (occasionally 1, 2, 3, 5) present, discoidal cell closed, median cell open, veins M and Cu₁ widely separate and crossvein between them normal, obvious. Male genitalia of Afrotropical species show no special differences from those elsewhere. Sternal plates of VIII in ♀ separated to base of segment (*cf.* Figs 6 & 25), distal margin of XI as in *Hydropsyche*, with one pair of cerci between two pairs of small lobes; median leg of ♀ dilated, fringed.

The genus is a very large one, and is represented in all regions except the Neotropical.

Cheumatopsyche thomasseti (Ulmer)

(Figs 20–42, Tables III, IV, also histogram, Fig. 214A)

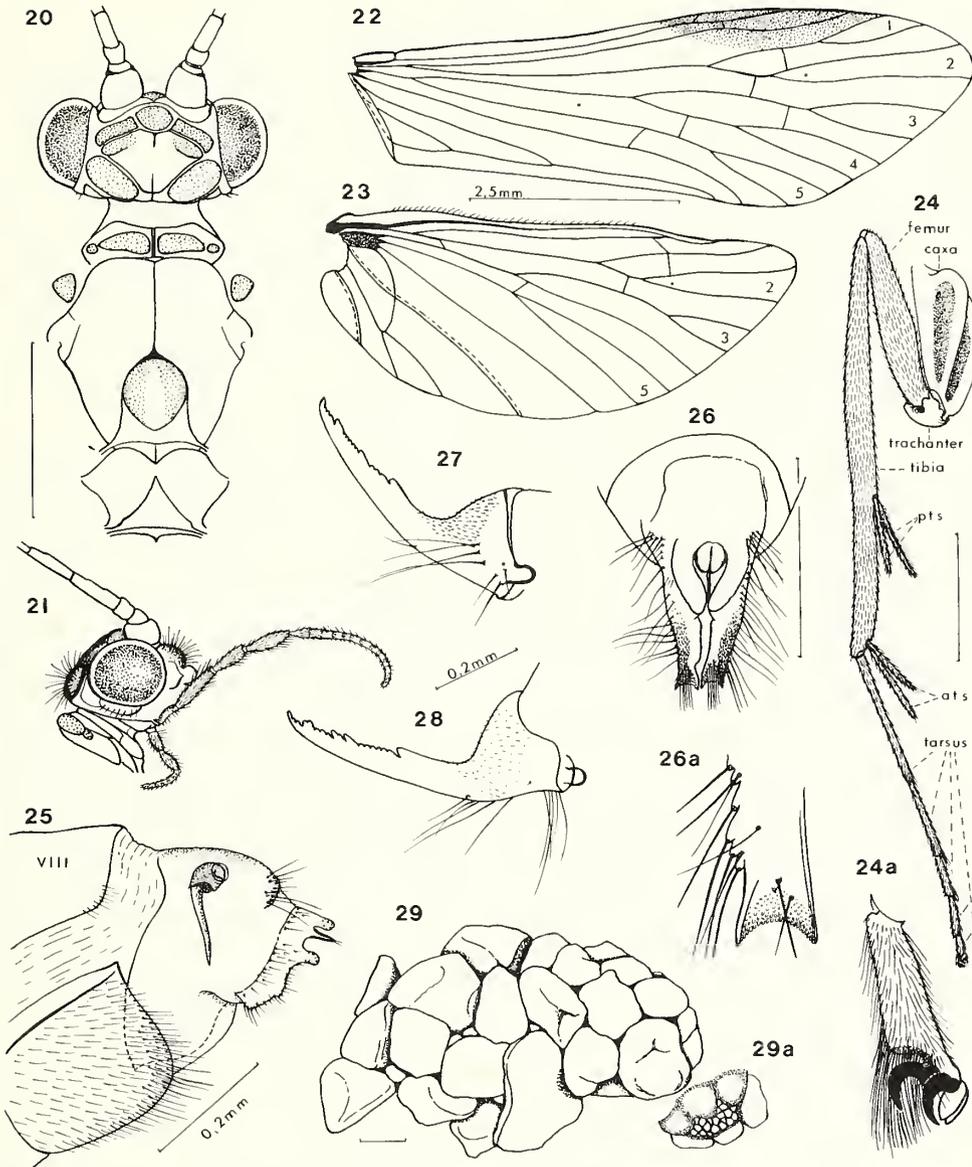
Cheumatopsyche thomasseti (Ulmer), 1931: 18–19, Figs 16, 17, (♂ genitalia) as *Hydropsychodes*. Natal, Weenen. ♂.

7 syntypes in British Museum (Nat. Hist.).

Distribution: South Africa: Natal, Cape Province, Transvaal, Orange Free State; South West Africa; Angola; Zimbabwe (Rhodesia). Larvae were also found in a collection from Kenya.

DESCRIPTION OF IMAGOS (Figs 20–25)

Male imago (described from fresh specimens; pinned and spirit material also available): a small-medium species, forewings 6–7 mm long, when alive silver-grey, wings densely pubescent, silvery mottled with darker grey, abdomen greenish to olive. Colour may vary in different areas as Ulmer described the type material (presumably pinned) as being light yellow to golden, the forewings marbled with dark brown, fringed with grey-brown setae, hind wings iridescent, abdomen greenish to blackish olive. Spirit material yellowish brown. Antennae slightly longer than wings, slender, very like those of *Hydropsyche*. Eyes large, black; head warts shown in Fig. 20, the anterior warts being somewhat variable in shape. Genitalia discussed and well figured by Kimmins (1960a: 263–265, Figs 28–31), who also gives a key to the then known



Figs 20-29. HYDROPSYCHINAE: *Cheumatopsyche thomasseti*, ♂, ♀, ♂ pupa and pupal case. 20. ♂: dorsal view of head and thoracic nota, 21. ♂: lateral view of head and palpi, 22, 23. ♂: fore and hind wings (right), 24. ♂: hind leg (left), 24a, same, fifth tarsal joint, paired claws and pulvilli, further enlarged, 25. ♀: lateral view of genitalia, 26. ♂ pupa: apex of abdomen showing anal appendages and pockets for ♂ genitalia, 26a, apex of anal appendage further enlarged, 27. right mandible of pupa, ventral, 28. left mandible of pupa, dorsal, 29. pupal case, lateral, 29a, end view of same, showing sieve plate.

species with comparative drawings of males and females of a number of them.

Female imago (in spirit): slightly larger, forewing 7–8 mm long, colour when alive as ♂: antennae shorter than wings; eyes, palpi *etc.* as in ♂. Sternal plates of VIII subquadrangular in shape with rounded apical angles, well separated right to base medially, setose and with long posterior fringe, X hood-like, clasper receptacle small with long groove (see Fig. 25 and Kimmins 1960a: 265, Fig. 71, ♀, drawn from specimens bred out from *Ch. thomasseti* larvae collected from the Great Berg River, Western Cape Province).

Material available in the Albany Museum Collection includes over 150 males, over 90 females (the latter not all with abdomen cleared, but Fig. 25 was drawn from cleared material compared with a Berg River specimen identified by D. E. Kimmins and bred out from a known larva). There are also hundreds of larvae and about ten ♂ and ♀ pupae, of which two mature male pupae with all relevant sclerites in their cases establish the correlation between adults, larvae and pupae of this species. The larvae, described below and illustrated, are very distinctive and easily distinguished from those of other *Cheumatopsyche* species of which we have correlated larvae.

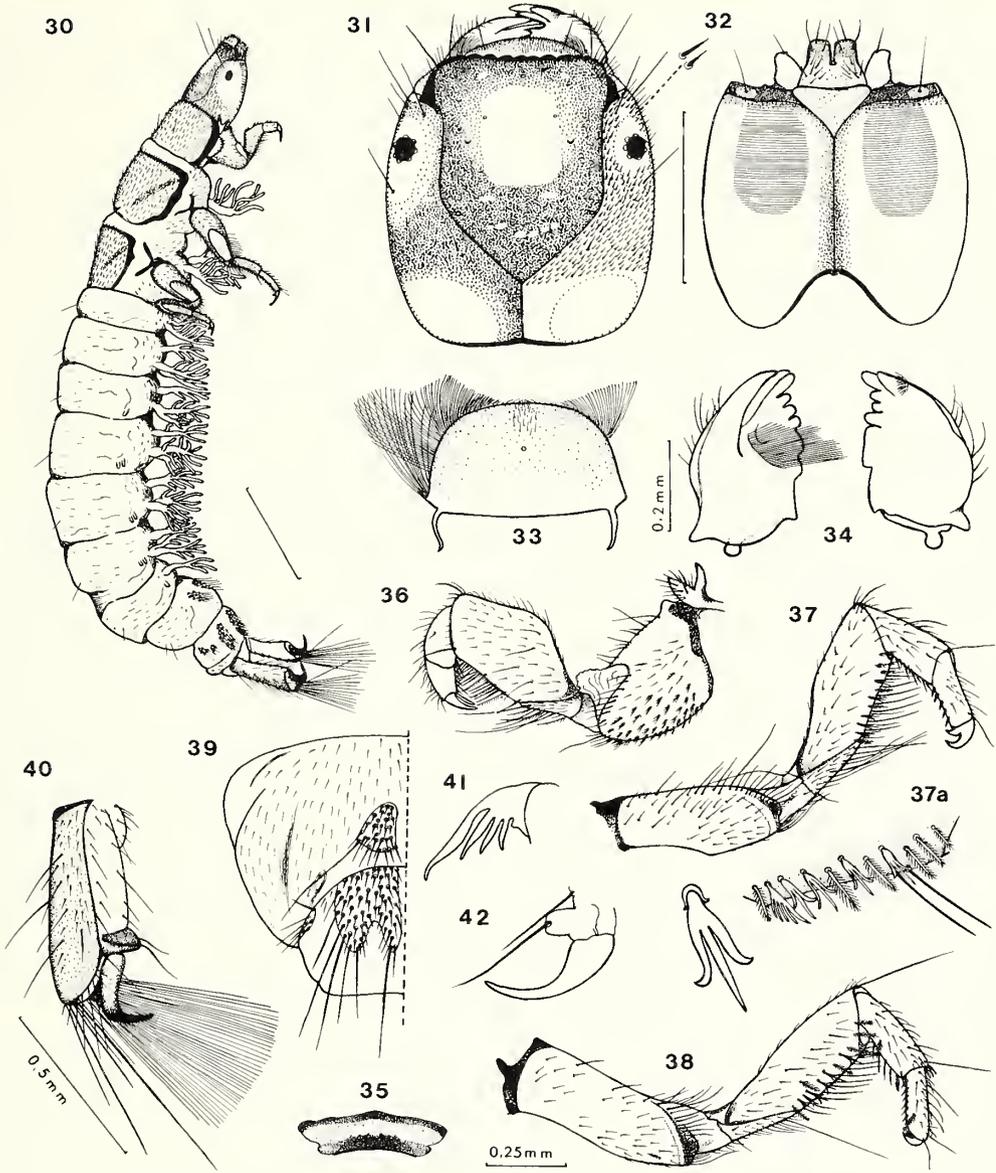
DESCRIPTION OF LARVA (Figs 30–42, Table III, histogram, Fig. 214A.)

Mature larva (in spirit Figs 30–40): length up to 8.0 mm, abdomen at widest point up to 1.3 mm, sclerotized parts light yellow to brown, head with strong brown and yellow pattern (Figs 30–32), abdomen in life olive brown to ochraceous in colour. The larvae are strongly setose, the setae on head and thoracic nota being short and sharply pointed, with none of the blunt setae so characteristic of *Hydropsyche* larvae.

Head (Figs 30–32): short, almost square, dorsal side flat but without carina, with very characteristic white or yellowish square on centre of frontoclypeal apotome, rest of head brown dorsally and laterally, apart from yellowish areas round eyes and near posterior margin as shown; ventral side yellowish. Dorsal side with many short setae except on frontoclypeal apotome which is minutely pitted but bears few setae, though it may often be covered with a woolly coat of "Aufwuchs", very characteristic of this species. Anterior margin of frontoclypeal apotome black, crenate, straight or slightly concave. Eyes medium-sized, black, placed well forward beneath small cuticular lenses. Stridulatory files present but not easily distinguishable as striae are fine and same colour as genae. Anterior ventral apotome light brown, posterior ventral apotome minute, brownish black.

Mouthparts (Figs 32–34): labrum sclerotized, pale brown, setose, without lateral expansion but with large ventral brushes of setae, usually partly or entirely retracted beneath it; anteclypeus membranous. Mandibles short, broad, three-sided, the narrow outer side bearing a few large setae. Left mandible with three terminal and three subterminal teeth, below these an irregular shelf-like protuberance across which lies a strong inner brush of setae. Right mandible with two terminal and three subterminal teeth, below the latter a shelf-like projection, no inner brush but a small tuft of setulae on upper apical tooth. Maxillary palpi short, stout, five-segmented, labium also short, thick, palpi not seen. Submentum light brown with deeply cleft apex, stipites paler brown.

Thorax (Figs 30, 35): thoracic nota ochraceous, pubescent, lateral margins blackish, meso- and metanota with faint brownish diagonal stripes, the former with crescent-shaped black mark in centre of posterior margin, the latter with a much smaller one. Anterior part of pronotum, particularly front edge, with scattered branched setulae in addition to simple ones. Pre-episternum bifid, dorsal branch smooth, ventral branch setose. Prosternal plate with dark anterior and posterior borders, no intersegmental sclerites posterior to it. Membranous parts of thorax whitish, with many small inconspicuous setae. One pair of mesosternal gills, three metasternal gills (one pair coxal gills, a single median gill).



Figs 30–42. HYDROPSYCHINAE: *Cheumatopsyche thomasseti*, mature larva. 30. habitus of mature larva, 31, 32. dorsal and ventral views of head, colour pattern shown on left gena and frontoclypeal apotome, setae on right, with 2 setae further enlarged, 33. labrum (dorsal), 34. left and right mandibles, dorsal view, 35. prosternal plate, 36. left foreleg (lateral view) with pre-episternum, 37. left mid-leg (median view), 37a. the same, femoral margin & single seta further enlarged, 38. left hind leg (median view), 39. ventral view of abdominal segments VIII & IX showing sclerites and setae, 40. right anal proleg and claw. *Cheumatopsyche thomasseti*, first instar larva. 41. claw of left mid-leg, 42. anal claw.

Legs (Figs 36–38): yellowish with a few dark markings, claws red-brown, with single basal spine. Foreleg relatively stout, particularly coxa and femur, claw large, strong, basal spine long, no tarsal brush, branched and plumose setae on coxa, trochanter and femur as indicated. Scraper of stridulator on femur much as in *Hydropsyche*. Mid-leg longer, hind leg longest, bearing feathered setae as shown, basal spines short, stout.

Abdomen (Figs 30, 39, 40): ochraceous in life, white in spirit, with many inconspicuous setulae which tend to disappear in larger individuals except in folds and on the ventral side of the body. Tufted tracheal gills present on abdomen in two to four rows (see Table III). Those abdominal gills which have two main stems retain a common basal stalk even in the largest specimens, and clearly arise as branches of a single gill. Single-stalked gills have 5–9 filaments, double-stemmed ones 9–16 filaments. Conical lateral gills present on segments III–VII, very small and inconspicuous. Sternum of segment VIII bears small pair of triangular sclerites set with short, stout setae and bordered posteriorly with long, dark ones; sternum of IX with a pair of much larger bifid sclerites similarly set with setae, also two pairs of smaller sclerites, lateral and dorsolateral, each with a few setae. Anal prolegs long, well developed, each with well sclerotized lateral sclerite and terminating in a fan of long, dark setae; anal claws right angled, plain. Four anal gills.

Earlier instars: the large number of larvae present in many of the samples studied has made it possible to work out the instars with reasonable accuracy, basing this primarily on the width of the head capsules at the eyes. Heads of 166 larvae collected from the Vaal River near Warrenton, North Cape, were measured, and the results are shown as a histogram (Fig. 214A), which indicates that there are five larval instars as is usual in the *Hydropsychinae*, the fifth showing two peaks, presumably representing males and females (the latter being the larger). Many specimens of each instar were present in the samples, and a brief description of their characteristics follows. All instars were clearly recognizable as *Cheumatopsyche*, of which only this species was encountered in the Warrenton area at the time.

First instar (Figs 41, 42): no tracheal gills; pre-episternum simple, head capsule and pronotum lightly sclerotized, the latter showing brown margins, no head pattern or stridulatory files visible as yet; meso- and metanota scarcely sclerotized, the latter barely distinguishable, no prosternal plate. Few setae, long and tapered, on head and limbs; legs with three basal spines to each claw (Fig. 41), a few feathered setae on tibiae. Anal claws (Fig. 42), simple, curved but not right-angled, no terminal fan.

Second instar: simple unbranched gills present on meso- and metathorax and abdomen. Pre-episternum shows second point, but may appear undivided except under compound microscope. Meso- and metanota clearly sclerotized, pubescent, head darker but pattern not yet visible. Stridulatory file distinguishable under compound microscope. Prosternal plate present. Tarsal claws with a single basal spine as in later instars, forelegs with a few feathered setae on femora. Anal prolegs without brushes, but with two long, strong setae next to each claw. Ventral plates on abdominal segments VIII and IX just visible.

Third instar: ventrolateral gills on abdominal segments II–VI, with with two main stems arising from a common base (ventral gills always remain single). All gills still unbranched (i.e. without lateral filaments). Pre-episternum with second point well-developed, but only clearly seen under compound microscope. Head darker, with heavy labrum, pattern not yet clear. Pro-, meso- and metanota with many fairly long setae. Ventral plates on VIII, IX clear, but stridulatory file still only visible under compound microscope. Foreleg with a few branched (trident or quadrident) setae on coxa, several plumose setae on trochanter and femur; mid- and hind legs with a few branched and plumose setae on femora; anal prolegs with thin brush of setae, anal claws not yet right-angled.

Fourth instar: meso- and metasternal gills with three filaments each, abdominal gills with one to three according to position. Head pattern fairly clear. Stridulatory file just visible under

SCOTT: HYDROPSYCHIDAE (TRICHOPTERA) OF SOUTHERN AFRICA WITH KEYS

stereomicroscope. Pre-episternum clearly bifid; forelegs with several long plumose setae on femora, many trident setae on coxae. Mid- and hind legs with a row of branched and feathered setae on femora and a few other feathered setae; a few branched setae on tarsi and coxae. Brushes on anal prolegs not yet fully developed.

Fifth instar: this is the final instar described above. See Table III for details of gills *etc.*

TABLE III:

Number and position of tracheal gills and other characters 1st to 5th larval instars of *Cheumatopsyche thomasseti*

Segment no.	1st instar		2nd instar		3rd instar		4th instar		5th instar	
Thoracic gills										
Mesosternal	—		1 pair		1 pair		1 pair		1 pair	
Metasternal	—		3 gills		3 gills		3 gills		3 gills	
Abdominal gills	VL	V	VL	V	VL	V	VL	V	VL	V
I	—	—	1	1	1	1	1	1	1	1
II	—	—	1	1	2*	1	2	1	2	1
III	—	—	1	1	2	1	2	1	2	1
IV	—	—	1	1	2	1	2	1	2	1
V	—	—	1	1	2	1	2	1	2	1
VI	—	—	1	1	2	1	2	1	2	1
VII	—	—	1	—	1	—	1	—	1	—
Tarsal claws:										
basal spines	3		1		1		1		1	
Gill branching	no gills		simple gills		simple gills		1-3 branches		5-9 branches per stem	
Head width at eyes in mm	0,12-0,20		0,23-0,32		0,37-0,45		0,55-0,65		0,78-0,81 ♂ 0,83-0,91 ♀	
Pre-episternum	simple,		simple with lateral point		bifid		bifid		bifid	

* The figure 2 denotes that the abdominal gill in question has two main stems arising from a common base (these originate as branches of a single gill and do not become completely separate basally). Gills of right side shown.

VL = ventrolateral gills.

V = ventral gills.

N.B. There are also very small conical lateral gills present on segments III-VII in the mature larva.

DESCRIPTION OF PUPA (Figs 26-29, Table IV)

There were some 10 pupae available for study, including two mature males, one almost mature male and three females (one nearly mature), each in case with larval sclerites, also pre-pupae in cases.

TABLE IV:
Tracheal gills, dorsal plates etc. of ♂ pupa of *Cheumatopsyche thomasseti* (Ulmer)

Abdominal segment no.	Tracheal gills (right side)		Dorsal plates	Setae and points (shagreening)
	L	V		
I	—	—	—	—
II	—	2	Presegmental pair (3-4 crochets)	fine shagreening; a few small ant. setae & 3 pairs post. setae
III	1	2	Presegmental pair (c. 6 crochets) Postsegmental pair (large, oval, 17-20 crochets)	fine shagreening over whole central area; some small ant. setae & 4 pairs post. setae
IV	2	2	Presegmental pair (c. 6 crochets) Postsegmental pair (smaller oval, 6-7 crochets)	fine shagreening in centre, post. band of long setae & a few small ant. setae
V	3	2	Presegmental pair (4 crochets)	fine shagreening down centre; c. 36 pairs of post. setae & some smaller ant. setae
VI	3	2	Presegmental pair (4 crochets)	fine shagreening over central area; c. 3 pairs setae
VII	2	—	Presegmental pair (4-5 crochets)	median shagreening & c. 6 pairs setae
VIII	—	—	Presegmental pair (4 crochets)	row of c. 10 long setae

L = lateral diverticula ("conical gills"); where there are two or three the anterior one is smallest, the posterior one largest.

V = ventrolateral tufted gills, the figure 2 denoting that the gill has two main stems.

The postsegmental dorsal plates have minute crochets or teeth, much smaller than those of the presegmental dorsal plates, projecting forwards not backwards.

Male pupa (pharate adult) (in spirit, Figs 26-28): length c. 5.5 mm, head rounded, pale yellow, with erect colourless setae on vertex, labrum and bases of antennae; imago visible through pupal pelt. Eyes large, dark. Antennae slender, about $1\frac{1}{2}$ times body length, ends forming a single coil. Labrum subtriangular, a tuft of setae on each side and a small median tuft near apex. Mandibles brown, slender, sharply pointed, right mandible with four teeth, left with five (two of them bicuspid), cutting edged serrated between teeth, each mandible with two tufts of 4-5 long setae on ventral side, a single small seta on outer margin, inner basal area with large patch of spinules. Maxillary and labial palpi as in adult. Forelegs fairly slender, mid-

and hind legs sturdier but not noticeably expanded, mid-legs with swimming fringe. Spurs 2.4.4. Tufted gills, conical lateral gills and dorsal plates present on abdomen as indicated in Table IV. Anal appendages fairly short, stout, almost straight, apices slightly curved dorsal, the tip of each appendage forming two sharp points between which is a shallow saddle covered with small protuberances; each appendage fringed with long, dark setae along outer margin, ventral side with apical patch of shorter, colourless setae, and spinules along outer edge. Genitalia in lobed pockets with light shagreening (raised points) on surface.

Female pupa (in spirit): length c. 6 mm; much as male, but antennae slightly shorter than body, straight; mid-legs expanded, with swimming fringe. Anal appendages almost straight, with fewer setae than in ♂, apices less symmetrical, the outer points being shorter than the inner. Genitalia not in special pockets.

Pupal case (Fig. 29): oval, about 8 mm long, rather roughly constructed of large sand grains or rock fragments with small ones filling interstices, not usually very rigid, completely lined with silk except for the rounded ends, which are partly closed with sand grains joined within by bands of silk forming a coarse network, allowing water to circulate; sides basally inturned and affixed to rock or stone, basal opening closed with silk lining only. Larval sclerites packed into posterior end of case.

REMARKS

Males and females in the Albany Museum collection are typical of the species, and cleared genitalia of both sexes have been compared with material identified by Mr D. E. Kimmins, who himself identified some of these specimens. The larvae and pupae have not, to my knowledge, previously been described, excepting that Barnard (1934: 63, fig. 38c) evidently had a mixed series of at least three species among the larvae he drew, because his fig. 38c, labelled "variations in the front margin of clypeus of *Hydropsychodes lateralis*", in fact shows what may be a variation of *Cheumatopsyche afra* (top drawing), *C. thomasseti* (middle drawing) and *C. maculata* (= *C. lateralis*), bottom drawing. The larva fully described (frontoclypeal apotome fig. 38b) appears to have been that of *C. afra*.

Ulmer (1957) discussed the larvae of the then known Hydropsychinae, including *inter alia* *Cheumatopsyche* and *Hydropsychodes* (now in synonymy), and providing a tentative key. Ulmer concluded from the evidence in his possession that *Cheumatopsyche* species had four metasternal and five anal gills, whereas *Hydropsychodes* species had three metasternal and four anal gills. As has been noted above, *C. thomasseti* has three metasternal gills and four anal gills, as has *C. afra* (described by Barnard as *C. lateralis* in 1934), though Marlier (1961) in describing *afra* larvae mentions five anal gills (see comment below). *C. tenerrima* on the other hand has three metasternal gills but appears to have five anal gills (Marlier 1961). *C. copiosa*, the larva of which was described by Hickin (1956) also has five anal gills (number of metasternal gills not given) and *C. maculata* (material collected by the author) definitely has three metasternal and five anal gills. Of the uncorrelated species of *Cheumatopsyche* described by Marlier, one (Marlier 1943a) has three metasternal gills (anal gills not mentioned); the other, Marlier's Larva B (1943b), is described as having three metasternal gills in the younger instars, four in mature larvae (anal gills not given). As regards Larva B, Ulmer suggests, I think with reason (there are also differences in the frontoclypeal apotome), that two different species were included in Marlier's material. Indeed from a careful consideration of Marlier's descriptions and figures, it appears to me probable that "Larva B" included two species of *Cheumatopsyche* (the small and medium-sized larvae respectively) and one of *Hydropsyche* (the large one); and that his "aged larva" seems to have been a specimen of the *Cheumatopsyche* sp. larva described in his 1943b paper. His "Hydropsychinae sp. C" larva (Marlier 1943c), sounds very like the plain brown *Hydropsyche* larvae mentioned under *H. longifurca*

above. The larva described by Jacquemart (1957) as *C. cf. leloupi* also has three metasternal gills.

Of the *Cheumatopsyche* larvae so far described from Africa, *C. tenerrima* (Marlier 1961) is the only species which might be confused with *C. thomasseti* as the larvae have the same almost straight crenate margin to the frontoclypeal apotome on which there is also a light patch. In *C. tenerrima* this light central patch broadens posteriorly to form a pale transverse band across the head behind the eyes whereas in *C. thomasseti* there is a dark transverse band in that position. There are also differences in shape of mandibles and the ventral plates on IX; these are clearly shown in the drawings. Gibbs (1973) describes two species (sp. A & sp. D, fig. 109A) with similarly shaped frontoclypeal apotomes, but both lack the central light square and show other differences from *C. thomasseti*.

It thus appears that in those Afrotropical species of *Cheumatopsyche*, the larvae of which have been described so far, the larvae have three metasternal gills and either four or five anal gills. Ulmer's Sunda Island species of *Hydropsychodes* (Ulmer 1957) also had three metasternal gills. His ascription of four to *Cheumatopsyche* was based on the description of *C. lepida* (Pictet), originally described as *Hydropsyche*, in which there are four metasternal gills (Silfvenius 1905) and his retention of the genus *Hydropsychodes*. As, however, *Hydropsychodes* has since been placed in synonymy with *Cheumatopsyche* (Kimmins 1963) and *C. lepida* is the type species of the genus and widespread in Europe and down into North Africa, it is advisable to regard *Cheumatopsyche* larvae as possessing two mesosternal gills and either three or four metasternal gills and either four or five anal gills. There would seem, nevertheless, to be stability in this count within a particular species; certainly in *C. thomasseti* larvae there appears to be no variation in thoracic gill numbers between the different instars, there being two mesosternal and three metasternal gills from the time of their first appearance in the second instar to the final instar.

The most useful characters for distinguishing between larvae of different *Cheumatopsyche* species in the Afrotropical Region appear to be the shape of the anterior margin of the frontoclypeal apotome and the colour pattern of the head, both of which seem to be reasonably stable characters, though there may be minor variations in the intensity of the colouration and in the shape of the margin. No doubt anal and metathoracic gill counts, setation, shape of mandibles and other characters can be used as additional criteria. Statzner (1981), in his study of the *Hydropsychidae* of the N'Zi River (Ivory Coast), concluded that the most useful characters for recognition of early instars of *Cheumatopsyche* species were the stridulatory ridges and secondary setae on the head; in later instars the size of the prosternal sclerites, the shape of the frontoclypeal apotome margin, shape of submentum and pre-episternum and the secondary setae on the head.

There are, in the Albany Museum collection, larvae representing at least a dozen species, of which, to date, three only have been correlated with their imagos, namely *C. thomasseti*, *C. afra* and *C. maculata* (unpublished data). Gibbs' "sp. A" is near South African *C. afra* larvae (Gibbs 1973), as of course is Marlier's *C. afra* larva from Kivu (Marlier 1961), which, however, differs from South African material in several respects. It is very possible that *C. afra* may eventually prove to be a complex of species as Kimmins (1960b) suggested might be the case.

In the same paper Marlier (1961) proposed the subdivision of the genus *Cheumatopsyche* into four subgenera, *Cheumatopsychodes*, *Achirocentra*, *Abacarioides* and *Cheumatopsyche sensu stricto*. He gave some discussion as to their relationships and differences and listed the species that he attributed to each. As I do not find the distinguishing characters very easy to use, I am not attempting to key out the proposed subgenera here. In the list of African species which follows, however, Marlier's placement into subgenera is indicated, and reference should be made to his paper if details are required.

BIOLOGY

Cheumatopsyche larvae are considerably smaller than those of *Hydropsyche*, but are similar in habits, also being predacious omnivores and building shelters with attached catching nets in which algae and smaller animals are trapped and from which they are collected and eaten. The catch taken includes small crustaceans, such as Copepoda and Cladocera, aquatic insect larvae, such as *Simulium* larvae and Ephemeroptera nymphs (Chutter 1968, 1971; Hynes & Williams 1962, and personal observations), and a higher proportion of algae than in the case of *Hydropsyche*. *Cheumatopsyche* larvae evidently prefer weaker currents to those favoured by *Hydropsyche* and build larger, flimsier nets which collapse on removal from water.

Much is known regarding the life cycle and habits of *Cheumatopsyche* species from work done in various parts of the world. Fremling (1960) in the study of *Hydropsyche orris* at Keokuk quoted above, also gave a detailed account of the almost equally common *C. campyla*. He noted that the larvae abounded in tailwaters and other areas of moderate current; that the adults sheltered during the day and swarming was not seen, though mating couples were collected; that females entered the water to oviposit, laying on submerged objects at depths of up to 12 ft (c. 360 cm), often re-entering the water on several occasions. In the case of eggs laid in the laboratory it took 51 days from hatching through five larval instars and pupation to the emergence of the adults. The pupal stage lasted for six days. In the river the larvae were found at depths of up to 24 ft (c. 720 cm), preferring deeper to shallower water. Only first instar larvae appeared to swim. Older larvae seemed to be continually active, feeding, cleaning nets and discarding inedible objects. New areas were populated by drifting of young larvae, this being compensated for by upstream flight of females. *C. campyla* appeared to be bivoltine, with peaks in early and late summer.

Cheumatopsyche thomasseti is a eurytopic species, widespread in Southern Africa, and is found in many types of flowing water. This species shows a wide range of tolerance to climatic, physical and chemical conditions, much more so than *Hydropsyche* and more so than some of the other species of *Cheumatopsyche* found in Southern Africa, though the genus as a whole is more tolerant of mild pollution of various kinds than are most other Trichoptera.

In the Berg River (West Cape) *C. thomasseti* larvae commonly occurred in the lower reaches during the summer months. Another species, *C. afra* (Mosely), was characteristic of the upper reaches, although in summer this species was present in small numbers, together with *thomasseti*, in the lengthy lowest zone. The main habitat of *thomasseti* thus lay in a stretch of river running through farmlands, where stony runs and stickles alternated with large, sandy, shallow pools, and where turbidity, dissolved solids, temperature and pH were higher than in the upper reaches. The whole river was subjected to periodic flooding during the winter rains. A few comparative values are shown below, taking Station 3 (a fast-flowing foothill stream) as being one at which *afra* was well represented, and Station 18 (on the lower Berg) for *thomasseti*, the only station where it was abundant (figures extracted from Harrison & Elsworth 1958).

Station	Temperatures ° C		pH	TDS ppm	Turbidity ppm SiO ₂
	winter min.	summer max.			
3: <i>C. afra</i>	9,0	29,0	4,7-6,8	19-78	0,0-6,0
18: <i>thomasseti</i>	10,0	31,7	6,4-8,2	45-584	0,0-13 000

In the East Cape the rivers may be broadly divided into two categories; highlylyng, often acid mountain streams; more or less highly mineralized, silty lowland rivers, subject to alter-

nate droughts and floods. The *Cheumatopsyche* species in the area show a clear distribution pattern, as might be anticipated, though perhaps not one that would have been expected.

In the upland streams on the Hogsback mountains (Amatola Range near Alice, altitude 1 200–1 500 m), the overwhelming preponderance of *Cheumatopsyche* larvae were a dark form of *C. afra*, *C. thomasseti* larvae being very rarely found. In the lower altitude (800–900 m) montane streams in the vicinity of Grahamstown, *C. afra* occurs, though rarely, unless two other possibly new species found prove to be variants of it. At present I tend to the opinion that they are different species as the larvae also appear to show consistent differences. The commonest of the local species is, however, *C. maculata* (Mosely). All these streams are clear, cold and clean, those on the Amatolas being permanent, whereas those near Grahamstown may be reduced to a trickle or to subsurface moisture during severe droughts.

Temperatures on the Hogsback ranged from snow cover at times in winter to 15–17° C (water temperature) in summer, and pH values ranged from 6,4 in summer to 7,5 in winter, the change to slight alkalinity being due to run-off during the rainy season, the rock formations being mainly basaltic. (Values from B. C. Wilmot, pers. com.) Highlying streams near Grahamstown drain Witteberg quartzites and remain acid throughout the year, pH values ranging from 6,0–6,9.

Two lowland rivers were studied in the course of other work (Scott 1974, Scott, Allanson & Chutter 1972), namely the Sundays River, which rises in the Sneeuberg mountains north of Graaff-Reinet and flows to the sea 35 km NE of Port Elizabeth, and the Great Fish River, which lies to the east of the Sundays, drains several mountainous areas and reaches the sea some 130 km to the east of Port Elizabeth. Both rivers lie largely in areas of rain shadow and flow over soft, easily eroded geological formations (mainly Beaufort and Ecce Series of the Karroo System, though the lower Sundays flows over cretaceous rocks of marine origin). Both rivers are liable to dry out during droughts and both are subject to catastrophic floods. Both had small resident Trichoptera populations limited to those parts which did not dry out completely. In the Sundays River the Hydropsychidae were represented by *C. afra* and in the Fish by *C. thomasseti*.

A brief summary of relevant water conditions encountered in the two is given below, extracted from Scott *et al.* (1972), including only values at which living, apparently healthy, *Cheumatopsyche* larvae were found:

		pH	TDS mg/l	Ca mg/l	Na mg/l
Fish River	<i>C. thomasseti</i>	8,2–9,0	511–3 368	27,7–115	110–830
Sundays River	<i>C. afra</i>	8,2–9,3	998–4 349	56	1 480

Such temperatures as were taken varied from 11,5–27° C. However, these do not really reflect the range obtaining, for air temperatures varied with the seasons from winter frosts to at least 46° C in summer and, as the water is often shallow, it tends to be directly affected. In extreme heat larvae could, however, seek shelter under stones and imagoes under bridges or vegetation. The Hydropsychid larvae also had other factors with which to contend, such as slow current, low water levels and heavy silt load during floods.

Calcium values have been included because the *C. thomasseti* larvae from most stations on the Fish River were more or less heavily encrusted with a white coating of CaCO₃, often with head completely covered and gills matted with calcareous material. This could have been due to a high load of calcium bicarbonate which can be precipitated as CaCO₃ on the bottom of the

river and evidently also on some of the animals. The larvae when caught, were alive, but must have been seriously hampered in their activities (Scott 1976).

The difference in *Cheumatopsyche* species between the two rivers may have been due to the very heavy silt load in the Fish River during floods, considerably heavier than in the Sundays, as it has been generally observed that *C. afra* usually occurs in larger numbers in the eroding zone, where the water is clean and silt-free whereas *thomasseti* is more abundant in lower, more turbid waters (Harrison & Elsworth 1958, Chutter 1969a, Scott et al. 1972). Since the above study was completed conditions may have changed considerably with the inflow of water from the Orange to the upper Fish River, via the Orange–Fish tunnel.

River studies in the Transvaal and Orange Free State (Chutter 1968, 1971) included observations on *C. thomasseti*, which was one of the commonest animals in stony runs in most parts of the Vaal River and its tributaries, particularly in areas of mild pollution. For example, such mild pollution, due to seepage of treated sewage effluent, occurred in the Vaal River below Standerton, resulting in increased particulate organic matter and algae (mainly diatoms), large numbers of Cladocera and Copepoda and, evidently feeding on all these, large numbers of *C. thomasseti* and *Amphipsyche scottae*. Chutter's work showed that *C. thomasseti* larvae were present all the year round, though most numerous in spring and autumn, and that the imagos were abundant in summer. Very few early instars were found in winter samples. Density of larvae was significantly correlated with current speed in certain areas, increasing sharply at speeds above 50 cm/sec.

Statzner's studies of emerging insects from the River Kalengo (Zaire) (Statzner 1976) also showed an all-year-round pattern but with two peaks for *C. explicanda* imagos and four smaller peaks for *C. boettgeri*. Statzner concluded that the main controlling factor could be light intensity. The Zaïrese climate is tropical.

Sharp (1976) made some laboratory observations on *C. maculata* larvae from hill streams near Grahamstown where they inhabit small falls and stony runs. In the latter situation they were usually under stones. Optimum conditions appeared to be a water temperature of about 10° C and a relatively high PO₂ level, indicating a high oxygen tension. Undulatory (respiratory) movements of the abdomen which increased both with rising temperature and with falling PO₂ levels did not occur at all in fast current when temperature and oxygen levels were favourable. If the temperature was increased too quickly or too much (25–30° C) or the PO₂ level dropped too low (less than 55 mg Hg) the larvae left their nets and attempted to escape, swimming with spiralling movements of the abdomen. Intraspecific fighting did sometimes occur but was not serious and did not result in injuries or death. Unlike *Hydropsyche*, *C. maculata* larvae spun nets at very low current speeds, and indeed did so in the laboratory even in still water provided that the substratum was suitable. In the small waterfalls they spun nets in the usual way, on open rock faces in the stream, usually in small crevices in the rock where there was some shelter (personal observations).

Gibbs (1973), in observations on Ghanaian species, noted that at times *C. digitata* larvae occurred in vast numbers (as many as 250 000/m² in a stream at Tafo), completely covering the bedrock with a dense incrustation of retreats, inhabited by fourth and fifth instar larvae, while younger larvae moved freely around them. Beneath these larvae retreats were pupal cases and beneath those older broken down cases occupied by chironomid larvae and worms. Gibbs noted that *Cheumatopsyche* larvae could be separated to species by their head markings and differences in secondary setation.

Statzner's study (1981) of hydropsychid larvae in the N'Zi River, a running water habitat with intermittent flow, included three species of *Cheumatopsyche*. The survey period of 15 months enabled him to study densities, life cycles and their relationship to discharge patterns. Parts of the N'Zi were treated with chlorphoxim to control Simuliidae, and Statzner concluded

inter alia that *Cheumatopsyche* larvae survived unfavourable periods in the larval stage and that they increased in numbers when flow slackened. He considered that there were only two to three generations per year.

AFRICAN SPECIES OF *CHEUMATOPSYCHE*

- C. afra* (Mosely), 1935: 229–231, figs 17–20 (wings, ♂ genitalia), as *Hydropsychodes*. ♂.
Mosely 1939b: 27, transfer to *Cheumatopsyche*.
Kimmins 1960a: 266–267, figs 36–67 (♂ genitalia), figs 72–76 (genitalia of probable ♀).
C. lateralis (Barnard), 1934, *partim* (as *Hydropsychodes*), is a synonym.
Marlier 1961: 162–164, figs 1–3 (♂ genitalia, larva), placed it in his new subgenus *Cheumatopsychodes*, and (1962a) proposed it as subgenus-type of this taxon.
Distribution: Sierra Leone, Tanganyika, Northern and Southern Rhodesia, South Africa, Belgian Congo, Ethiopia, Angola and possibly Ghana. It is thus widespread in Africa from the West Cape in the south to Ethiopia in the north-east and Sierra-Leone in the north-west, but may prove to be a complex of closely related species (Kimmins 1960a).
- C. albomaculata* (Ulmer), 1905a: 34, 35, fig. 22 (wings), as *Hydropsychodes*. ♂ ♀.
Marlier 1957: 289–292, figs 7, 8 (wings, head & thorax of ♀), as *Hydropsychodes*. ♀.
Kimmins 1963: 132–134, figs 36–39 (wings, ♂ genitalia), as *Cheumatopsyche*.
Distribution: Belgian Congo, Katanga, Lakes Edward & Albert, Angola, Ghana, Ethiopia.
- C. alferii* (Navás), 1927: 212–213, as *Hydropsychodes*. ♀.
Distribution: Egypt.
- C. amboinica* (Navás), 1928b: 112, 113, fig. 9 (♂ genitalia, labelled *C. ambonica*), as *Hydropsychodes*. ♂.
Distribution: British East Africa (Amboni).
- C. anema* Marlier, 1959: 111–114, figs 4, 5 (wings, ♂ genitalia; 5c, not labelled as such, appears to be ♀ genitalia). ♂ ♀.
Distribution: Sao Tomé Island, Gulf of Guinea.
- C. apicata* (Navás), 1931a: 126, 127, as *Hydropsychodes*. ♂.
Distribution: Belgian Congo.
- C. aterrima* Marlier, 1961: 159, 172–174, figs 11A–E (wings, ♂ genitalia, palps). ♂. Marlier places this in his new subgenus *Achirocentra* in the same paper.
Distribution: Kivu.
- C. atlantis* (Navás), 1930b: 142–143, fig. 48 (hind wing), as *Hydropsychodes*. ♀.
Distribution: N. Africa, Grand Atlas Mountains.
- C. bifida* Statzner, 1975: 382, 383, figs 13–17, 31 (♂ genitalia & wings), figs 21–23 (♀ genitalia). ♂ ♀.
Distribution: Zaïre.
- C. bimaculata* (Ulmer), 1930: 491–493, fig. 15 (wings), as *Hydropsychodes*. ♀.
Mosely 1939b: 27, transfers it to *Cheumatopsyche*.
Kimmins 1963: 132, fig. 35 (♀ genitalia).
Distribution: Abyssinia.
- C. bimaculata* (Jacquemart) 1966b: 45, fig. 10 (wings), as *Hydropsychodes*. ♂.
Distribution: Congo.

Note: *C. bimaculata* Ulmer was described from the ♀ only; if this is regarded as the ♂ of his species it should be attributed to Ulmer, if not, it would have to be renamed, as *Hydropsychodes* has been placed in synonymy with *Cheumatopsyche* (Kimmins 1963). Jacquemart gives no drawings of the genitalia.

- C. boettgeri* Statzner, 1975: 382, 383, 388–397, figs 18–20, 32 (♂ genitalia & wings), figs 24–26 (♀ genitalia). ♂ ♀.
Distribution: Zaïre.
- C. brunnea* Jacquemart, 1961d: 228. ♂.
Jacquemart 1961b: 23–25, fig. 14 (wing & ♂ genitalia).
Distribution: Congo.
- C. brunnea* (Jacquemart), 1963a: 378–379, fig 33A–D (wings & ♂ genitalia), as *Hydropsychodes*. ♂.
Distribution: South Africa (West and East Cape).
Note: As *Hydropsychodes* is now in synonymy with *Cheumatopsyche*, this species should be renamed.
- C. burgeonia* (Navás), 1931b: 138–139, fig. 74 (♀ hind wing), as *Hydropsychodes*. ♀.
Distribution: Belgian Congo.
- C. comorina* (Navás), 1931a: 125–126, fig. 63 (hind wing), as *Ulmeria*. ♂ ♀.
Distribution: Comoro Islands.
- C. copiosa* Kimmins, 1956: 196–197, figs 1–4 (♂, ♀ genitalia). ♂ ♀.
Hickin 1956b: 132–133, figs 1–7 (larva), description of larva.
Distribution: Uganda, Gold Coast, Dakar.
- C. digitata* (Mosely), 1935: 228–229, figs 14–16 (wing & ♂ genitalia), as *Hydropsychodes*. ♂.
Gibbs 1973: 393, 397, fig. 109a (larval head *cf.* with other species). Brief description of larval head and habitat.
Distribution: Belgian Congo (not Tanganyika, Mosely 1936), Uganda, Ghana, Nigeria. Cape Verde Islands (Nybom 1960: 3, ♂ ♀).
- ‘*C. digitifera* Mosely’, Jacquemart 1966b, is presumably a mis-spelling of *C. digitata*.
- C. diminuta* (Walker), 1852: 115, as *Hydropsyche*.
Ulmer 1931: 16–18, figs 13–15 (wing & ♂ genitalia), as *Hydropsychodes*. ♂.
Betten & Mosely 1940: 187–188, fig. 92 (♀ wings), as *Cheumatopsyche*. Original description plus further description.
Marlier 1961: 160, 161, proposed this as subgenus-type of his subgenus *Cheumatopsychodes*, but later withdrew it and substituted *C. afra* (1962a).
Distribution: Sierra Leone, Congo, German East Africa, South Africa, Cameroons, Sudan, Egypt.
- C. explicanda* Statzner, 1975: 382–387, 394, figs 1–4, 9–13, 30 (♂ genitalia & wings), figs 5–8 (♀ genitalia), fig 14 (♂ & ♀ genitalia *in copula*). ♂ ♀.
Distribution: Zaïre.
- C. falcifera* (Ulmer), 1930: 482–485, figs 4–7 (wings, ♂ genitalia), as *Hydropsychodes*. ♂.
Barnard 1934: 360–362, figs 37h–j (♂ genitalia), as *Hydropsychodes zuluensis* Barnard.
Mosely 1939b: 27, transfer to *Cheumatopsyche*.
Kimmins 1960a: 263, figs 24–27 (♂ genitalia); synonymy of *H. zuluensis* Barnard with *C. falcifera* (Ulmer).

- Kimmins 1963: 130–131, fig. 46 (♀ genitalia), as *Cheumatopsyche*. ♀. He notes that *C. falcifera* var., Ulmer 1930, is actually *C. afra* (Mosely).
Corbet 1958: 208–210, fig. 3a-f (larval parts & pupal case).
Distribution: Abyssinia, South Africa, former Belgian Congo, Uganda, Ghana.
- C. kimminsi* Marlier, 1961: 159, 165–168, figs 5–7 (wings & ♂ genitalia). ♂ ♀.
Marlier places it in his new subgenus *Cheumatopsychodes* in the same paper.
Distribution: Kivu.
- C. kissi* Marlier, 1961: 159, 170–172, figs 9–10 (wings, ♂ genitalia & palp). ♂.
Placed in Marlier's new subgenus *Cheumatopsychodes* in the same paper.
Distribution: Kivu.
- C. kitutuensis* Marlier, 1962a: 3, fig. 1 (♀ maxillary palps). ♀.
Marlier uses it as subgenus-type of his new subgenus *Hydrocheumatopsyche*. Originally described in Marlier 1961: 186–188, figs 16, 17A (wing & leg) as *Cheumatopsyche* sp. ♀.
Distribution: Kivu.
- C. lateralis* (Barnard), 1934: 362–364, as *Hydropsychodes*. It proved to be a synonym of *C. maculata* (Mosely); part of his material was, however, *C. afra* (Mosely).
- C. leleupi* Marlier, 1961: 159, 177–180, figs 13a–c (wings, ♂ genitalia). ♂.
Placed in Marlier's subgenus *Abacarioides* in the same paper.
Distribution: Kivu.
- C. leloupi* Jacquemart, 1957: 94–95, figs 78–83 (♂ genitalia & wings), pp. 95–100, figs 61a, 63, 75 (parts of probable larva). ♂.
Marlier, 1961, suggests that *leloupi* may be synonymous with *C. digitata* (Mosely), to which it is certainly very similar.
Distribution: Lakes Kivu, Edward and Albert (Belgian Congo).
- C. lepida* (Pictet), 1834: 207, pl. 18f, also larva & case, as *Hydropsyche*.
Fischer 1963: 114–122, as *Cheumatopsyche*.
Distribution: Europe, North Africa (Algeria).
- C. lesnei* (Mosely), 1932: 4, pl. 1 & figs 1–3 (wings, ♂ genitalia), as *Hydropsychodes*. ♂ ♀.
Mosely 1939b: 27, transfer to *Cheumatopsyche*.
Kimmins 1957b: 11–12, fig. 7 (♂ & ♀ genitalia), as *C. uncatata* sp. n. in error; he discovered it was synonymous with *lesnei*, appending a note to that effect in the same publication.
Distribution: Mozambique, Uganda, Dakar, Rhodesia, as well as probable material from Natal.
- C. lestoni* Gibbs, 1973: 395, figs 99–101 (♂ genitalia). ♂.
Distribution: Ghana.
- C. lobata* Marlier, 1943a: 10, 11, fig. 6 (♂ genitalia). ♂ ♀.
Distribution: Belgian Congo.
- C. maculata* (Mosely), 1934: 22–24, figs 11–13 (♂ genitalia), as *Hydropsychodes*. ♂.
Mosely 1939b: 27, transfer to *Cheumatopsyche*.
C. lateralis (Barnard) 1934: 362 falls into synonymy with *maculata*, his drawings were, however, of *afra* (Kimmins 1960a).
Distribution: South Africa (West and East Cape).

- C. madagassa* (Navás), 1923: 27, fig. 38 (♂ hind wing), as *Hydropsychodes*. ♂.
Distribution: Madagascar.
- C. marieni* (Jacquemart), 1965: 1–3, figs 1, 2 (wings & ♂ genitalia), as *Hydropsychodes*. ♂.
Distribution: South Africa (Natal).
- C. meruana* Navás, 1934d: 21–22, fig. 107 (hind wing). ♀.
Kimmins 1960a, notes that the ♂ is unknown and regards it as unidentifiable at present.
Distribution: Kenya.
- C. nubila* Kimmins, 1963: 137–138, figs 47–50 (♂, ♀ genitalia). ♂ ♀.
Distribution: Ethiopia, South Africa (Natal).
- C. obscurata* (Ulmer), 1930: 485–488, figs 8–10 (wings, ♂ genitalia), as *Hydropsychodes*. ♂.
Mosely 1939b: 27, transfer to *Cheumatopsyche*.
Kimmins 1963: 130, fig. 45 (♀ with description).
Distribution: Abyssinia.
- C. obtusa* (Jacquemart), 1963a: 380, fig. 35a–c (wings, ♂ genitalia), as *Hydropsychodes*. ♂.
Distribution: South Africa (Orange River, Upington).
- C. pallida* (Banks), 1920: 357–358, pl. 7, fig. 89, as *Hydropsychodes*. ♂.
Distribution: Madagascar.
- C. plutonis* (Banks), 1913: 239, pl. 23, figs 2, 4, 5 (♂ & ♀ genitalia, wings), as *Symphitopsyche*.
♂ ♀.
Mosely 1939b: 27, transferred it to *Cheumatopsyche*.
Distribution: Abyssinia.
- C. pulverulenta* Gibbs, 1973: 393–395, figs 95–98 (♂ genitalia & forewing). ♂ ♀.
Distribution: Ghana.
- C. punctata* (Jacquemart), 1961d: 228, also 1961b: 25–26, fig. 15 (forewing & ♂ genitalia), as *Hydropsychodes*. ♂.
Distribution: Congo.
- C. rhodesiana* (Jacquemart), 1963a: 375–378, figs 32A–D (wing & ♂ genitalia), as *Hydropsychodes*. ♂.
Distribution: South Africa (East Cape, Natal), Basutoland, Southern Rhodesia, Katanga.
- C. roscida* (Navás), 1934c: 71, 72, fig. 13 (forewing), as *Hydropsychodes*. ♂ ♀.
Distribution: Madagascar.
- C. sessilis* Marlier, 1961: 159, 168–170, figs 8A–E (wings, ♂ & ♀ genitalia), placed in his new subgenus *Cheumatopsychodes* in this paper. ♂ ♀.
Distribution: Kivu.
- C. sexfasciata* (Ulmer), 1904b: 421, figs 10, 11, 12 (wings, ♂ genitalia), as *Hydropsyche*. ♂ ♀.
Kimmins 1963: 131, figs 30–34 (wings, ♂ & ♀ genitalia); transfer to *Cheumatopsyche*.
Marlier 1961: 159, 175–177, figs 12A, B (wings, ♂ genitalia), places it in his new subgenus *Abacarioides*, which he describes here.
Gibbs 1973: *C. striata* Jacquemart is doubtfully distinct.
Distribution: Cameroons, Ethiopia, Kivu, Belgian Congo, Angola, Ghana, Gabon.
- C. simplex* Kimmins, 1963: 134–135, figs 40–44 (wings, ♂ & ♀ genitalia). ♂ ♀.
Distribution: Ethiopia.
- C. socia* (Navás), 1927: 213, fig. 9 (♂ genitalia), as *Hydropsychodes*. ♂ ♀.
Ulmer 1963: 258, 260, figs 4, 5 (♂ genitalia), description and transfer to *Cheumatopsyche*.
Distribution: Egypt.

- C. spinifera* (Jacquemart), 1966b: 43, 44, figs 8, 9 (wings, ♂ genitalia), as *Hydropsychodes*. ♂.
Distribution: Congo.
- C. striata* (Jacquemart), 1959: 125, figs 39–43 (wings & ♂ genitalia), as *Hydropsychodes*. ♂.
Gibbs 1973: doubtfully distinct from *C. sexfasciata* (Ulmer).
Distribution: Lake Albert.
- C. tectifera* Marlier, 1959: 115–117, figs 6–8 (wings, ♂ & ♀ genitalia). ♂ ♀.
Distribution: Sao Tomé Island, Gulf of Guinea.
- C. tenerrima* Marlier, 1961: 159, 180–186, figs 14, 15 (wings, ♂ genitalia, larval & pupal parts), larva and pupa described. Marlier left this species in *Cheumatopsyche sensu stricto* in this paper, but in his 1962b paper placed it in his subgenus *Ethiopsyche*. ♂.
Distribution: Kivu.
- C. thaba* Mosely, 1948: 70–71, figs 9, 10 (♂ genitalia). ♂.
Distribution: Yemen (South-west Arabia is regarded as a part of the Afrotropical Region).
- C. thomasseti* (Ulmer). 1931: 18, figs 16, 17 (♂ genitalia), as *Hydropsychodes*. ♂ ♀.
Kimmins 1960a: 263–265, figs 28–31 (♂ genitalia), fig. 71 (♀ genitalia); fig. 70, which he gave as ? *thomasseti*, he later transferred to *C. nubila* Kimmins (1963).
Distribution: South Africa (all Provinces), Angola, Rhodesia, South-west Africa, probably Kenya (larvae).
- C. triangularis* (Ulmer), 1931: 19, figs 18, 19 (♂ genitalia), as *Hydropsychodes*. ♂.
Kimmins 1960a: 275, figs 1–4 (♂ genitalia), figs 68, 69 (Probable ♀ genitalia).
Distribution: South Africa (Natal, Transvaal).
- C. trifida* (Mosely), 1935: 228, figs 11–13 (wing & ♂ genitalia), as *Hydropsychodes*. ♂ ♀.
Mosely 1939b: 27, transferred it to *Cheumatopsyche*.
Kimmins 1960a: 257–259, figs 5, 6 (♂ genitalia).
Distribution: Belgian Congo, Southern Rhodesia, Uganda.
- C. uncata* Kimmins 1957b: synonym of *C. lesnei* (Mosely), q.v.
- C. urema* Mosely, 1936: 436–437, figs 15–17 (♂ wings & genitalia).
Kimmins 1960a: 257, 265, figs 32–35, stated that *urema* might be a synonym of *thomasseti* (Ulmer).
Marlier 1961: 159 et seq., 165, fig. 4 (♂ genitalia) placed it in his newly erected subgenus *Cheumatopsychodes*.
Distribution: Kenya, Uganda, Kivu.
- C. villosa* (Navás), 1934d: 22–23, fig. 108 (♀ posterior wing), as *Hydropsychodes*. ♀.
Mosely 1935 commented that the ♀ hind wing hardly suggested the genus *Hydropsychodes*, with which I would agree.
Distribution: Africa.
- C. zuluensis* (Barnard), 1934: 360–362, fig. 37h–j, as *Hydropsychodes*. ♂ ♀.
Kimmins 1960a: 263, placed *zuluensis* in synonymy with *C. falcifera* (Ulmer).

Genus *HYDROMANICUS* Brauer 1865

Hydromanicus Brauer 1865: 420.

Type species *irroratus* Brauer. ♀. Java.

Hydromanicus Brauer; Ulmer 1907a: 168 (key to genera), 172, 173 (characters & species list); pl. 23, fig. 211 (wings).

Hydromanicus Brauer; Ulmer 1951: 226, 227, 275–281 (imagos).

Hydromanicus Brauer; Ulmer 1957: 388, 390 (larval & pupal keys).

Hydromanicus Brauer; Fischer 1963: 93, 94; 1972: 127.

Generic diagnosis (derived from Ulmer 1907a: 172 & 1951: 279):

In general this genus is very similar to *Hydropsyche*.

Imago: tibial spurs of ♂, ♀, 2.4.4, inner spurs longer than outer, tarsal claws usually smaller in ♂ than in ♀. Maxillary palpi with fourth segment clearly longer than third, fifth articulated. Head with large median wart and pair of large lateral warts; antennae little longer than fore wings in ♂, shorter in ♀, without spiral black line. Wings broad; forewing with apical forks, 1, 2, 3, 4, 5, discoidal and median cells closed; hind wing with apical forks 1, 2, 3, 5 (1 may be diminutive), discoidal cell closed, median cell open, M and Cu₁ well separated, with a clear crossvein between them. ♂ with large superior appendages and apically cleft tenth tergite; claspers (inferior appendages) two-jointed; copulatory organ prominent, large (lacking the long ventral endothelial lobe characterising Afrotropical species of *Hydropsyche*). ♀ mid-legs not widened.

The genus is not a very large one, mainly represented in India, Indonesia, the Far East and Borneo, with a single species in the Seychelles, hence its inclusion here.

Hydromanicus seychellensis Ulmer

Hydromanicus seychellensis Ulmer, 1910: 47–49, figs 11–14 (wings & ♂ genitalia). Mahé, Seychelles Islands. ♂ ♀.

Syntypes comprised 10 ♂♂, 5 ♀♀, divided between the Museums in Cambridge and London and Ulmer's private collection.

Hydromanicus seychellensis Ulmer; Marlier 1978b: 34–38, pl. 2, figs 12–27 (larva & pupa).

Distribution: endemic to the Seychelles Islands.

REMARKS

Ulmer's description of this species accords with his generic diagnosis, except that he neither draws nor mentions superior appendages in the ♂ genitalia, and although M and Cu₁ are clearly separate in the hind wing, they do lie close together. The ♂ genitalia are, however, very easily recognizable on account of the distinctive apical joints of the claspers, sharply pointed, blackened, and thickly clothed with dark setae. Length of ♂ forewing 7–7.8 mm, ♀ 8–10 mm.

H. seychellensis appears to be the sole Hydropsychid found on the Seychelles Islands, where Marlier (1978b) found it to be widespread and the commonest Trichoptera species. He found the larvae and pupae in all streams on the Island of Mahé, even slightly polluted ones, and also on the Island of Praslin. Marlier, who reported on the results of collections made both by himself, in 1976, and by Professor F. Starmühlner of the University of Vienna in 1974, recorded that the larvae were found under similar conditions to European species of *Hydropsyche*, also constructing wide-mouthed catching nets and building rigid pupal cases of pebbles and sand.

Distinguishing characters of imagos, larvae and pupae of this species as described in the literature have been used to separate *Hydromanicus* from other genera in the keys, together with generic characters used by Ulmer (1951). The keys are not, therefore, necessarily applicable to species of *Hydromanicus* from other parts of the world.

The larvae and pupae of *Hydromanicus* appear to be remarkably similar to those of *Hydropsyche*, though there are minor differences such as the proportions of the dorsal and ventral branches of the pre-episternum, number of metasternal gills and type of setation in the larva. The anal appendages of the pupa are simpler than those of *Hydropsyche*, lacking the two points seen there; presegmental dorsal plates on III–VIII; tracheal gills on II–VII, and ♂ antennae wound once round apex of abdomen. Length of *Hydromanicus* larva up to 15 mm, length of pupal exuviae 13 mm.

Reference should be made to Ulmer (1910) for description and figures of ♂ imagos, and to Marlier (1978b) for illustrated accounts of larva and pupa.

AFRICAN SPECIES OF *HYDROMANICUS*

- H. seychellensis* Ulmer, 1910: 47–49, figs 11–14 (wings & ♂ genitalia).
 Mahé, Seychelles Islands. ♂ ♀.
 Marlier 1978b: 34–38, pl. 2, figs 12–27 (larva & pupa).
 Distribution: Seychelles Islands only.

Subfamily DIPLECTRONINAE Ulmer 1951

Genus *SCIADORUS* Barnard 1934

- Sciadorus* Barnard 1934: 358 (key), 364 (diagnosis) (also metam.)
 Type species *acutus* Barnard (original designation).
 South Africa (Cape Province). ♂ ♀ larva, pupa.
Sciadorus Barnard; Scott 1975: 47, figs 8–13, 31, 32 (larva).
Sciadorus Barnard; Fischer 1963: 151, 1972: 154.

Generic diagnosis (amplified from Barnard 1934: 364):

Imago: tibial spurs of ♂, ♀, 2.4.4; anterior tarsal claws of ♂ normal. Maxillary and labial palpi relatively small, slender, the former with 1st segment short, 2nd, 3rd, 4th subequal, longer than 1st, 5th longest, articulated, the latter 3-segmented, 3rd segment longest, articulated. Head: vertex with very large paired posterior warts, anterior warts narrow strips, median wart inconspicuous, mid-cranial sulcus present, may be incomplete; eyes noticeably small, anteriorly placed, sparsely pubescent; antennae with flagellum slender, about length of forewings in ♂, shorter in ♀, with the serrated appearance usual in this subfamily. Forewing with apical forks 1, 2, 3, 4, 5 present, discoidal and median cells closed, forks 1 & 3 with long footstalks, Cu₂ and 1A meet at arculus; ♂ forewing 5–9 mm, ♀ slightly larger. Hind wing narrower than in *Diplectronella*, forks 2, 3, 5 present (occasionally a minute fork 1), discoidal cell closed, median cell open, Sc and R₁ entirely separate, united by cross-vein, little upturned at ends; fork 2 shortly stalked or sessile. Abdomen: 5th sternum (♂ & ♀) bears a pair of short, tubular ventrolateral filaments, each arising from an internal gland; two pairs of large, rounded, reticulated sacs present in ♂ only, opening on posterior margins of VI and VII and extending forward over two or more segments. Abdomen thicker than is usual in males, presumably due to presence of these organs. ♂ genitalia with tenth tergum bifid, copulatory organ large, apically truncate, claspers slender, two-segmented, apical segment small. Small lateral tufts sometimes present on pleura of II–VII. ♀ genitalia with sternal plates of VIII completely separate ventrally, as in *Cheumatopsyche*, and the usual two pairs of small papillae separated by a pair of small cerci; mid-legs not expanded, but fringed with setae in pupa.

This small genus is endemic to the Afrotropical Region, to date comprising two South African species, one from the West Cape, the other from the South-west and South Cape. A third, *S. sinuatus*, was described by Marlier (1943a) from the former Belgian Congo, but this should be transferred to the genus *Diplectronella* (see under Remarks below).

Sciadorus obtusus Barnard

(Figs 43–65, Tables V, VI)

Sciadorus obtusus Barnard, 1934: 366, fig. 39a-i (wings, ♂ genitalia, detail of abdomen, antenna etc.). Swartberg Range, South-west Cape. ♂.

Syntypes (♂) in collection of South African Museum.

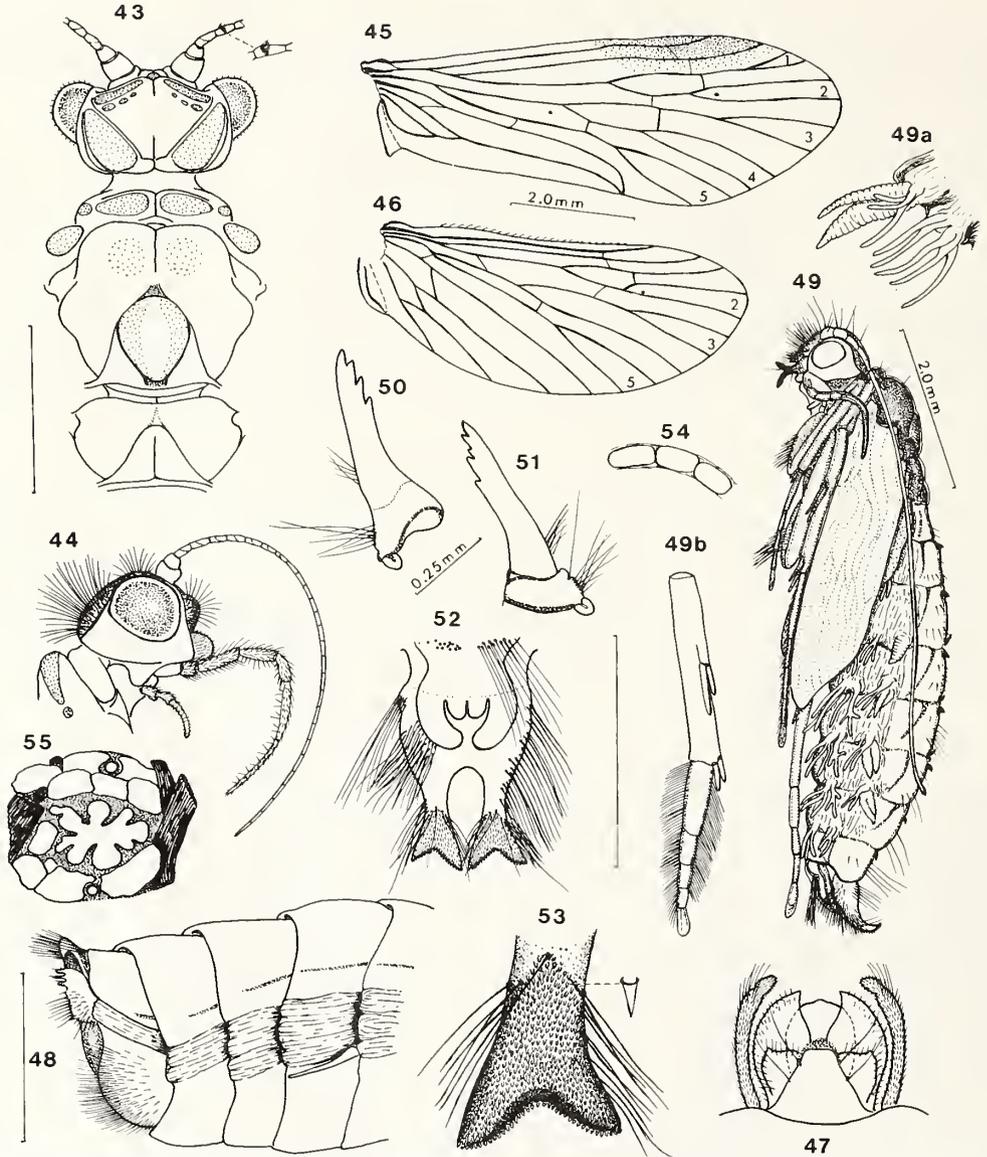
Distribution: South Africa: Cape Province (Swartberg Range, various streams, forest stream on Robinson Pass, Vet River on Garcia's Pass near Riversdale, Storm's River tributary and Blaauwkrantz River, all South or South-west Cape; also recorded by Jacquemart (1963a) from Upington on the Orange River (North Cape) and the Swartberg Pass (but see under Remarks).

DESCRIPTION OF IMAGOS (Figs 43–48)

Male imago (in spirit, Figs 43–47): (colour description from Barnard 1934: 364, 365 as his spirit material is old and faded); a medium-sized species, forewings 7–8.5 mm long, pale brown, veins darker, when fresh hyaline marks visible on distal cross-vein of discoidal cell, r-m cross-vein and M_{1+2} proximal to it, also on distal part of Cu_2 . Head, thorax and abdomen mainly brown, antennae brown, legs ochraceous. Vertex: a line of setate spots present, close behind each narrow anterior wart (not seen in *S. acutus*); mid-cranial sulcus present, incomplete. Lateral filaments on V no longer than segment, may be shorter, not easily seen. Easily separable from the other Cape species, *S. acutus*, by the shape of the 9th and 10th terga, larger size, darker colour and presence of lines of setate spots on vertex.

Female imago (in spirit, Fig. 48): Barnard had no females, larvae or pupae of this species, but all three are represented in the Albany Museum collection, which includes one good ♀ from a forest stream above the Storm's River Pass (SU 68, 25.IX.1959); it was together with two larvae of *S. obtusus*, and its size, locality and association with the larvae all indicate that it is the female of this species. There are also good ♀ pupae, evidently of the same species, from the Vet River, which were associated with an identifiable ♂ pupa, prepupal larvae and larvae (personally collected). The female imago is larger than the male (♀ forewing 10.2 mm in length), but is very similar in general appearance, colouring and wing venation. Head and thorax mainly dark brown, warts cream; abdomen mid-brown with lighter marks on dorsal side, pleura purplish, paired filaments on V not longer than segment, inconspicuous; legs ochraceous; palpi almost colourless, smaller than in ♂. Genitalia: IX almost entirely contracted within VIII, scarcely visible, though XI can be seen, with the usual small cerci and papillae; sternal plates of VIII rounded, brown, apices with blunter, shorter dorsolateral points than in *acutus*, hairy, completely separated ventrally.

Material available comprises Barnard's spirit specimens from the Swartberg Range (several males, mainly fragmented, including cleared abdomens showing genitalia and reticulated internal sacs), on loan from the South African Museum. Also 21 larvae, 9 prepupal larvae and 8 pupae (including 4 ♂ pupae, one good, fully mature, three immature, damaged, four good ♀ pupae, two mature, two immature) from the Vet River, Garcia's Pass, near Riversdale (MISC 306f, g); 22 larvae from the Ruitersbos Forest Station on Robinson Pass (MISC 282), all in the Albany Museum Collection. In addition one larva from the Blaauwkrantz Pass, and one good ♀ and two larvae from a forest stream with falls above the Storm's River Pass, collected by Dr H. Bertrand (also in the Albany Museum Collection).



Figs 43-55. DIPLECTRONINAE: *Sciadorus obtusus*, ♂, ♀, ♂ pupa. 43. ♂: dorsal view of head and thoracic nota, 44. ♂: lateral view of head and palpi, 45, 46. ♂: fore and hind wings (right), 47. ♂: dorsal view of genitalia, 48. ♀: lateral view of genitalia, showing process on abdomen V, 49. ♂ pupa: habitus; left appendages only shown, 49a. ♀ pupa: part of abdomen VI showing gill arrangement: gills spring from distal part of pleuron. Note that lateral branchial gills arise from base of conical gills, 49b. same: mid-leg showing swimming fringe, 50, 51. ♂ pupa: left and right mandibles, 52. same: apex of abdomen, ventral, 53. same: apex of left anal appendage further enlarged, 54. part of egg string from ♀ pupal case, 55. apex of ♂ pupal case showing meandrine opening and smaller lateral openings; larger surrounding stones omitted.

DESCRIPTION OF LARVA (Figs 56–65, Table V)

Mature larva (in spirit, Figs 56–65, Table V): length 13–14 mm, larvae large, similar to *Hydropsyche* in size, but with the characteristic Dipletronine head and thoracic nota. Sclerites dark brown in colour, almost black in life, with cream abdomen (in spirit abdomen turns pale purplish and sclerites fade somewhat); rough and setose in appearance.

Head (Figs 56, 57): rounded, without carina, frontoclypeal apotome very broad, widest in centre, with deep indentations opposite eyes, behind which it is strongly expanded; ventral side with very large anterior and posterior apotomes, together much longer than the mid-ventral ecdysial line; stridulatory files present, large, broadly oval, inconspicuous because same colour as genae, lines fine, even, close together. Dorsal side of head blackish to dark brown except for two small light patches on frontoclypeal apotome and pale areas round eyes; thickly set with short, dark, pointed setae. Eyes small, set well forward beneath clusters of cuticular lenses. Ventral side of head brown, mainly dark.

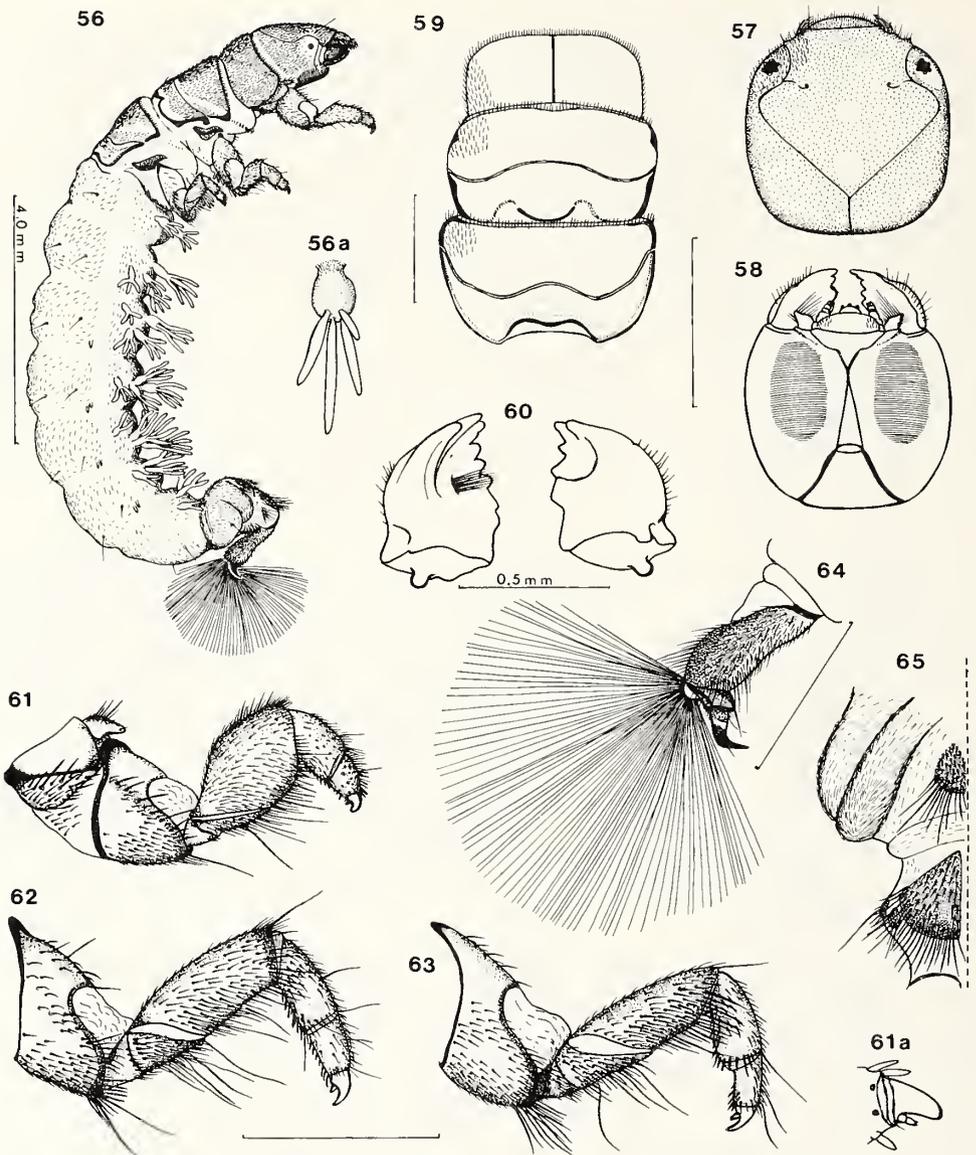
Mouthparts (Figs 58, 60): labrum rounded, sclerotized, dark brown, setose, frequently largely retracted, with thick lateral brushes of setae, anteclypeus membranous. Mandibles blackish, heavily built, strong, triangular in section, the left one with 3 apical and 4 lateral teeth, the proximal tooth bicuspid, and inner brush of bristles; the right mandible with 2 apical and 3 lateral teeth, the proximal tooth shelf-like; no lines of setulae on either mandible. Outer surface of both mandibles with a number of short setae. Maxillary palpi short, stout, five-segmented; labium short, thick, palpi minute. Submentum with rounded apex, it and stipites dark brown.

Thorax (Figs 56, 59): pro- and mesonota very dark brown, the latter paling slightly posteriorly, pronotum with thickened black posterior and lateral margins, thickly set with simple dark setae, metanotum paler brown; meso- and metanota pubescent, with black lateral margins and transverse lines where nota break at ecdysis, common to the Dipletroninae; both with sinuous posterior margins, each with a conspicuous median black mark. Pre-episternum simple, it and pleural sclerites dark brown, setose. Prosternal plate angled, light brown with darker marks; membranous parts of thorax cream with scattered dark setae; single mesosternal tracheal gill (Fig. 56a), two pairs of metasternal gills, the median pair close together but not joined.

Legs (Figs 61–63): forelegs stout, strong, dark to mid-brown, strongly setose, claws blunt with short blunt basal spine; scraper of stridulator on femur as usual. Mid- and hind legs less stout, light brown with darker markings, thickly fringed with strong dark setae; many of them sword-like; most other setae paler, less conspicuous, claws with stout basal spine, less blunt than foreclaws. Lightly feathered setae present on coxa, trochanter and tibia of foreleg and tibiae of mid- and hind legs.

Abdomen (Figs 56, 64, 65): cream in life, mauve-tinged in spirit; many short dark setae scattered over whole abdomen, those on venter very small, inconspicuous. Tufted tracheal gills present in four to six rows (see Table V). In this genus the gill filaments are few in number, usually 3–4 filaments (branches) per gill, occasionally 2 or 5. Minute conical lateral gills ('Zipfelkiemen' of Ulmer) on segments III (1), VI (2), V (2), VI (2). Sternum of segment VIII bears small pair of triangular sclerites set with yellow spines and fringed posteriorly with long dark setae, these sclerites are joined medially by a glabrous sclerotised area. Segment IX bears a pair of much larger triangular spine-clad sclerites on venter, a small pair of setose lateral sclerites and a larger pair of setose dorsolateral sclerites. Anal prolegs fairly long, with well-developed lateral sclerites and strong, plain claws, each leg terminating in a large fan of black setae. Five anal gills.

Earlier instars: few immature larvae were present in the material available; one of these appeared to be in the fourth instar, six in the third. These are briefly described below.



Figs 56–65. DIPLECTRONINAE: *Sciadorus obtusus*, mature larva. 56. habitus of mature larva, 56a. mesothoracic gill, further enlarged, 57, 58. dorsal and ventral views of head, 59. dorsal view of thoracic nota showing transverse ecdysial lines, 60. left and right mandibles, dorsal, 61. right foreleg, with pre-episternum, episternum & epimeron, 61a. foreclaw further enlarged, 62, 63. right mid- & hind legs, 64. right anal proleg, claw and brush, 65. ventral view of abdominal segments VIII & IX to show sclerites & setae.

SCOTT: HYDROPSYCHIDAE (TRICHOPTERA) OF SOUTHERN AFRICA WITH KEYS

Third instar: three larvae in the Vet River sample, one from the Blaauwkrantz River and two from the Storms River tributary. Length 5–7 mm, gill count as in mature larva, the gills on the whole longer relative to size of larva than in final instar, nearly all gills with one or two filaments per gill, occasionally three in ventral gills. Colour of head and nota varies from dark brown (Vet River) to mid-brown (Blaauwkrantz and Storms Rivers), light spots on head variable in intensity, not always easy to distinguish. Colour differences possibly attributable to altitude differences. Small conical gills absent. Anal setal fans very thin.

Fourth instar: single larva in sample from Vet River, much as final (fifth) instar in appearance; length 10 mm. All gills present, smaller than in final instar, with two to three branches. Conical gills present, minute, on segments III–VI. Colour markings on head etc. as in final instar. Anal fans thicker but not as dense as in final instar.

I would expect first instar larvae to lack tracheal gills entirely, second instar larvae to have the full number of gills found in later instars, those gills being simple and all or almost all unbranched.

TABLE V.

Number and position of tracheal gills in mature larvae of *Sciadorus obtusus* and *S. acutus* (right side, abdominal)

Segment no.	<i>Sciadorus obtusus</i>			<i>Sciadorus acutus</i>		
Thoracic gills	single (median)			—		
Mesosternal	2 pairs			3 gills (1 pair & 1 median gill with 2 stems)		
Metasternal						
Abdominal gills	DL	VL	V	DL	VL	V
I		1	1		1	1
II	1	2*	1	1	2	1
III	1	2	1	1	2	1
IV	1	2	1	1	2	1
V	1	2	1	1	2	1
VI	1	2	1	1	2	1
VII		1	2		1	2

*The figure 2 denotes that the gill has 2 main stems, either joined basally or contiguous within the same basal circle.

DL = dorsolateral gills: 2–3 filaments per stem.

VL = ventrolateral gills: 3–4 filaments per stem.

V = ventral gills: 4 filaments per stem as a rule.

Note: There are also very small simple conical gills (lateral) on segments III–VI, dorsal to the lateral line area (no visible lateral line). (See Fig. 56)

DESCRIPTION OF PUPA (Figs 49–53, Table VI)

Specimens available for study comprised 8 pupae together with their cases. Of these four were males (one good, mature, one fairly good, one very poor and one very immature), and four were females, two of them very good. All came from the Vet River on Garcia's Pass, and were collected in February, 1976. Of these, the good, mature male pupa proved to be *Sciado-*

rus obtusus Barnard, thus providing the correlation between larvae, ♂ and ♀ pupae and imago. Although none of the *Sciadorus* pupal cases contained larval sclerites, which is very unusual in Hydropsychidae, there was evidently only a single species involved, hence the possibility of correlation. The loss of larval sclerites from the pupal cases could well have been due to the large size of the terminal openings (Fig. 55) combined with pupal movements and fast flowing water.

Male pupa (pharate imago) (in spirit, Figs 49–53): length 7–7.5 mm, imago clearly seen through pupal pelt, mainly dark brown with cream warts set with long, dark brown setae, flattened beneath pelt; mesoscutum with two large patches of setae, mesoscutellum with long setae, antennae appearing serratulate even within the pupal pelt. Face of pupa with scattered dark setae and four clumps of setae just above labrum; labrum small, brown, oval, thickly set with dark, shorter setae; mandibles brown, strong, the left one with five apical and subapical teeth, the right with four. Maxillary and labial palpi as in imago, but pale, the labial palpi very small and inconspicuous. Forelegs and mid-legs with tufts of long dark setae on the coxae, mid-legs slightly flattened, with swimming setae; tibial spurs 2.4.4. Fore-, mid- and hind legs reach to distal end of abdominal segments II and V and apex of abdomen respectively. Wings (unexpanded in sheaths), dark golden brown, strongly setose, fore- and hind wings reaching to distal end of segments VII and VI respectively. Tufted gills, conical lateral gills and dorsal plates present on abdomen as shown in Table VI and Figs 49, 49a. Conical gills smaller than in *Diplectronella*, and ventrolateral branchial gills actually arise from proximal side of conical gills. Anal appendages shortly bifurcated, both apices curving to a point with a saddle between, outer point slightly shorter than inner; appendages apically strongly denticulate, set with short, heavy spines and long, strong, dark lateral setae. Both sexes with a small, inconspicuous pair of filaments on abdomen V, towards ventral side of pleura. Usual pockets enclosing male genitalia.

Female pupa (in spirit): length 7–7.5 mm, cases as in males. As male pupa, but gills larger and very clear and dorsal plates appear smaller though otherwise similar. One female had an egg string tangled up inside its case, a small part is shown in Fig. 54.

Pupal case: oval, about 9–10 mm long, strongly built, usually very shaggy in appearance, incorporating much vegetable matter (pieces of wood and charcoal) as well as sand grains (white quartz) and small rock fragments. Both ends have large, somewhat meandrine openings with silk flaps. No larval sclerites found within cases.

REMARKS

Comments on the genus *Sciadorus* Barnard and the two Cape species, *S. acutus* and *S. obtusus*, appear above. It may be noted here, however, that *S. obtusus* imagos differ from those of *acutus* not only in detail of genitalia and head warts, but also in size and colouring, being larger and much darker. The same applies to the larvae, which are larger, with almost black sclerites, but the simplest distinction is the possession by *obtusus* larvae of a single well-developed mesosternal gill (Fig. 56a) and two pairs of metasternal gills, whereas *acutus* larvae have no mesosternal gills and three metasternal, of which the median gill has two branches joined basally.

Jacquemart's record (1963a: 383, 384, Fig. 38A-D) of *S. obtusus* from the Orange River, Upington, has been omitted from the distribution of this species because his drawings appear to indicate two different taxa. He also recorded *S. obtusus* from the Swartberg Pass, S. W. Cape (altitude c. 1525 m), which is a known habitat of that species, and his Fig. 38D (genitalia, lateral) could be of *S. obtusus*, as could Fig. 38A, B (wings). Fig. 38C (genitalia, ventrodorsal) does not, however, appear to be *obtusus* and many well not be of a *Sciadorus* at all. This is a possibility as Jacquemart worked entirely from specimens already prepared and mounted on

TABLE VI.

Tracheal gills and dorsal plates of ♂ pupa of *Sciadorus obtusus* Barnard

Abdominal segment no.	Tracheal gills (right side)			Dorsal plates
	Lc	Lb	V	
I	—	—	—	
II		1	2*	Presegmental pair
III	(1)	1	2	Presegmental pair
IV	(2)	1	2	Postsegmental pair
V	(2)	1	2	Presegmental pair
VI	(2)	1	2	Postsegmental pair
VII	(1)	1	2	Presegmental pair
VIII	—	—	—	Presegmental pair

*2 indicates double tracheal gills, either with a common base or contiguous bases.

(1) Brackets indicate conical gills (lateral diverticula). (See Fig. 49a)

Lc = lateral conical gills.

Lb = lateral branchial gills.

V = ventral branchial gills.

slides so that a lateral and a "ventrodorsal" view could not be drawn from the same specimen. *Sciadorus* has small, slender claspers and simple genitalia lacking the long, spiny processes the drawing shows. The lower Orange River at Upington is not a known habitat for *Sciadorus*, which is usually confined to the upper reaches of fast-flowing mountain streams (see also under Biology).

S. sinuatus Marlier (1943a) was described as having longer lateral filaments on V than either of the Cape species, as long as in *Diplectronella*, and there appeared to be other resemblances to that genus. Study of imago kindly lent to me by Dr Decelle (Tervuren) revealed that the male abdomen lacked the large paired reticulated organs found in *Sciadorus* and *Diplectrona*, but not in *Diplectronella*, and that the wings were almost identical with those of *D. medialis* Marlier (also borrowed from Tervuren). A careful comparison was therefore made, and it is clear that *Sciadorus sinuatus* must in fact be transferred to the genus *Diplectronella*, becoming *D. sinuata* (Marlier) (Stat. nov.). *D. sinuata* is very similar to *D. medialis* Marlier, differing in a few minor details such as the position of some of the cross-veins in the wings and the shape of the apices of the tenth tergum in the ♂ genitalia. On that account I have left them as separate species for the present although it is possible they may prove to be synonymous should series of both species be studied.

The genus is said to resemble closely the genus *Diplectrona* apart from the usual absence of fork 1 from the hind wings. Their hind wings, however, also differ in shape, and in *Sciadorus* the apices of S_2 and R_1 are not strongly upturned as in *Diplectrona* and *Diplectronella*, and the lateral filaments on V are short, not long. The larvae and pupae also show consistent differences. Males of both *Diplectrona* and *Sciadorus* possess in the abdomen the large reticulated

organs the function of which is still obscure. These organs also occur in one or two other Dipteronine genera not found in Africa.

BIOLOGY

Little is known about the biology of *Sciadorus* species. Being endemic to the Cape Province and usually somewhat inaccessible they have not to my knowledge been reared in the laboratory or used in any experimental work. Field observations indicate that *Sciadorus* appears to be a high altitude genus, infrequently encountered in highlying, fast-flowing, clean cold streams, where the species occur higher up than *Cheumatopsyche* although there may be a small overlap. It is not possible to compare their distribution directly with that of *Hydropsyche* species, as that genus has not as yet been recorded from the same areas.

Barnard (1934) collected *S. acutus* from the West Cape (French Hoek and Hottentots Holland Mountains) between altitudes of 2 000 and 4 000 ft (610–1 220 m), *S. obtusus* from the Zwartberg Range, South-West Cape, between 3 000 and 5 000 ft (915–1 525 m). Streams at such levels are highlying and fast-flowing, often torrential, the mountains themselves rising from the coastal plain. The Albany Museum material of *S. obtusus* was collected from the South-West Cape mountains at altitudes of 500–600 m, in similar streams, where it was the only Hydropsychid present. Bertrand's specimens from the Blaauwkrantz River (at 180 m) and Storms River tributary (no altitude given) were, however, found much lower down. This can probably be explained by the fact that both are "drowned rivers", their original estuaries and lower reaches now lying submerged beneath the sea, as is the case with all the rivers in that part of the South-West Cape. The Storms River specimens were taken together with a single larva of *Cheumatopsyche afra*.

On the Robinson Pass *S. obtusus* larvae were taken from strongly flowing water in a forest stream, from the outer face of a weir and from adjacent rock faces. There they had built thick-walled, rather untidy shelters incorporating much vegetable matter such as twigs and charcoal fragments as well as sand grains. Attached to each shelter, facing full into the current, was a neat, coarse-meshed, wide-mouthed catching net, attached to the rock on one side, often by means of a line of small stones, and held open and reinforced laterally and along the outer edge by bundles of twiglets bound together by silk secretion. Within this shelter lay the sturdy, powerfully built larva, usually facing upwards and into the current. The posterior exit was surrounded by a double or treble ring of stones, cemented together and smoothed over with secretion. Gut contents included many insect sclerites and some detritus, indicating that the larvae are undoubtedly predators. The shelters were unusual in that some also contained a walled-off compartment filled with detritus, possibly simply sealed off with silk when much extraneous material had accumulated, perhaps at a time of low flow. Some shelters contained half-eaten prey, such as Corixid bugs.

The Garcia's Pass specimens came from a small fast flowing mountain stream near the summit, on a rocky bush-covered hillside. The shelters and nets were of similar type to the others, but incorporated a higher admixture of charcoal blocks, probably reflecting a recent mountain fire.

The larvae pupate in stout cases of the same materials as the larval shelters, with a thick soft lining, affixed to the rock and with rather large terminal openings, meandrine and guarded by silken flaps (flaps closed in early prepupal case, later ones and pupal cases open). The openings are evidently large enough to allow the larval sclerites to escape with the water flowing through during ventilation. Mature pupae were found in February (late summer), together with mature larvae and prepupae, so emergence could well have continued into the autumn. Bertrand's female imago was taken in late September (spring), and Barnard's males in November and February (late spring and summer), as were his *S. acutus* (possibly a function of collecting dates rather than of life cycles). At any rate it would appear that these species probably

emerge during the spring, summer and autumn months, no doubt overwintering as young larvae.

AFRICAN SPECIES OF *SCIADORUS*

- S. acutus* Barnard, 1934: 364–366, fig. 39j-n (♂, ♀ genitalia, larval head). ♂ ♀ metam.
Distribution: South Africa (West Cape).
- S. obtusus* Barnard, 1934: 366, fig. 39a-i (♂ wings, genitalia, antenna, ventrolateral process on abdomen V, internal vesicles). ♂.
Distribution: South Africa (South-West Cape).
- S. sinuatus* Marlier, 1943a: 11, 12, fig. 7 (♂ genitalia). ♂ (♀ not described). Distribution: Congo (Albert National Park).
Transferred to *Dipletronella* in this paper, as *D. sinuata* (Marlier).

Genus *DIPLECTRONELLA* Ulmer 1928

Dipletronella Ulmer 1928: 317.

Type species *Hydropsyche taprobanes* Hagen (selected by Fischer 1963: 150).

Dipletronella Ulmer; Mosely 1931: 195, 196 (discussion and redefinition of genus).

Dipletronella Ulmer; Marlier 1962b: 140–142.

Dipletronella Ulmer; Fischer 1963: 150, 151, 1972: 153.

Generic diagnosis (based on Mosely 1931, Marlier 1962b, Ulmer 1951):

Imago: tibial spurs of ♂, ♀, 2.4.4, claws normal. Maxillary palpi with 1st segment short, 2nd longer, dilated, with tuft of setae on truncate apex (inner side), 3rd and 4th progressively shorter, 5th about as long as rest together, articulated. Labial palpi 3-segmented, 3rd longest, articulated. Vertex with fairly large bean-shaped anterolateral warts, posterior warts larger, oval, median wart clear; eyes strongly hairy. Antennae fairly short, thick, of usual *Dipletronina* type, each segment with short spines or setae and slight dilatation, giving the antenna a serrated appearance (Fig. 67). Forewing with apical forks 1, 2, 3, 4, 5, discoidal and median cells closed, forks 1 and 3 stalked; wing apically broad, apex obliquely truncate; subcosta and radius much thickened from base to cross-vein; length about 7–11 mm. Hind wing very broad, lower margin almost semicircular, forks, 2, 3, 5 present, occasionally a small fork 1 (very small *cf.* with that in *Dipletrona*); discoidal cell closed, median cell absent; subcosta elbows downwards nearly meeting radius near apex of wing, so may appear to form a false fork; cubitus often pigmented. Venation sometimes variable. Abdomen: 5th sternum (♂ & ♀) bears a long pair of ventrolateral filaments, reaching apex of abdomen in ♂, to mid-VI in ♀; each arises from an internal gland. No large internal vesicles such as characterize ♂ *Dipletrona* and *Sciadorus*. ♂ genitalia with tergum of X forming a pair of large, apically pointed lobes, each bearing a setose lateral boss; between them lies a smaller pair of slender lobes; copulatory organ dilated at apex to form a cup-like depression containing four stylets (*cf.* Fig. 78), lateral to which is a pair of small erectile lobes; claspers long, two-segmented, basal part long, apically thickened, apical part shorter (but much longer than in *Sciadorus*). ♀ genitalia with sternal plates of VIII separated to base and the usual small cerci and papillae; mid-legs not expanded.

Diplectronella medialis Marlier

(Figs 66–87, Tables VII, VIII)

Diplectronella medialis Marlier, 1961: 159, 191–197, figs 19–20 (wings, larval parts). ♂ ♀. Kivu, Belgian Congo.

Type material in Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

D. medialis Marlier; 1962b: 140, 142, figs 76, 79 (larval & pupal parts).

Distribution: Belgian Congo (Kivu); Zaïre (River Kalengo).

NOTE: The material described below was very kindly sent to me on loan by Dr Decelle of the Musée Royal de l'Afrique Centrale at Tervuren, and forms part of that originally described by Dr Georges Marlier (1961, 1962b). It comprised 3 male, 2 female imagos in spirit, ♂ parts on slides, 6 larvae and a male pupa. In addition I had a few *Diplectronella* larvae collected by Dr J. O. Young in Kenya, which were useful for comparison; they could well have been of *D. afra* Mosely.

DESCRIPTION OF IMAGOS (Figs 66–73)

Male imago (in spirit, Figs 66–71 and *cf.* 78): (colour description from Marlier 1961); a medium-sized species, forewings (both sexes) 7.5–9.5 mm, membrane brownish-yellow, venation distinct, hyaline mark on r–m cross-vein; insect generally brownish-yellow in colour, head yellowish, warts paler. Vertex with clear median wart, bean-shaped anterolateral warts and large, oval posterior warts, mid-cranial sulcus clear, complete; a pair of conical tubercles on vertex. Lateral filaments on V long, reaching end of VIII. Marlier remarks that the genitalia are very similar to those of *D. afra* Mosely, but does not illustrate them, separating the two species on the basis of forewing venation, particularly the position of the r–m cross-vein in relation to that closing the median cell, which in *D. medialis* is in fact very similar to that in *D. indica* Mosely (1931) from India. The male genitalia are figured here (Figs 70, 71) and show the pubescent median processes of X.

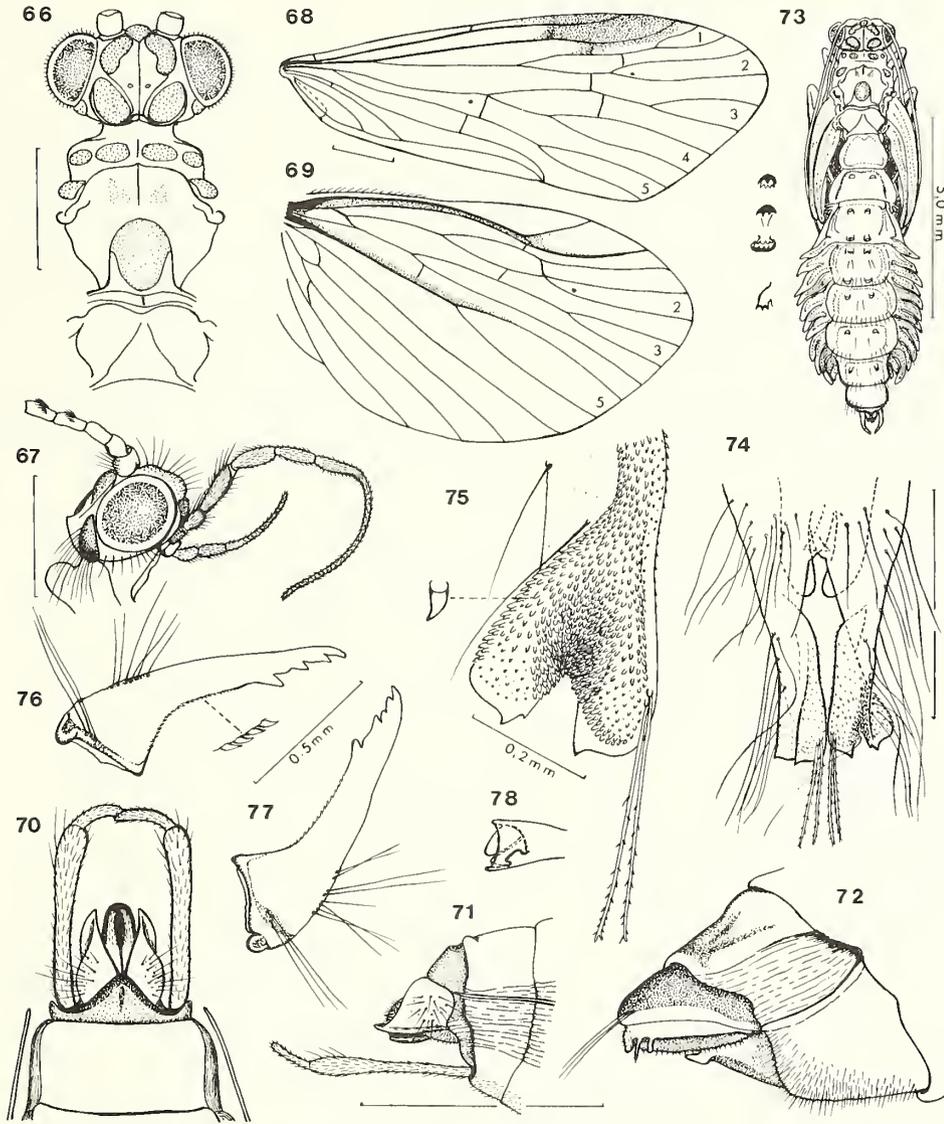
Female imago (in spirit, Fig. 73): as male in colour and general appearance. Lateral appendages of V shorter than in ♂, reaching to middle of VI. Genitalia: IX not retracted within VIII, XI with usual small cerci and papillae; sternal plates subrectangular, subgenital plate with prominent terminal lip, downturned in lateral view.

DESCRIPTION OF LARVA (Figs 79–87, Table VII)

Mature larva (in spirit, Figs 79–87, Table VII): length 16–18 mm, larvae fairly large, of typical Diplectronine type, with transverse ecdysial lines on meso- and metanota, and frontoclypeal apotome which widens behind eyes, though less so than in *Sciadorus*; abdomen rough in appearance due to presence of small setae and minute scales. Sclerites pale brown, abdomen yellowish. Although the larva is quite strongly setose it appears much less so than *Sciadorus* as the setae are pale brown in colour and inconspicuous. There are few anal setae, not forming a fan.

Head (Figs 79–81): oblong, brownish with paler patches as indicated, without carina, frontoclypeal apotome about as broad behind eyes as in front; anterior and posterior ventral apotomes fairly large, but together shorter than ventral ecdysial line; head thickly set with both blunt and pointed setae. Stridulatory files present, shortly oval. Eyes small, set well forward under usual cuticular lenses.

Mouthparts (Figs 80–82): labrum semicircular, yellowish brown, finely setose with large lateral brushes, anteclypeus membranous. Mandibles brown, triangular in section, setose on outer side; left one with two large apical teeth, between these a smaller tooth, four lateral teeth (one on dorsal side) and an inner brush of setae; right mandible with one apical and four



Figs 66-78. DIPLECTRONINAE: *Diplectronella medialis*, ♂, ♀, ♂ pupa. 66. ♂: dorsal view of head and thoracic nota, 67. ♂: lateral view of head and palpi, 68, 69. ♂: fore and hind wings (right) (from 2 individuals, hence hind wing relatively larger than forewing), 70, 71. ♂: dorsal and lateral views of genitalia, showing apices of processes on abdomen V, 72. ♀: lateral view of genitalia, 73. ♂ pupa: habitus (dorsal), left dorsal plates of segment II (presegmental), III (pre- & postsegmental), VI (presegmental) shown further enlarged; apical parts of exuviae removed, 74. same: apical part of exuviae (dorsal view), from slide, 75. same: apex of right anal appendage further enlarged (ventral view), 76, 77. same: left and right mandibles; part of dentate margin shown further enlarged. *Diplectronella sinuata*, ♂: 78. Apex of copulatory organ (right lateral view) showing cup-like tip containing 2 pairs of stylets (of which 2 are visible), also small erectile lateral lobe.

lateral teeth, no inner brush; a line of setulae on the dorsal tooth or teeth in both mandibles. Maxillary palpi short, thick, five-jointed, much as in *Sciadorus*. Submentum with rounded apex, slightly concave anteriorly, pale brown.

Thorax: (Fig. 79): thoracic nota brownish with narrow black margins as indicated, set with small brownish setae, again including both blunt and pointed types. Pre-episternum simple, setose, pro-epimeron wraps round base of foreleg. Prosternal plate stout, brown anteriorly, blackish posteriorly, angled as in *Sciadorus*. One pair of mesosternal gills, three metasternal gills (coxal pair and single two-stemmed median gill).

Legs (Figs 83–85): foreleg stout, mid- and hind legs longer and more slender than in *Sciadorus*, brownish, densely setose, but setae pale and inapparent except under compound microscope; foreleg with plumose setae on coxae, trochanter and femur; mid- and hind legs with feathered setae on femora, tibiae and tarsi. A scraper is present on the fore-femur, as in many other hydropsychids, but is not easily seen as it projects inwards; it is clear in ventral view, forming a small triangular projection.

Abdomen (Figs 79, 86, 87): tufted tracheal gills present in four rows (see Table VII). Gills clear, with more filaments than in *Sciadorus*, usually 7–12 per gill stem. Small conical lateral gills (“Zipfelkiemen”) present on segments III (1), IV (3), V (3), VI (3) and VII (3), larger

TABLE VII:

Number and position of tracheal gills in mature larvae of *Diplectronella medialis* (right side, abdominal)

Segment no.	<i>Diplectronella medialis</i>	
Thoracic gills		
Mesosternal	1 pair gills	
Metasternal	1 pair coxal gills, single median gill	
Abdominal gills	VL	V
I	1	1
II	2*	1
III	2	1
IV	2	1
V	2	1
VI	1	1
VII	—	—

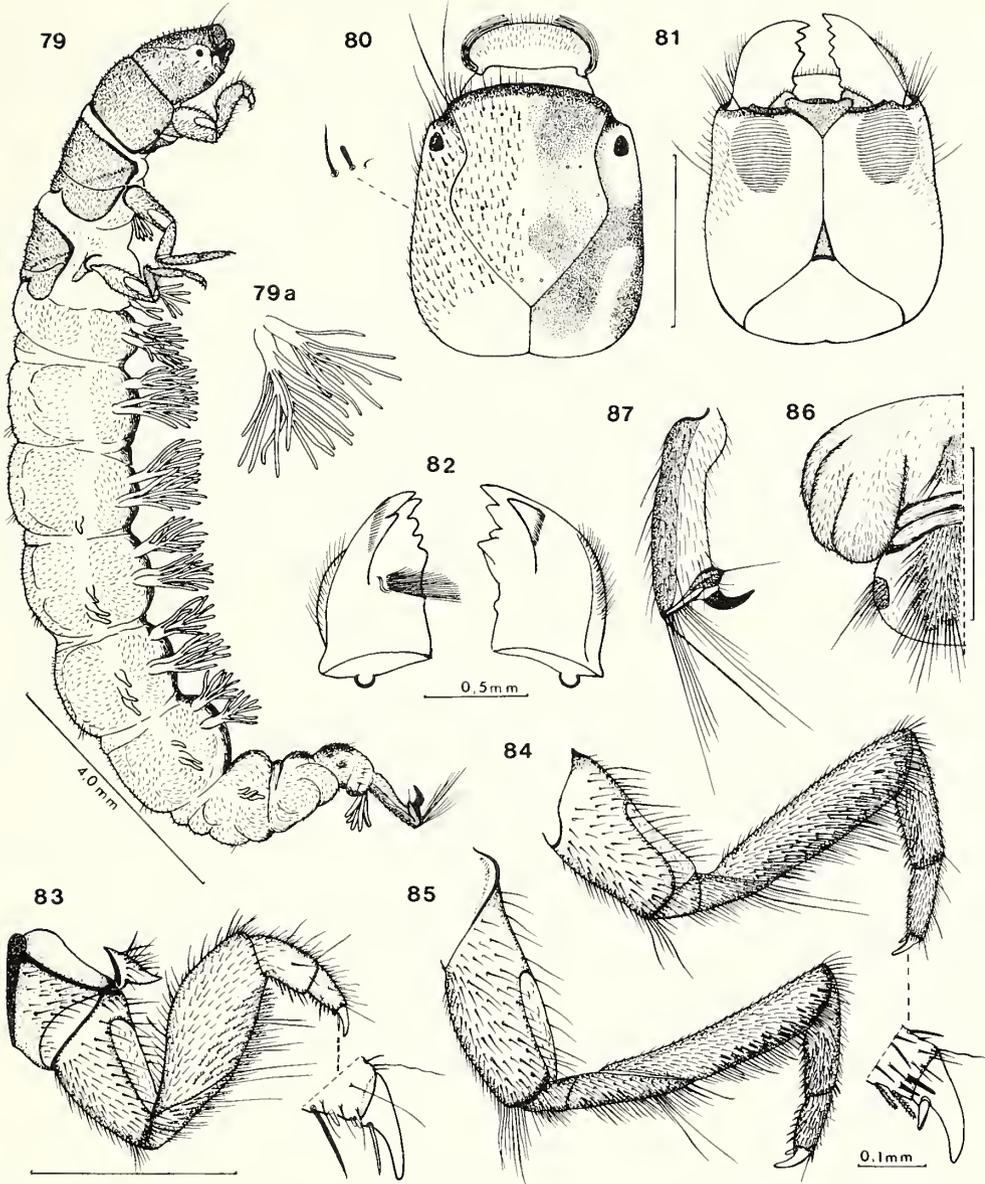
2*: denotes that the gill has 2 main stems, joined basally. Tracheal gills bushy, with 7–12 filaments per stem, roughly in whorls.

VL = ventrolateral gills.

V = ventral gills.

Dorsolateral gills are absent in this genus in contrast to *Sciadorus*.

Note: The conical lateral gills on the pleural area of *Diplectronella* larvae are conspicuous and much larger than in *Sciadorus*, occurring on segments III–VII (see Fig. 79).



Figs 79-87. DIPLECTRONINAE: *Dipletronella medialis*, mature larva. 79. habitus, lateral (right appendages only shown), 79a. ventrolateral gill (double) of segment III, spread out & enlarged, 80, 81. dorsal & ventral views of head; dorsal view shows colour pattern on right half, setation on left, types of setae further enlarged, 82. left & right mandibles, dorsal, 83, 84, 85. right foreleg, mid- and hind legs, foreleg with pleural sclerites; foreclaws and mid-claws further enlarged, 86. ventral view of abdominal segments VIII & IX showing sclerites & setae, 87. right anal proleg, lateral.

than in other genera so far described. Sternum of VIII with a pair of small sclerites each bearing a few stout setae, apparently joined medially by a very lightly sclerotized area. Sternum of IX has larger paired patches of spine-like setae, not confluent medially, and a pair of small lateral setate sclerites, but no dorsal ones. Anal prolegs with pale brown lateral sclerites and a few terminal setae, no fans; anal claws plain, strong; five anal gills.

DESCRIPTION OF PUPA (Figs 73–77, Table VIII)

A good male pupa was kindly made available to me for study by Dr Decelle; the following description was based on it and compared with Marlier's own account. A few larval sclerites accompanied the pupa. The anal appendages and mandibles had been removed and mounted on a slide.

Male pupa (pharate imago) (in spirit, Figs 73–77): length about 11 mm, imago clearly visible through pupal pelt. Antennae clearly serratulate even through pelt, short, thick, about 5/6 body length. Labrum rounded, with pair of strongly setose lateral protuberances and median area; mandibles slightly bowed, each with several setae on outer side, inner margin appearing finely serrated due to presence of blade-like spinules; left mandible with four apical and subapical teeth, right with five. Maxillary and labial palpi large, clear. Wings (unexpanded) short, just over half body length. Abdomen with anterior dorsal plates on segments II–VII, posterior dorsal plates on III and IV; lateral gills very large and prominent, including ventral tufted gills and conical, branched, pouch-like lateral gills (see Table VIII). Genitalia relatively small, clear (Figs 70, 71). The anal appendages are forked, apices broadly squared (not sharply pointed);

TABLE VIII:

Tracheal gills and dorsal plates of ♂ pupa of *Diplectronella medialis* Marlier

Abdominal segment no.	Tracheal gills (right side)		Dorsal plates
	Lc	V	
I	—	—	—
II	(1)	1	Presegmental pair
III	(3)	2*	Presegmental pair Postsegmental pair
IV	(3)	2	presegmental pair postsegmental pair
V	(3)	2	presegmental pair
VI	(3)	1	presegmental pair
VII	(3)	—	presegmental pair
VIII	—	—	—

*2 indicates double tracheal gills, either with a common base or contiguous bases. Tracheal gills are bushy, with about 20 long, fine filaments per double gill.

(3) Brackets indicate conical pocketlike gills (lateral diverticula); these are large, long and prominent.

Lc = lateral conical gills (1–3 pockets superimposed).

V = ventral branchial gills.

There are no lateral branchial gills as in *Sciadorus*.

apices densely covered (particularly on ventral side) with strong, closely set denticles, a few long lateral setae present, also a pair of long, stout, shortly feathered setae on the inner side of each appendage (Figs 74, 75).

Pupal case: an oval case made of small stones affixed to the substrate.

REMARKS

Mosely (1931) states that the paired ventrolateral filaments on the abdomen arise from segment IV, but this is an error, as they definitely arise from segment V (Marlier 1961 and personal observation).

Marlier (1962b) mentions "three species of *Diplelectronella* in Africa"; I only know of two, however, namely *D. afra* Mosely (1931) and his own *D. medialis* (Marlier 1961, 1962b). Marlier's *sinuata* of course makes a third, but that was regarded at the time of his writing as a species of *Sciadorus*. He notes that the genus *Diplelectronella* appears to occur only in small localized populations, remarking that the resulting inbreeding may be the cause of the aberrations in wing venation known to occur in this genus (1961 p. 193).

As indicated under "Remarks" on the genus *Sciadorus*, *S. sinuatus* Marlier (1943a) is in fact a species of *Diplelectronella*, as is evidenced by the general appearance of the imago and more particularly by the shape of the hind wings and their venation, the head warts, the ♂ genitalia and the length of the lateral appendages on V. Most of these points (and others) will be clearly seen on comparison of the figures for the two genera, as *D. sinuata* is very similar to *D. medialis*. The acid test is, however, the possession of large paired reticulated internal organs by the ♂ of *Sciadorus* (and *Dipletrona*) and not by *Diplelectronella* males.

BIOLOGY

Marlier (1962b) commented that *Diplelectronella* larvae lived in cold, clear running water, on stony bottoms in highlying streams or cascades, being found in small numbers in crevices between stones where they wove their silken nets. Larvae collected had been feeding on vegetable matter (débris of higher plants) and on small crustaceans (*Darwinula* sp., Ostracoda) (Marlier 1961). Known African species are mountain dwellers, living almost entirely at high altitudes in Central Africa; the lowest found was at 950 m (over 3 000 ft).

Little else was known about their biology until the publication of Statzner's work on the emergence of Trichoptera imagos from a Central African stream, the Kalengo, which flows from the highlands of Zaïre into Lake Kivu (Statzner 1976). From his studies it became clear that *Diplelectronella medialis* imagos, male and female, emerged throughout the year (though occasionally only one sex was taken). Numbers were always low, from one or two to a maximum of eighteen, and (at least from September to February) males were somewhat more numerous than females. Statzner calculated the numbers collected twice monthly, the total numbers of both sexes and their dry weight, and gave the percentages of females to males and of total dry weight of *D. medialis* to dry weight of the whole catch. These are listed below (extracted from Statzner 1976, using his figures for the period April 1972–March 1973 inclusive). The numbers given had been extrapolated to cover days when no collecting was done.

Diplelectronella medialis Marlier

Total ♂♂	Total ♀♀	♀%	%Abundance	Dry wt♂	Dry wt♀	%, Total dry wt
184	85	31,6%	2,56%	372,97 mg	277,70 mg	14,08%

Statzner (1976) also contributed to a knowledge of their food, since he found that *D. medialis* larval guts contained parts of Trichoptera, Diptera and water mites as well as plant

material. Life cycles appeared to take roughly four months, which would give three peaks of emergence during the year in a tropical climate. The actual peaks on the graph (Fig. 21), occurred in October and February of 1972 (both in the rainy season) and June, July of 1973, in the dry season (the sampling was not continued beyond July). Statzner suggested that the factor controlling emergence was neither rainfall nor phases of the moon nor waterlevel (the latter did not decrease in the Kalengo during the dry season), but changes in light intensity, which occurred at the beginning and end of the dry season. Emergence values as counted, might have been affected by the fact that breeding and egg-laying could take place in the emergence house, which was sited over a portion of the river.

AFRICAN SPECIES OF *DIPLECTRONELLA*

D. afra Mosely, 1931: 202–205, figs 10–13 (♂ wings & genitalia). ♂.

Uganda: Kampala.

Distribution: Uganda (Kampala, Ruwenzori), Ethiopia.

D. medialis Marlier, 1961: 159, 191–197, figs 19, 20 (wings & larval parts). ♂ ♀.

Belgian Congo: Kivu. Larva also described.

Marlier 1962b: 140–142, fig. 79 (pupal parts); further description of adults, larvae and pupae.

Distribution: Congo (Kivu), Zaïre (River Kalengo).

D. sinuata (Marlier), 1943a: 11–12, fig. 7 (♂ genitalia), as *Sciadorus*. ♂ ♀.

Belgian Congo.

Transferred in the present paper to *Diplectronella*.

Distribution: Belgian Congo.

May prove to be synonymous with *D. medialis* Marlier; see discussion under "Remarks" on *Sciadorus*.

Genus *DIPLECTRONA* Westwood 1840

Diplectrona Westwood 1840: 49

Type species: *Aphelocheira flavomaculata* Stephens 1836 *nec* Pictet 1834, syn. of *felix* McLachlan (original designation). Europe, North Africa.

Diplectrona Westwood; Ulmer 1957: 329, 331, 414 (larva and pupa).

Diplectrona Westwood; Wiggins 1977: 102, 103, figs A-G (larva).

Generic diagnosis (based on Mosely 1939c, Mosely & Kimmins 1953, Ulmer 1951, Schmid 1980 and others):

Imago: tibial spurs of ♂, ♀, 2.4.4, anterior tarsal claws of ♂ normal. Maxillary palpi with basal segment short, second, third and fourth long (second being longest), fifth articulated, scarcely as long as rest together. Head: warts on vertex of usual *Diplectronine* type, two large pairs present, posterior ones largest; antennae slender, about length of forewings, distal segments slightly inflated in middle, appearing serrated. Forewing short, broad, with apical forks 1, 2, 3, 4, 5; 1 and 3 having long footstalks, discoidal cell short, closed, median cell longer, closed, thyridial long, narrow, Cu₂ and 1A meet, or almost meet, at arculus. Hind wings shorter, broad, blunt, with forks 1, 2, 3, 5 (1 being large), discoidal cell closed, median open, R₁, and often Sc, strongly curved upwards near apices to meet costa, in both fore and hind wings. Abdomen: fifth sternum bears a pair of very long, slender ventrolateral tubular filaments, each arising from an internal gland (these glands being larger in the ♂ than in the ♀); the filaments may reach beyond the end of the abdomen. Within the abdomen in the ♂ there are also two pairs of large, rounded reticulate, internal sacs, opening on the posterior margins of VI and VII, and

frequently extending over two or more segments (usually four sacs, but number varies according to species). ♂ genitalia usually with dorsal plate of X divided into two or more lobes. Claspers with long, stout basal segment, short, narrower apical segment. Phallic apparatus large, simple. ♀ genitalia of usual Diplectronine type, sternal plates of VIII separated to base, mid-legs not widened.

The genus occurs in North Africa, *Diplectrona felix* McLachlan having been recorded from there, but nowhere in the Afrotropical Region. It does not occur in the Neotropical Region either, but is widespread in the Northern Hemisphere and Australian Region.

Diplectrona felix McLachlan

Diplectrona felix McLachlan 1878: 376, pl. 40, figs 1–9. ♂ ♀. Britain, France, Guernsey.

Diplectrona felix McLachlan; Gauthier 1928: 26. North Africa.

Diplectrona felix McLachlan; Mosely 1939c: 194, figs 411–415. ♂ ♀. (Wings and genitalia).

This is a European species whose distribution extends into North Africa, which forms part of the Palaearctic Region, not the Afrotropical. Should further information about it be required, Fischer (1963 and 1972) gives many references, including ones to the larval and pupal stages.

REMARKS

Larvae of this genus are excellently illustrated and described in Wiggins (1977). Characters distinguishing them from *Sciadorus* and *Diplectronella* will be found in the keys at the beginning of the present paper. The larvae are typically Diplectronine in shape of head, frontoclypeal and ventral apotomes and in method of ecdysis by rupture of transverse ecdysial lines on the meso- and metanota. Meso- and metasternal gills are present, and the larvae have four rows of tracheal gills on the abdomen, most ventrolateral ones being double, as have *Diplectronella* larvae. *Sciadorus* has six, most ventrolateral ones also being double, and there are dorsolateral gills in addition to the others. Older larvae in all three genera possess in addition the smaller conical lateral gills termed by Ulmer "Zipfelkiemen".

Diplectrona larvae inhabit small, cool swift-flowing streams, often in vegetation, constructing shelters and catching nets in the usual way. Their normal life cycle appears to be one year, and swarming adults have been observed in August (Edington & Hildrew 1981).

AFRICAN SPECIES OF *DIPLECTRONA*

D. felix McLachlan, 1878: 376, pl. 40 figs 1–9. ♂ ♀. Britain, France, Guernsey.

Fischer 1963: 142–145, 1972: 148, 149.

Gauthier 1928: 26. North Africa (Algeria, Tunisia).

Mosely 1939c: 194, figs 411–415 (♂ wings & genitalia). Britain.

Tobias 1972: 395, figs 158–161 (Genitalia). ♂ ♀.

Lestage 1921: 544–546, fig. 183a-i (larval & pupal parts).

Distribution: Europe, North Africa.

Subfamily MACRONEMATINAE Ulmer 195

Genus *MACROSTEMUM* Kolenati 1859

Macrostemum Kolenati, 1859: 168, 239.

Type species *Macronema hyalinum* (Pictet) (described as *Hydropsyche*), mentioned by Ulmer 1957: 339 as one of Kolenati's two *Macrostemum* species; selected by Fischer (1963: 176). (For description of *M. hyalinum* see Ulmer 1907d: 75, 76, fig. 78 & col. pl. III figs 15, 16 ♂ imagos.)

Macrostemum Kolenati; Barnard 1934: 372, key to South African species and varieties (as *Macronema*): larva (as *Chloropsyche*?), p. 368 & figs 40h-1.

Macrostemum Kolenati; Wiggins 1977: 110-111, figs 6.8A-E (larva), as *Macronema*.

Macrostemum Kolenati; Flint & Bueno-Soria 1982: 358-9, 367-369, resurrection of name *Macrostemum* for their second group of *Macronema* species (for reasons see under Remarks below).

Generic diagnosis (derived from Flint & Bueno-Soria, 1982, and other sources and checked against all other African species as far as descriptions and figures allow, as well as some from other regions; diagnosis is applicable to African species but not necessarily to those from elsewhere).

Image: tibial spurs of ♂, ♀, usually 2.4.4, sometimes 1.4.4, apical spurs on foreleg sometimes small but always present. Antennae very long, threadlike, twice to thrice forewing length in ♂, shorter in ♀. Maxillary palpi well developed, labial palpi relatively small. Head: vertex with large pair of anterior warts, sometimes a median wart, small posterior pair. Forewing elongate, rounded at apex, rarely pubescent (if so, setose not scaly), usually translucent, shining, membrane often brightly patterned; discoidal and median cells present, closed, discoidal cell small but not minute, median cell larger than discoidal, thyridial cell very long, costal cross-veins may be present, Sc united to R₁ shortly before reaching wing margin; forks 1-5 present (occasionally only 1-4 in ♂, or a false 5 present). Hind wing hyaline, sometimes iridescent, shorter than forewing, broad, anal portion much widened in ♂, less so in ♀, folded, discoidal and median cells absent, forks 1, 2, 3, 5 or 2, 3, 5 present; costal margin excised before apex, partially bordered with hooked macrotrichia. Length of forewing 9-21 mm, in ♀ less (♀ usually smaller than ♂). Fifth abdominal sternum bears a pair of short filamentous appendages in males, each arising from an internal gland, not present in females. ♂ claspers two-segmented, tenth tergum elongate, usually simple, lacking additional lobes or processes, tip of copulatory organ bulbous without special structures.

The genus *Macrostemum* as defined and delimited by Flint & Bueno-Soria (1982) still remains a large and widespread one of almost world-wide occurrence; it is not, however, found in Europe.

Macrostemum capense (Walker)

(Figs 88-113, Tables IX, X, histogram Fig. 214B)

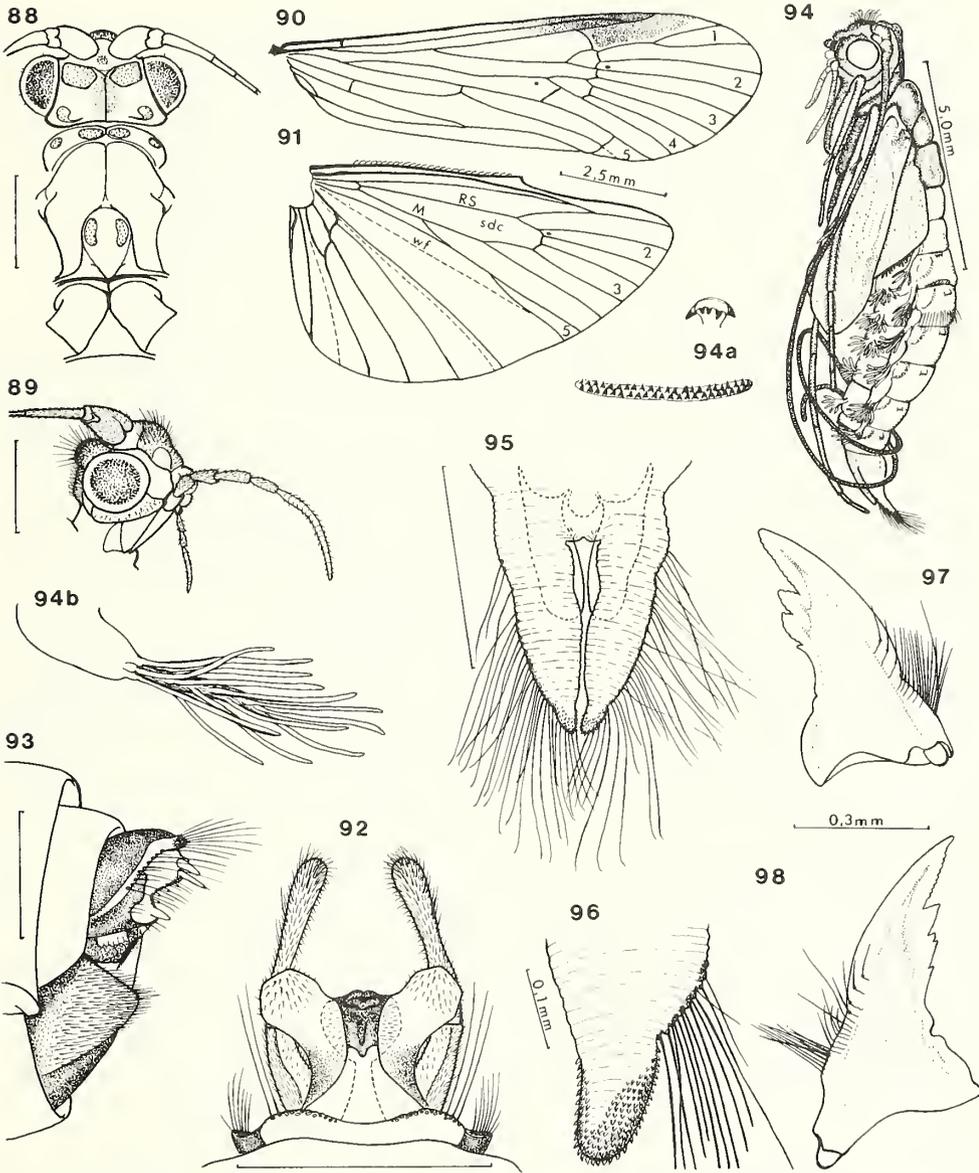
Macrostemum capense (Walker), 1852: 77 (as *Macronema capensis*)

Macrostemum capense (Walker); Betten & Mosely 1940: 194-199, figs 96-99, as *Macronema capense*; synonymy with many other African species and varieties and re-description of imagos (♂, ♀) Holotype ♀ in British Museum (Nat. Hist.). Port Natal.

Macrostemum capense (Walker); Barnard 1934: 368, 372, figs 42f-g, also larva, described as? *Chloropsyche*, p. 368, figs 40h-1.

Macrostemum capense (Walker); Gibbs 1973: 386-389, figs 62, 72, 84-86, imago, larva & pupa (as *Macronema capensis*).

Distribution: widely distributed over Southern and Central Africa; includes several colour var-



Figs 88–98. MACRONEMATINAE: *Macrostemum capense*, ♂, ♀, ♂ pupa. 88. ♂: dorsal view of head and thoracic nota, 89. ♂: lateral view of head and palpi, 90, 91. ♂: fore and hind wings (right), 92. ♂: dorsal view of genitalia (copulatory organ indicated mainly by dotted lines), 93. ♀: lateral view of genitalia, 94. ♂ pupa: habitus (lateral), 94a. pre- and postsegmental dorsal plates of segment III, further enlarged, 94b. lateral gill from segment IV, further enlarged (stem shaded), 95. ♂ pupa: apical part of exuviae (dorsal), from slide (not all setae shown), 96. same: apex of right anal appendage further enlarged, 97, 98. ♂ pupa: right and left mandibles (dorsal).

ieties earlier described as separate species or subspecies. Colour of head and body ranges from dark brown to yellow, of forewings from dark brown to fawn, yellow or orange, plain or variously patterned with brown, orange, yellow or white (see Ulmer 1907d, pl. V, for coloured figures of several varieties); hind wings paler, plain, iridescent. Recorded from South Africa (all four Provinces), through Zimbabwe, Zambia, Angola, Mozambique to West and East Africa (Sierra Leone to Zanzibar). Material in the Albany Museum includes specimens from South Africa (all Provinces), Malawi and Zimbabwe, mainly of typical *capense* but also including the colour variation earlier termed *Macronema inscripta* Walker, then *M. capense* var. *inscriptum*, and later placed in the synonymy of *M. capense*, now *Macrostemum capense* (Walker).

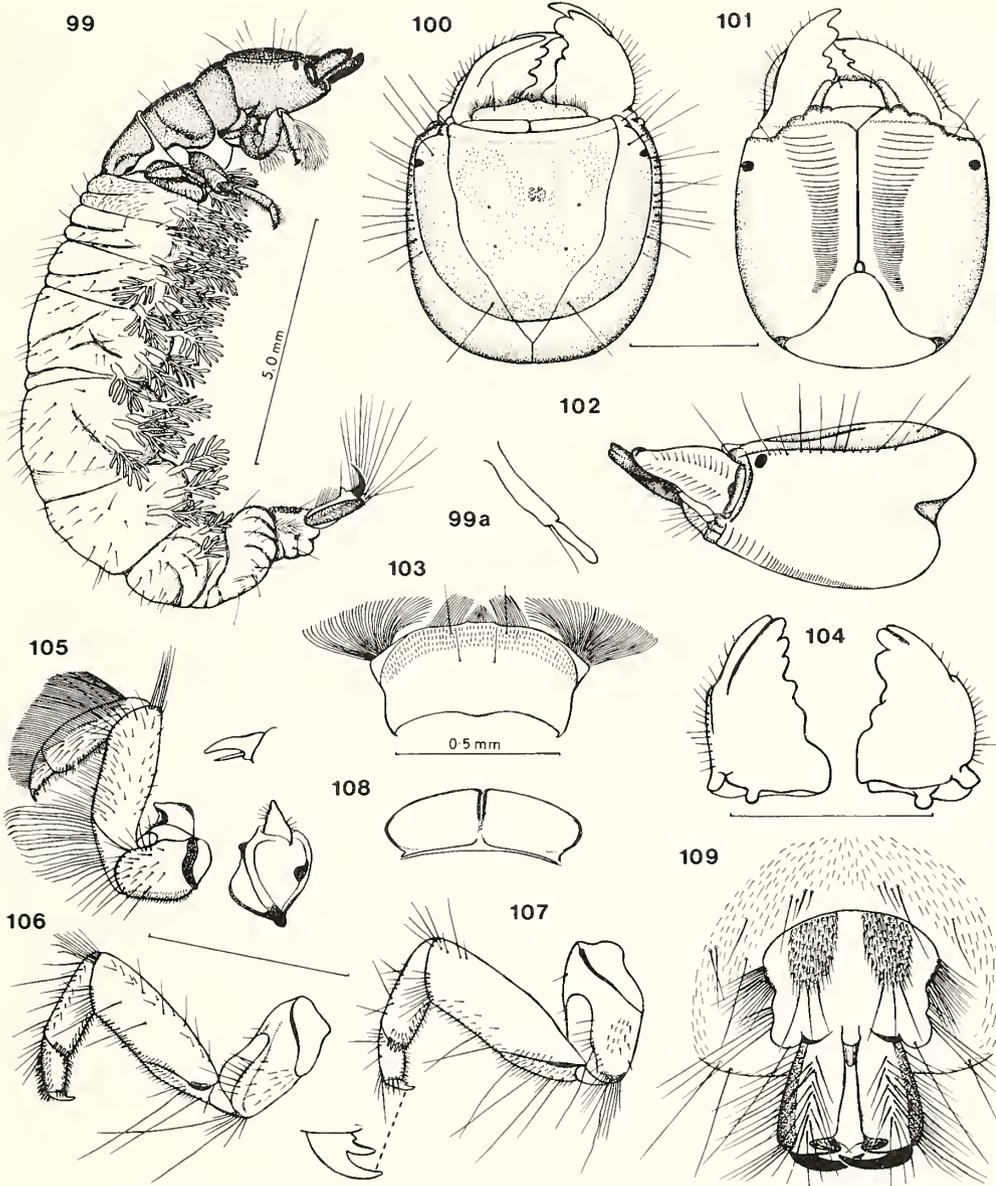
DESCRIPTION OF IMAGOS (Figs 88–93)

Imagos (in spirit, Figs 88–93): dark form, earlier described as *Macronema capense* var. *capense*, now of course *Macrostemum capense*. Males dark brown in general appearance, with pubescent brown forewings obscurely marked with deeper brown, hind wings paler. Head and thorax dark, shining chestnut brown, mesoscutum without warts, mesoscutellum with a pair of pale warts. Antennae very long, slender, brown, minutely pubescent; maxillary palpi well developed, fuscous, finely pubescent; labial palpi comparatively small, pale. Legs yellowish brown, tibial spurs 2.4.4. ♂ abdomen with a pair of short filamentous processes on segment V; genitalia simple, lacking cerci, claspers two-segmented, terminal segment long, strong; copulatory organ with large round apex and narrow stem. Females similar to males but paler, with shorter antennae, and without filamentous abdominal processes on fifth sternum. ♀ genitalia of usual hydropsychid type; sternal plates widely separated medially. Specimens in our collection appear to be considerably darker in colour than those described in the literature, but colour in this species is known to be highly variable, and as these are in fluid accurate colour description is not possible. Gibbs (1973: 387) described *M. capense* imagos from Ghana (evidently fresh material) as the dark form and as having an orange-brown head, orange-brown antennae with thick grey pubescence, especially basally, dark brown thorax, yellow legs and palpi, wings with pale brown membrane, forewings with short brown pubescence. (Wing length (♂ forewing) 9–12 mm, ♀ usually smaller. Fig. 110 depicts an imago of *M. capense* var. *inscriptum* with spread wings.

DESCRIPTION OF LARVA (Figs 99–109, 111–113, Table IX, Figs. 214B)

Mature larva (in spirit, Figs 99–102, 104–109, 111, Table IX): length up to 16 mm. Fairly large larvae, brightly coloured, with typically macronematine head, flattened, with carina; prepisternum simple, ventral sclerites on IX but not on VIII; no setal fan on anal prolegs.

Head (Figs 99–102): bright chestnut, shortly rounded, with strong carina; frontoclypeal apotome broadly triangular, with two pairs of slight lateral indentations, clypeal portion partly sunk over a semicircular area anterior to the epistomal sulcus, frontal portion slightly raised above level of carina, apex cut off by carina, which traverses it. Dorsal surface of head finely punctate within the carina in certain areas only (indicated by stippling in Fig. 100), colour almost uniform bright red-brown, with a few small paler muscle marks. Anteclypeus with one pair of sclerites. Each parietal sclerite bears a row of long, stiff setae dorsally, bordering the carina. Eyes small, black, situated fairly far forward close to carina, within a paler area; no cuticular lenses visible. Antennae minute, close to base of mandibles. Submentum almost semicircular, the anterior margin flattened and slightly indented, anterior ventral apotome showing suture at one side only; posterior ventral apotome minute. Stridulatory files present, large, curved, the distance between striae greater in the wider distal part than in the narrower proximal part.



Figs 99–109. MACRONEMATINAE: *Macrostemum capense*, mature larva (except for Figs 99a & 103). 99. habitus, lateral (right appendages only shown), 99a. ventral gill bearing seta, further enlarged, from 3rd instar larva, 100, 101, 102. dorsal, ventral & lateral views of head, 103. labrum of 4th instar larva, 104. left and right mandibles (dorsal), 105. fore-leg with claw further enlarged, also propleural sclerites including pre-episternum, on right, 106, 107. mid- and hind legs, hind claw shown further enlarged, 108. prosternum, 109. ventral view of abdominal segment IX, with part of VIII and anal prolegs (somewhat tilted).

Mouthparts (Figs 101, 103, 104): labrum dark brown, retractile, sclerotized, with small paired lateral membranous expansions each bearing a very large brush of setae, sometimes tucked in beneath labrum, which is usually strongly retracted and mandibles extended in preserved specimens. Mandibles large, broadly three-cornered, heavily sclerotized, with strong, blunt teeth, mainly in the apical half, the triangular outer side of each mandible set with small setae below a strong ridge; no inner bristles.

Thorax (Figs 99–111): castaneous, pronotum with blackened lateral margins and posterior division, meso- and metanota with lateral margins blackened, a medio-dorsal crescent-shaped black spot near hind margin of former, a smaller oval spot on latter, diagonal brownish stripes present but faint, no transverse ecdysial lines as in the Diplelectroninae. Prosternal plate partly divided by a sulcus. Mesosternum with one pair of branched tracheal gills, metasternum with two pairs. Pre-episternum small, bluntly triangular.

Legs (Figs 105–107): strong, brownish yellow. Foreleg: coxa with strong basal process, femur with basal process on inner side, tibia and tarsus with dense brush of silky white setae, claw with single slender basal spine. Mid- and hind limb claws apparently with two thick basal spines, the proximal one small. Ulmer suggests that the proximal basal spine on each claw may in fact merely be a basal extension of the claw itself (Ulmer 1957: 368–9). In the penultimate instar it is, however, clearly socketed. The mid-tarsus bears a short, fine brush. As Gibbs (1973: 389) points out, there is a basket-like arrangement of long setae on the trochanter of the foreleg; this is very clearly seen in our larvae too, and in one or two this contains a fluffy mass which could have been detritus or algal material collected from the net.

Abdomen (Figs 99, 109): dorsal side covered with short, fine setae and sparsely scattered longer ones; tufted gills present on abdominal segments II and III in eight rows, on IV–VI in six rows (see Table XI). Segment IX with one pair of ventral and two pairs of lateral sclerites, all bearing bristles or setae; the ventral ones are of the usual type, but only occur on IX, there are none on VIII. Anal prolegs of medium length, stout, with strong lateral sclerite and a few long setae, no anal fan. Five anal gills.

Earlier instars: The Vaal River material included third to fifth instars of *M. capense* in addition to the mature (sixth instar) larvae described above, and the Natal material included all six instars, there being many specimens of all except the first, of which there were only three, probably due to their passing through the meshes of the nets used. The instars were separated as before, on the basis of head width, gill type etc. From the third instar on, the larvae showed the characteristic head shape and colour seen in the mature larvae, although with slight differences in gill development (see Table IX) and other features. (See histogram Fig. 214B.)

First instar: head rounded, head capsule approximately 0,17 mm in width at eyes; labrum small, with a few setae but no brushes. No gills apart from the five anal gills. Only pronotum clearly defined and complete, pre-episternum scarcely visible, mesonotum partially and very faintly sclerotized, metanotum practically unsclerotized. Legs: foreleg with four large feathered setae on tarsus, claw with three basal spines; mid- and hind claws with three basal spines and a spinule. Ninth abdominal segment with two large feathered setae where ventral sclerites appear in later instars. Anal claw plain, curved, with single large seta. (See Figs 112, 113 a–c)

Second instar: head rounded, head capsule approximately 0,26 mm in width at eyes, labrum prominent, with strong lateral brushes; no stridulatory files visible. No abdominal or thoracic gills. All three thoracic nota well sclerotized; pre-episternum clearly visible. Legs: foreleg with three feathered setae on tibia, two on tarsus, claw with two basal spines and two spinules (all four graduated in size); claws of mid- and hind legs with two basal spines and several spinules. No feathered setae or ventral sclerites on ninth abdominal segment, other setae long, sparse.

TABLE IX.

Number and position of tracheal gills in 3rd to 6th larval instars of *Macrostemum capense*

Segment	3rd instar				4th, 5th, 6th instars			
Mesothorax	1 pair				1 pair			
Metathorax	2 pairs				2 pairs			
Abdomen (right side)	Post	Pre	VI	V	Post	Pre	VI	V
I	—	1	1	1	—	1	1	1
II	—	1	1	1	1	2*	2	1
III	—	1	1	1	1	2	2	1
IV	—	—	1	1	1	—	2	1
V	—	—	1	1	1	—	2	1
VI	—	—	1	1	1	—	1	1
VII	—	—	1	—	1	—	1	—
VIII	—	—	—	—	—	—	—	—

*Abdominal gills marked 2 each have two main stems, either arising from a common base or separately.
 Post = postsegmental lateral gill.
 Pre = presegmental lateral gill.
 VI = ventrolateral gill.
 V = ventral gill.

Third instar: head flattened, carina visible; head width 0,37–0,50 mm at eyes; stridulatory file and presumed scraper present on head and foreleg respectively. One pair mesothoracic and two pairs metathoracic gills present, also abdominal gills as in Table IX; all abdominal gills simple, unbranched, arising from one stem only, each ventral gill bears a long seta. No postsegmental lateral gills present as yet. Forelimb claw with one slender basal spine; mid- and hind claws with two thick basal spines, the proximal one very small; thin brush of setae on forelegs, no feathered setae found; abdomen smooth, paired ventral sclerites now present on IX. (See Fig. 99a and Table IX)

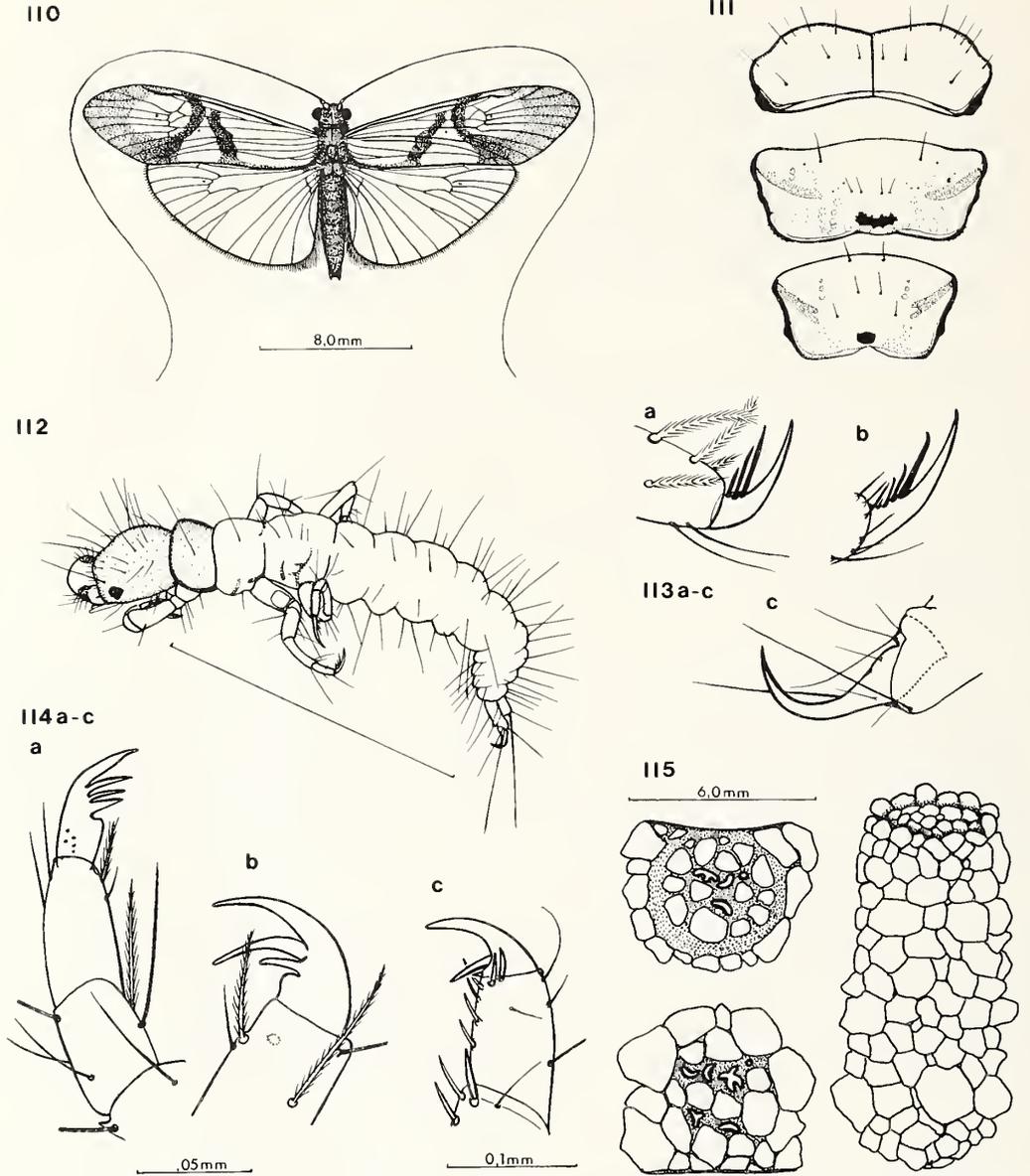
Fourth instar: head capsule 0,69–0,81 mm wide at eyes; abdominal gills as in mature larva, postsegmental lateral gills present, gills that will develop double stems have done so, but gills only bear 1–4 branches; ventral gills without setae. Fore claw with slender basal spine, mid- and hind claws with two thick basal spines, the proximal one small, as in later instars. Abdomen smooth. Brush on foreleg denser than in third instar. (See Fig. 103, labrum)

Fifth instar: head capsule 1,06–1,38 mm wide at eyes; abdominal gills as in mature larva, usually with 4–8 branches. Brush on foreleg fairly well developed. Abdomen hairy in appearance, as in final instar. As mentioned above, the proximal basal spine of each limb claw is clearly socketed.

Sixth instar: this is the mature larva, described above. Head capsule 1,56–1,94 mm in width at eyes; gills with 15–23 branches.

DESCRIPTION OF PUPA (Figs 94–98, Table X)

Material available included a number of mature male and female pupae with cases and larval sclerites, thus establishing the correlation with *M. capense* imagos. Length of pupae 9–10 mm. Mature larvae were present in some instances, substantiating the correlation.



Figs 110–115. MACRONEMATINAE: *Macrostemum capense*. 110. *M. capense* var. *inscriptum*: ♂ imago with wings spread (legs omitted), 111. *M. capense*: pro-, meso- and metanotal shields of mature larva (larval sclerites from pupal case), 112. *M. capense*: first instar larva, whole mount, 113. *M. capense*: first instar larva, claws (drawn freehand, × 400): a. claw of foreleg, b. claw of mid-leg, c. anal claw. MACRONEMATINAE: *Amphipsyche scottae*. 114. mesothoracic claws of larvae: a. first instar, b. second instar, c. third instar., 115. dorsal view of pupal case, showing end plates on left, further enlarged, to show respiratory holes.

SCOTT: HYDROPSYCHIDAE (TRICHOPTERA) OF SOUTHERN AFRICA WITH KEYS

Male pupa (pharate imago—in spirit) (Figs 94–98, Table X): head rounded, brownish yellow, surmounted by two sparse flattened tufts of brown setae with bent tips, anterior ones projecting forwards, posterior ones backwards. Eyes large, dark; antennae long, slender, curled round end of abdomen (two coils per antenna). Labrum semicircular, flattened; mandibles small, each with an apical and three lateral slightly serrated teeth (proximal one small, distal ones large, in left mandible second tooth from base has two cusps), strong setae along the outer margin. Maxillary and labial palpi well developed. All legs fairly stout, middle pair fringed to form oars; spurs 2.4.4. Tufted gills and dorsal plates present as indicated in Table X. Lateral gills on segments IV–VI each with a swollen pouch-like base from which arises a single, long, much-branched gill (Fig. 94b). Anal appendages of medium length, strongly curved dorsad, plump, with small “bare” finger-like apices (these lack long setae but are minutely spinose), apart from the apices the appendages are heavily fringed with strong setae, some laterally but most ventrally placed. Male genitalia enclosed in ventral pockets as usual.

Female pupa (pharate imago—in spirit): similar to male but antennae shorter, recurved not coiled; middle swimming legs more strongly broadened; anal appendages similar but lacking pockets for genitalia. Gill count as in male, but pouches at bases of dorsolateral gills less pronounced; dorsal plates, setae etc. similar.

Pupal case: length 10–12 mm; a straight, rigid case of variously sized sand grains, mainly medium to large in size, lower edges inturned where case rests on substratum, completely lined with secretion except at ends. Secretion forms a loose inner lining, cocooning the pupa. Poste-

TABLE X.

Branchial gills, dorsal plates etc. of ♂ pupa of *Macrostemum capense*

Abdominal segment no.	Tufted gills (right side)			Dorsal plates	Setae, sclerotised points etc. on dorsal side of abdomen
	Dl	VI	V		
I	—	—	—	—	2–3 pairs setae
II	1	2*	2	—	4 small pairs setae; scattered points over whole
III	(1)	2	2	1 ant. pair 1 post. pair	4 pairs setae; scattered points over whole
IV	(1)	—	2	1 ant. pair	Band of long setae along post. margin; scattered points over whole
V	(1)	—	2	1 ant. pair	Scattered points over whole
VI	(1)	—	1	1 ant. pair	Scattered points over whole
VII	1	—	1	1 ant. pair	—
VIII	—	—	—	1 ant. pair	—

*The figure 2 denotes that the gill in question has 2 main stems.

(1) The brackets denote that the gill in question has a swollen pouch-like base, from which arises a single long, much branched gill.

Dl = dorsolateral gills.

VI = ventrolateral gills.

V = ventral gills.

rior end of case rounded, of smaller grains connected by perforated sieve plates, anterior end flatter, with lid of small sand grains between which are several holes guarded within by sieve plates. Larval sclerites tucked into posterior end of case.

REMARKS

Over the years there has been considerable confusion in regard to the nomenclature of *Macronema* species in Africa, largely on account of the great variability in colour and small amount of difference in other characters between the specimens being studied. Specimens have frequently been made new species which have later proved to be colour variations of existing species. Names have changed in rank from species to subspecies or variety and back and many have later fallen into synonymy. The list of African species given below reflects this.

Although this background and position remain unaltered, there has been a recent change in the generic name of all African species from *Macronema* Pictet to *Macrostemum* Kolenati (Flint & Bueno-Soria 1982). As Flint and Bueno-Soria point out in their paper, it had long been recognized that *Macronema* species fell into two groups (e.g. Ulmer 1907d, 1957 & others). They had defined differences in an earlier paper (Flint & Bueno-Soria 1979) in which they separated the Neotropical species of *Macronema* into two groups, the *hyalinum* group and the *percitans* group, based on clear differences in adult structure, particularly in wing colour and in shape and complexity of male genitalia. Whereas larvae of a number of species in the *hyalinum* group were well known, no larvae had then been correlated with imagos of any species of the *percitans* group. Thus the matter stood until Bueno-Soria was able to collect and rear some *Macronematinae* larvae of a type previously attributed to the genus *Centromacronema* by Marlier (1964), a very different larva from the well-known "*Macronema*" larva. These larvae proved to be those of *Macronema variipenne*, a member of the *percitans* group, the larvae of *Centromacronema* thus remaining unknown.

Flint & Bueno-Soria (1982) point out that *variipenne* larvae are so different from those of previously described *Macronema* larvae (exemplified by their having been attributed to *Centromacronema*) that the two divisions of *Macronema* must be regarded not as species groups but as different genera. The *percitans* group includes both *M. variipenne* and *M. lineatum*, the latter being the type species of the genus *Macronema*. The *percitans* group (which is exclusively South American) therefore retains the name *Macronema*. A new name has therefore had to be found for the *hyalinum* group which comprises some South American species, all African species and all species from the rest of the world. To this group Flint & Bueno-Soria (1982) have allocated the name *Macrostemum* Kolenati 1859, of which the type species is *Hydropsyche hyalina* Pictet, selected by Fischer (1963: 176). *Macrostemum* had been listed as a synonym of *Macronema* by Fischer (1963: 176) so was available for the *hyalinum* group.

Flint & Bueno-Soria (1982, table 1) give a useful comparison of the larvae and pupae of *Macronema* and *Macrostemum* species. The food and probably the net of South African *Macrostemum* larvae, however, evidently differ considerably from those of South American ones (see under Biology).

Larvae and pupae of non-African species of *Macronema* (i.e. *Macrostemum*) have been described by a number of authors, mainly from American and Asian material. Of African species, the only valid descriptions to my knowledge are those of *M. capense* larvae and pupae by Gibbs (1973) and of an unidentified species of *Macronema* by Barnard (1934) as *Chloropsyche*? which was also *M. capense*. Descriptions of *Macronema* larvae were also given by Ulmer (1912) and Marlier (1943b) as *Aethaloptera*. Marlier (1965/6) described a pupa but gave no figures.

Neither larvae nor pupae show clear interspecific differences, though it might well be possible to find reliable characters should sufficient material of several species be available for study. Comparison of *M. capense* larvae with figures and descriptions in the literature indicates

that shape of mandibles differs from one species to another and that colour differences may also exist. Statzner (1981) separates four species of *Macronema* (i.e. *Macrostemum*) on the basis of shape of head and submentum and differences between stridulatory ridges and setae on the ventral sclerites of IX. These differences are regrettably not illustrated.

Barnard (1934: 373) pointed out that *M. natalense* Ulmer (1931) only differed from *M. capense* Walker in the length of the fifth segment of the maxillary palpi relative to that of the other four segments, a difference which seems minimal in available material, if indeed present. The recorded distribution of *natalense* coincides with part of that of *capense* and the larvae appear to be identical (comparison of specimens in the Albany Museum collections, considered on a geographical basis). *M. natalense* is a dark form; *capense* has dark forms, *inter alia*. I therefore feel that *natalense* should be placed in the synonymy of *capense* (**Syn. nov.**).

BIOLOGY

In contrast to most of the other Macronematinae, much detailed and elegant work has been carried out in various parts of the world on the biology and behaviour of *Macronema* (= *Macrostemum*) species, particularly by the late Dr Werner Sattler on larvae living in forest streams in the Amazon basin (Sattler 1963, 1965); see also Wallace (1975, 1976) and Wallace and Sherberger (1974, 1975), working on North American material, and others.

Macrostemum larvae tend to inhabit large rivers and the larger streams, living in sandy or gravelly bottoms, on or under rocks and large stones, or in and on the bark of submerged trees or branches. There they make beautiful and complex retreats, varying somewhat in detail according to species and site, but usually incorporating a U-shaped tube, comprising a longer funnel-like tube, facing upstream, down which the water enters, and a second, shorter tube for its exit. At the bend of the U a very fine-meshed net is placed (mesh openings $2-4\mu \times 14-32\mu$ in Amazonian species), in which incoming food particles are trapped, and just anterior to which a third tube opens, which evidently houses the larva, enabling it to collect food from the net. The net traps microstemon (fine particulate organic matter, phytoplankton and bacteria) in contrast to the much larger organisms commonly taken by most other Hydropsychidae in their coarser nets. The tubes are made of silk secretion in which embedded sand grains act as stiffening. Dense brushes on forelegs and labrum and setose tracts within the oral region enable the *Macrostemum* larvae to sweep the food particles collected by the net into the mouth. When not feeding the larva can block the opening of the dwelling tube with its flat head.

When the tubes are situated in sandy bottoms they are vertically placed with the arms of the U-tube projecting into the current and the dwelling tube penetrating into the substratum. When under stones, as was the case with some South African specimens that I collected, the tubes were horizontal, facing upstream, and usually situated between a large stone and the substratum whether gravel or underlying rock or stone. Thus they did not need to be as complete and the walls were only partly of sand or gravel and silk and partly formed by the sheltering stone and the substratum. Gibbs (1973) found similar retreats under stones in a river in Ghana where the anterior tube was roughly made of rather large stones.

The South African stream-dwelling species, *M. capense*, evidently has a different feeding pattern from that of South American species studied by Sattler. Chutter (1968), working on the ecology of *Simulium* species in the Vaal River (South Africa), also studied their predators which included several hydropsychid genera of which *Macrostemum* (as *Macronema*) was one. The *Macrostemum* larvae had a strongly toothed gizzard and large amounts of insect sclerites were found in their guts. He concluded that large *M. capense* larvae were mainly carnivorous and would probably readily eat *Simulium* larvae and, of course, other insect larvae.

M. capense imagos and pupae, in the Albany Museum material, were collected from September through to April (thus not in the winter months) and larvae all the year round.

AFRICAN SPECIES OF *MACROSTEMUM* (all described as *Macronema*)

M. adpictum (Navás), 1934c: 70, 71, fig. 12. ♀.

Distribution: Madagascar.

M. alienum (Ulmer), 1907d: 107–108, fig. 109. ♂ ♀.

Distribution: Sudan, Ghana.

M. bouvieri (Navás), (1922) 1923: 49, 50, fig. 16. ♂.

Distribution: Congo.

M. capense (Walker), 1852: 77. ♂ ♀.

Synonyms: *M. capense* var. *signatum* Walker, 1852: 77.

M. capense var. *inscriptum* Walker, 1852: 77.

M. capense var. *pulcherrimum* Walker, 1852: 77.

M. sansibaricum Kolbe, 1897: 39.

M. sjöstedti Ulmer, 1904b: 419, fig. 9.

M. capense var. *rhodesianum* Ulmer, 1931: 14, 15, fig. 12.

M. capense var. *stigmatum* Navás, 1930a: 331, fig. 46.

M. fulva Jacquemart, 1961b: 19.

M. natalense Ulmer, 1931: 12, fig. 11. Placed in the synonymy of *M. capense* in this paper (**Syn. nov.**); see above under Remarks.

See Fischer 1963: 179–181 for full references. Most of the above varieties have been treated as full species at times. All now fall into synonymy.

Distribution: widely distributed in Africa, from Sierra Leone and Ghana in the West to Uganda and Zanzibar in the East, down to South Africa (all four Provinces), and including the Comoros, Fernando Po and São Tomé.

M. colini (Navás), 1932a: 289, fig. 86. ♀. Belgian Congo.

Marlier (1960) states that this is undoubtedly a species of *Dipseudopsis* (Dipseudopsidae).

M. displicens (Navás), 1935: 73, 74, fig. 34. ♂.

Distribution: Madagascar.

Sýkora (1964: 281, figs 13–16) redescribes the species and transfers it to the genus *Leptonema*.

M. distinctum (Ulmer), 1912: 100–102, fig. 22. ♂.

Distribution: Spanish Guinea, Ghana.

M. furcata (Jacquemart & Statzner), 1981: 15, pls X figs 1, 2, XV fig. 9. ♂.

The wings illustrated resemble those of a *Protomacronema* rather than those of a *Macrostemum*.

Distribution: Zaïre.

M. graphicum (Navás), 1934c: 69, 70, fig. 11. ♂.

Distribution: Madagascar.

M. lacroixi (Navás), 1923: 25, 26, fig. 36. ♂.

Distribution: Madagascar.

M. madagascariense (Ulmer), 1905b: 31, fig. 18. ♂.

Distribution: Madagascar.

M. nigriceps (Navás), 1932a: 290, fig. 87. ♀. Congo.

Marlier (1960) notes that this is a mistaken identification of *Protodipseudopsis congolana* Navás (Dipseudopsidae).

- M. obscurum* (Banks), 1920: 355. (Sex not stated.)
Distribution: Madagascar.
- M. placidum* (Navás), 1935: 72, 73, fig. 33. ♂.
Distribution: Madagascar.
- M. pseudodistinctum* (Marlier), 1965/66: 22, 43, 44, figs 14a, b. ♂.
Distribution: Angola.
- M. scriptum* (Rambur), 1842: 507. Sex not given but evidently ♂. Holotype in Coll. Selys.
Ulmer 1907d: 108, 109, fig. 111 (wings). ♂.
Distribution: Madagascar.
- M. subscriptum* (Jacquemart), 1966b: 42. Listed from the Congo.
I can find no reference to a description. If there is none, it is a *Nomen Nudum*.
- M. trilineata* (Jacquemart), 1961a: 1–3, figs 1, 2. ♀.
Jacquemart 1966a: 8. ♂.
Distribution: Congo (♀), Katanga (♂).
- Macronema* sp. Marlier, 1978a: 292–294, fig. 4 (♀ wings & genitalia). ♀. (= *Macrostemum*)
Distribution: Mali.
Described as a new species but not named, awaiting ♂.

Genus *AMPHIPSYCHE* McLachlan 1872

- Amphipsyche* McLachlan, 1872: 68, pl. 2, figs 7–7e.
Type species *Amphipsyche proclata* McLachlan, 1872. Amur.
- Phanostoma* Brauer, 1875: 69, pl. 4, figs 5–5e.
Type species *Phanostoma senegalense* Brauer, 1875. Senegal.
- Phanostoma* Brauer; Barnard 1934: 369.
- Amphipsyche* McLachlan; Kimmins 1962a: 84–85, synonymy and discussion; key to then known African species (males).
- Amphipsyche* McLachlan; Lepneva 1964 (1970): 604–617, description of larval and pupal stages.

Generic diagnosis (derived from McLachlan 1872, Ulmer 1907d & Kimmins 1962a, 1963) Imago: Spur formula ♂, ♀, 1.4.4, 1.4.3, 1.4.2, 0.4.3, 0.4.2, 0.3.2 or 0.2.2. Mid-tibia and first three basal tarsal segments moderately flattened in ♂, very strongly so in ♀, fringed with setae. Antennae very long, scape bulbous, flagellum threadlike, about 2½ times forewing length in ♂, shorter in ♀; eyes rather small, face somewhat inflated, vertex with paired anterior warts very large. Maxillary palpi weak, rather short, five-segmented, labial palpi very small, three-segmented, segments two and three subequal, not clearly separated. Forewing long, rounded apically, excised in postcostal area proximal to arculus, particularly in ♂; wing forks 1, 2, 3, 4, 5 present, several false costal cross-veins in ♂, not in ♀; discoidal cell absent, median cell closed, short, a false discoidal cell present or absent. Hind wing subtriangular, very wide at base in ♂, less so in ♀, with forks 2, 3, 5, discoidal and median cells absent, hooked macrotrichia present along costa; folded when at rest. ♂ and ♀ wings differ in shape and venation (Kimmins 1962a gives figures of both sexes). Wings colourless to pale green or pale brown, naked. Length of ♂ forewing 11–18 mm, of ♀ 9–14 mm, in African species. ♂ genitalia simple, tenth tergite divided, copulatory organ with or without spiniform “parameres” (endothelial spines); claspers slender. ♀ smaller than ♂. ♀ genitalia with sternal plates of VII widely separated medially, as in *Macrostemum*.

The genus occurs not only in Africa, but also in Russia, China and the Oriental Region as far south-east as Borneo.

Amphipsyche scottae Kimmins

(Figs 114–136, Tables XI, XII, histogram Fig. 214C)

Amphipsyche scottae Kimmins, 1962a: 93–94, figs 29–37 (♂ palpi, ♂, ♀ wings and genitalia).

Holotype ♂, Wilge River (tributary of Vaal), 5 miles downstream from Harrismith, 10.ii.1959; Allotype ♀, Vaal River below Barrage, 23.viii.1957, both in British Museum (Nat. Hist.). Paratypes in British Museum (Nat. Hist.), Albany Museum and South African Museum collections.

Amphipsyche scottae Kimmins; Scott 1975: 48, figs 35, 36 (larva).

Distribution: this species appears to be endemic to South Africa, where it has been recorded from the Transvaal, Orange Free State and Northern Cape, always from the Vaal River and its tributaries; it has also been found in the Mooi River, Natal.

Kimmins' material all came from the National Institute for Water Research collections, (now housed in the Albany Museum and forming part of their Collection of Freshwater Invertebrates), and the rest of his specimens are now housed in the Albany Museum together with further material from the same areas. Additional material is extensive, including male and female imagos, larvae and pupae; almost all are from the Vaal River System, a few from the Mooi River, Natal.

DESCRIPTION OF IMAGOS (Figs 116–121)

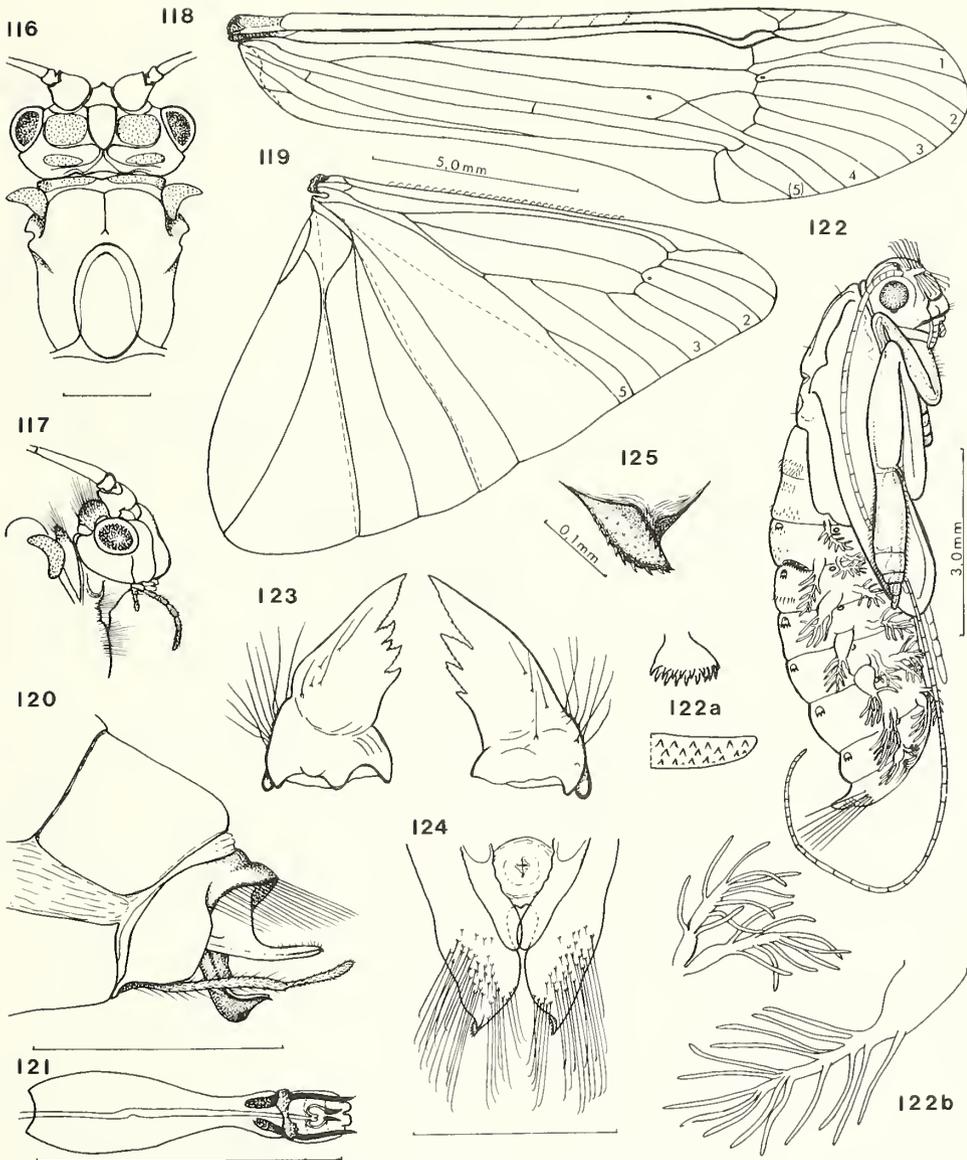
Imagos (in spirit, Figs 116–121): large, cream to tawny yellow in colour with glassy wings; hind wings very wide, males more brightly tinted than females. Antennae finely annulated with red-brown at joints, very slender. Maxillary and labial palpi present, small. Legs with small black spots on each trochanter and at apical end of fore and mid-tibiae. Mid-legs of male somewhat flattened, of female strongly flattened and expanded, fringed. Tibial spurs 0.4.2. Wings slightly clouded, iridescent, membrane covered with microtrichia and, particularly in ♂, with a sparse scattering of larger setae; setae also present along some wing veins. ♂ forewing length c. 18 mm, ♀ c. 14 mm. Vertex with pair of large anterior warts separated by a shield-shaped raised median area, representing the dorsal triangle; posterior warts narrow. Mesoscutum and mesoscutellum without warts. Females almost entirely glabrous, males with a fuzz of pale hairs on parts of thorax and legs. Abdomen reddish purple. Male genitalia are simple, the claspers slender and the copulatory organ has a pair of "parameres" (Kimmins and other authors) inserted into its dorsal side. According to Schmid (1979 and other papers), these are not true parameres but neoformations, endothecal spines.

DESCRIPTION OF LARVA (Figs 126–136, Table XI, Fig. 214C)

Amphipsyche larvae are very characteristic in appearance, the larger instars always being easily recognizable from the head shape and pattern. Even young larvae of *A. scottae* are often separable from other Hydropsychidae by the comparatively large, broad, flat brown head with paired whitish marks, the large humped labrum (occasionally retracted, in which case the mandibles are usually everted), and the relatively short, rapidly narrowing abdomen.

Mature larva (in spirit, Figs 126–136, Table XI): length up to 12 mm, width of abdomen up to 3 mm.

Head (Figs 126–128): short, rounded, frontoclypeal apotome and surrounding area flattened and bounded by a carina; top of head mainly dark brown in colour, dark colour extending slightly beyond carina except where indented by yellowish areas round eyes; paired yellowish patches on frontoclypeal apotome. Head not uniformly dark brown, but spotted with minute yellow pits from each of which arises a small seta. Carina runs exactly through apex of frontoclypeal apotome, which is short and widely triangular; setae sparse, small, pale, apart



Figs 116-125. MACRONEMATINAE: *Amphipsyche scottae*, ♂, ♀ pupa, ♂ pupa. 116. ♂: dorsal view of head & thoracic nota, 117. ♂: lateral view of head and palpi, 118, 119. ♂: fore and hind wings (right), 120. ♂: lateral view of genitalia, 121. ♂: copulatory organ (dorsal); "parameres", shown by transparency, lie mainly within the copulatory organ on dorsal side; the apical internal sclerites lie below & between them, 122. ♀ pupa: habitus, lateral, 122a. pre-segmental dorsal plate from V & postsegmental dorsal plate from III (part), 122b. ventrolateral and dorsolateral gills from III & V respectively, 123. ♀ pupa: left & right mandibles, dorsal, 124. ♂ pupa: apical part of exuviae (ventral) from slide (not all setae shown; long setae practically all on ventral side, 125. same: apex of right appendage further enlarged.

from two pairs of longer, dark ones near anterior margin. Eyes (clusters of ocelli), black, placed well forward, beneath a few small cuticular lenses, not easily seen. Antennae minute, at base of mandibles. Parietal sclerites yellow laterally, brownish ventrally, patterned with paler muscle spots; stridulatory files triangular, anterior margin of head capsule heavily sclerotized, dark. Anterior ventral apotome represented by a small sclerite, with cleavage line on left side only, posterior ventral apotome smaller.

Mouthparts (Figs 129–131): labrum brown, largely sclerotized, with membranous anterolateral lobes, anterior margin with long tufts of pale, silky setae, dorsal surface with small secondary setae in addition to the primary ones. Labrum retractile, when fully retracted scarcely visible; membranous base of labrum (anteclypeus) bears four brown sclerotized plates. Mandibles broad, powerful; right mandible with four apical teeth, narrowing below, then widening midway to the base where a blunt, three-cusped lateral tooth arises; left mandible with five apical teeth and two lateral teeth, the latter with two or three cusps each, no inner brushes; mandibles triangular in cross-section, as is usually the case in hydropsychids, the outer surface setose, enclosed by lateral flanges. Maxillo-labium: palpifers with strong tufts of setae, maxillary palpi stout, five-jointed, galeae narrow, tipped with sensilla; submentum triangular, brown, bearing curved setae; labium shorter than maxillae, labial palpi minute, not easily distinguished.

Thorax (Fig. 126) thoracic segments short, little narrower than abdomen; pronotum with paired sclerites, brownish, with narrow darker anterior and posterior borders and black lateral thickenings, a transverse sulcus near posterior margin; meso- and metanota undivided, brownish with black lateral margins and darker diagonal stripes, a small central black mark near posterior margin of each. Prosternal plate narrow, dark; meso- and metasterna membranous; one pair of tufted gills present on mesosternum, two pairs on metasternum. Propleuron with pre-episternum (first pleural sclerite) simple, shortly pointed, bearing a few bristles (see Fig. 132).

Legs (Figs 132–134): comparatively short, strong, yellowish to brownish in colour, with darker markings as indicated in figures, anterior pair (particularly tibiae and tarsi) darker than rest, claws brown. Legs with many secondary setae. Forelegs: coxa with stout, striated basal projection which articulates with propleuron, femur with short, blunt projection on inner side of proximal end, this appears to have no function unless it serves as scraper, as I could find no other in the usual place along the anterior margin of the femur. Tibia and tarsus have a weak brush of hairs, some finely plumose, appearing serrated, and a short fringe of stout setae along the posterior margin. Limb claws each with a single short stout spine at base.

Abdomen (Fig. 126): not deeply segmented, dorsal surface largely covered with minute, blunt microchaetae, occasional longer setae and a few very long ones, the microchaetae become smaller laterally, disappearing at the pleura. They are usually more abundant in the intersegmental folds, and may be lacking in patches dorsally, for example along transverse, indented bands on segments I and II, which instead are set with bent spinules several times as long as the microchaetae. Tufted tracheal gills are present in six rows on segments I and VII, eight rows on segments II–VI, and two rows on segment VIII, there are none on IX. These gills are borne on the lateral, ventrolateral and ventral surface of the abdomen (see Table XI), lateral gills have both presegmental and postsegmental tufts. Gill filaments arise from the sides and apex of a common stalk (in thoracic gills along one side only). On segment IX there is a pair of ventral sclerites bearing spines, also a small pair of lateral sclerites and a larger pair of dorsolateral sclerites, both setose; there are no such sclerites on VIII. Anal prolegs short, stout, with strong lateral sclerites, anal claws large, incurved; five anal blood gills.

Earlier instars: The differences between the larval instars were noted as in the other genera, and they appeared to fall naturally into six groups, which have been taken as representing

TABLE XI:

Number and position of tracheal gills and other characters in 3rd to 6th larval instars of *Amphipsyche scottae*

Segment No.	3rd instar				4th instar				5th instar				6th instar			
Mesosternal gills	1 pair				1 pair				1 pair				1 pair			
Metasternal gills	2 pairs				2 pairs				2 pairs				2 pairs			
Abdominal gills	Post	Pre	VI	V	Post	Pre	VI	V	Post	Pre	VI	V	Post	Pre	VI	V
I	—	—	1	1	—	—	1	1	—	—	1	1	—	1	1	1
II	—	1	1	1	1	2*	2	1	1	2	2	1	1	2	2	1
III	—	1	1	1	1	2	2	1	1	2	2	1	1	2	2	1
IV	—	—	1	1	1	1	2	1	1	1	2	1	1	1	2	1
V	—	—	1	1	1	1	2	1	1	1	2	1	1	1	2	1
VI	—	—	1	1	1	1	2	1	1	1	2	1	1	1	2	1
VII	—	—	1	—	—	1	2	—	1	1	2	—	1	1	2	—
VIII	—	—	1	—	—	—	2	—	—	—	2	—	—	—	2	—
Tarsal claws	2 spines (1 minute)				2 spines (1 minute)				1 spine				1 spine			
Gills	unbranched				c. 2-4 branches				c. 6-10 branches				c. 16-24 branches			
Head width at eyes	0,5mm				0,75-0,80mm				1,1mm				1,5-1,7mm			

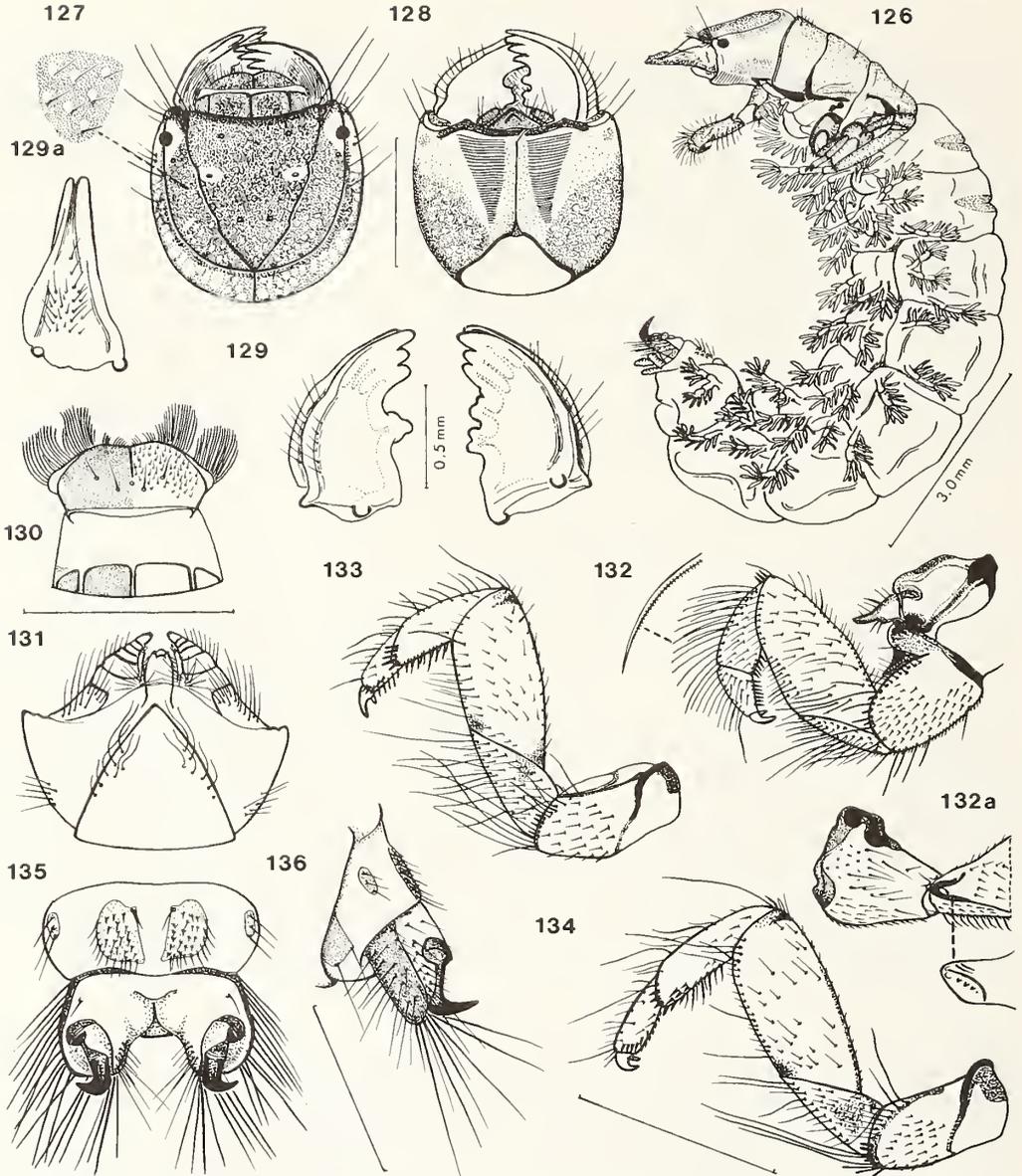
* The figure 2 in this section of Table I indicates that the abdominal gill in question has 2 main stems, either arising from a common base or separately.

Post = postsegmental lateral gill; Pre = presegmental lateral gill; VI = ventrolateral gill; V = ventral gill.

six larval instars, as was the case in *Macrostemum capense*. Only 69 larvae were available for study, so the histogram derived was not as good as that for *Cheumatopsyche*, nevertheless it tallied with the other larval features observed, see Fig. 214C (histogram).

First instar: head rounded, neither flattened nor with carina, uniformly pale brown in colour but with the characteristic extensile labrum; thoracic nota very lightly chitinized, scarcely darkened marginally; tarsal claws of all legs with three large basal spines, several large feathered setae on tibiae, tarsi and femora (Fig. 114a); no tracheal gills on thorax or abdomen. Average head width of available specimens at eyes 0,17 mm.

Second instar: similar to first, but head darker, sometimes faintly patterned; thoracic nota more heavily sclerotized, pronotum strongly darkened marginally; tarsal claws of all legs with



Figs 126-136. MACRONEMATINAE: *Amphipsyche scoutae*, mature larva. 126. habitus, lateral (right appendages only shown), 127, 128. dorsal & ventral views of head; small portion of surface shown further enlarged, 129. left & right mandibles, ventral view, 129a. right mandible, lateral view, 130. labrum and anteclypeus, dorsal, 131. labium, ventral, 132, 133, 134. foreleg, mid- & hind legs (left); foreleg with pleural sclerites attached & serrate seta further enlarged, 132a. fore-coxa & part of femur, median view; process of femur further enlarged, 135. ventral view of abdominal segment IX, including anal prolegs, 136. right anal proleg, lateral.

two large basal spines (Fig. 114b), large feathered setae on tibia, tarsus and femur of foreleg, less strongly feathered setae on tibiae and tarsi of mid- and hind legs; files of stridulators not yet visible on head, but basal processes present on anterior femora and coxae; no tracheal gills. Average head width 0,33 mm.

Third instar: carina sometimes recognisable on head, but dorsal surface still convex, characteristic colour pattern faint but discernible; stridulatory files present; tarsal claws of all legs with one large basal spine and one minute one (Fig. 114c); normal setation of the type found in the final instar developing, strongly plumose setae absent, but some setae on tibia and tarsus with very fine, short feathering ("serrated"), as in later instars. Simple tracheal gills present on both thorax and abdomen (nearly all unbranched), no postsegmental gills present and few presegmental gills, so that gill count is less than in later instars (see Table XI); all gills arise from one stem only, and each ventral gill bears a subterminal seta, as in *Macrostemum*. Average head width 0,5 mm.

Fourth instar: typical flattened frontoclypeal apotome, colour pattern strong (whole area bounded by carina is not completely flattened even in mature larvae); full number of gills present except for presegmental gill on segment I and postsegmental gill on VII, but gills usually only have one to four branches, although nearly all those that will develop double stems have already done so; forelegs more strongly setose, but as yet no proper brush; tarsal claws as in third instar. Average head width 0,75–0,80 mm.

Fifth instar: full number of gills present except for presegmental gill on segment I; gills more fully branched, usually having from six to ten branches; a thin brush present on forelegs, tarsal claws with one basal spine only, as in mature larva. Average head width 1,1 mm.

Sixth (final) instar, fully described above: all gills present and fully branched (usually 16–24 branches per gill). While the actual number of gills per segment appears to be constant, the number with two main stems seems to be slightly variable, and an occasional larva may have from one to three more gills with double stems than is indicated in the table. Forelegs with full brush; this is not, however, as thick as in, for example, *Macrostemum* or *Aethaloptera*. Average head width 1,5–1,7 mm.

DESCRIPTION OF PUPA (Figs 115, 122–125, Table XII)

Female pupa (in spirit; Figs 122, 123): length 9,5 mm. Head somewhat flattened, vertex dark brown surmounted by four flattened tufts of dark setae with bent tips, of which the two smaller tufts project forwards, the two larger backwards; each seta arises from a white circle, giving the head a spotted appearance. Eyes large, dark; antennae very slender, about $1\frac{1}{2}$ times length of pupa, not curled round body but loosely recurved; labrum short, rounded, with three setae at each side; mandibles strong, with large serrated teeth (left mandible with five teeth, including apical teeth, right with four), tufts of setae on outer side near base and a few setae near outer edge of dorsal face; maxillary and labial palpi small but present. Forelegs fairly slender, mid-legs much broadened, flattened and fringed with setae to form swimming oars; hind legs very slender. Tibial spurs 0.4.2. Tufted gills and dorsal plates present on abdomen as indicated in Fig. 122 and Table XII. Gill branches are slightly variable in size and number, and branches are easily broken off (gill numbers are a more reliable character in larvae than in pupae). While the dorsolateral and ventrolateral gills are clearly separate on segments II and III, where the ventrolateral gills are double, from segment IV caudad they draw closer and closer together until on segment VII both could be branches of the same gill. On VIII the dorsolateral gills are definitely two-branched and there are no others. Those dorsolateral gills on segments III–VI arise from broad pouch-like bases, from which may arise one, two or three different stems bearing gill filaments. Anal appendages fairly short, bluntly rounded, directed somewhat dorsad, bearing strong, dark setae on the ventral side.

Male pupa (pharate imago, in spirit, Figs 124, 125): as female, but mid-leg narrower, less expanded, though still fringed and oar-like; antennae much longer than in female, and more slender, ends forming a coil on the posterior half of the dorsal side of the pupa, four turns of each antenna in the coil; dorsal plates and gills as in female. Anal appendages less rounded (Fig. 124), with pockets for male genitalia, more heavily setate, ending posteriorly in small vertical plates fringed with spinules.

Pupal case (Fig. 115): oval, constructed of variously sized sand grains (mainly large), lined with silk; sides basally inturned to rest on substrate, case closed ventrally with silk only; head end of case (cover) flattened, edged with closely set sand grains which surround a silken lid in which are set a number of sand grains, between which are several small slits for the passage of water; posterior end of case rounded, with about six slits between larger, more closely set sand grains. Case rigid, sand grains very firmly cemented together, completely lined with silk except at ends. Larval sclerites tucked into posterior end of case as is usual.

TABLE XII:

Tracheal gills, dorsal plates etc. of ♀ pupa of *Amphipsyche scottae*

Abdominal segment no.	Tufted gills (right side)			Dorsal plates	Setae, points (shagreening)
	DI	VI	V		
I	—	—	—	—	irregular band of setae
II	1	2*	2	—	broad anterior band of scattered points; narrow posterior band of scattered points
III	(1)	2	2	1 anterior pair 1 posterior pair (strips)	scattered points anteriorly; band of points posteriorly
IV	(1)	1	2	1 anterior pair	anterior patch and posterior band of long setae
V	(1)	1	2	1 anterior pair	
VI	(1)	1	2	1 anterior pair	
VII	(1)	1	2 or 2	1 anterior pair	
VIII	2	—	—	1 anterior pair	

* The figure 2 denotes that the gill in question usually has 2 main branches or stems.

(1) Brackets indicate that the gill in question has a broad, pouch-like base.

DI = dorsolateral gill; VI = ventrolateral gill; V = ventral gill.

REMARKS

Ulmer distinguished between the larvae of *Amphipsyche* and *Phanostoma* on the basis of length of tarsal claws compared with tarsus (Ulmer 1963). In view of the combination of the two genera by Martynov (1935) and Kimmins (1962a) this difference would be specific rather than generic.

A comparison of the larvae of *Amphipsyche scottae* with the descriptions of the larvae of *senegalensis* (Brauer) as given by Hickin (1955) and Jacquemart (1957) and with those of the presumed larvae of *curvinerve* Navás given by Ulmer (1963), of *meridiana* Ulmer (Ulmer 1957) and of *proluta* McLachlan (Lepneva 1964 (1970)) indicates that whereas they are very similar one to another, as might be expected, there are noticeable though often small differences in such characters as the mandibular teeth and the colour pattern and basic colour of the head. The basic colour of the head may be brown, as in *scottae* and *senegalensis*, or yellow. In *curvinerve* the head is yellow and lacks the typical pair of pale spots; *proluta* also lacks these and has a paler transverse stripe. The setose ventral plates on the last abdominal segment may differ somewhat in shape from species to species. Similarly the labrum may differ in shape and extent of sclerotization. There also appear to be slight differences in gill counts (where these are available) and in the suture or sutures shown as bounding the anterior ventral apotome laterally (though this may reflect inaccurate observation in some cases).

Only the central part of the transverse bar in *senegalensis*, tentatively called the gular sclerite by Hickin (1955), represents the anterior ventral apotome. This is small and triangular with a suture on the left side only (Fig. 128). Marlier (1943b) described as *Aethaloptera* sp. an *Amphipsyche* larva, from the Parc National Albert, which could be *senegalensis*.

Kimmins (1962a) suggested that Ulmer's *curvinerve*, described from females only, might be synonymous with *senegalensis*, for though their wing venation differed from that of the male *senegalensis*, normal in this genus, it was similar to that of the females assigned to *senegalensis* on a locality basis. Ulmer's description of the probable larva (Ulmer 1963) is not of *senegalensis* but might well prove to be that of *ulmeri* not *curvinerve* larvae. In the Albany Museum collection there are two larvae (and an immature pupa), very kindly sent to me by Mr Gibbs from his Ivory Coast material, which may be of *ulmeri*. They are fourth or fifth instar and have some gills missing. They correspond to some extent to Ulmer's colour description of *curvinerve* as the heads are yellow to brownish yellow, however, they are not entirely unpatterned, as Ulmer's appear to have been, but, as in *proluta*, show the two paler marks faintly on the fronto-clypeal apotome and a pale stripe close to the anterior margin. The gill count is different from the other known species. These larvae are evidently neither *senegalensis* nor *scottae* and could thus well be those of *ulmeri* as Gibbs considered likely (Gibbs 1973). To establish the facts with certainty it would be necessary to correlate the larvae of both kinds (*ulmeri* and *curvinerve*) with their male and female imagoes (and incidentally establish the status of *curvinerve*).

The presumed larvae of *senegalensis* in the Albany Museum collection are more like the *scottae* larvae than I would have expected from the published descriptions. However, they do differ in having narrower setose plates on the ninth abdominal sternum, in the shape of the mandibles, and in that the brown coloration of the head and nota lacks the slight reddish tinge seen in *scottae*. Neither account of the larva of *senegalensis* gives the gill count in mature specimens.

Statzner (1981) distinguishes between two species of *Amphipsyche* larvae from Ivory Coast by using stridulatory ridges, submentum, and shape of sclerites on IX as a basis for comparison, but as far as I know no general scheme for distinguishing all known African species has as yet been worked out.

The pupa of *scottae* can be compared with those of *senegalensis* (Marlier 1978a, Gibbs 1973) and *ulmeri* (immature pupa from Ivory Coast); descriptions of the non-African species *meridiana* (Ulmer 1957), *proluta* (Lepneva 1964 (1970)) and *indica* (Hafiz 1937) are also available. Pupae of the different species are very similar in general appearance, but do show minor differences in gill counts, in the shape of the anal appendages and their setation, particularly in males, and in the shape of the pupal cases, which may be rounded apically or urn-shaped, with lip, as in most species other than *scottae*.

In imagos of *A. scottae* fork 5 has been shown as present in both ♂ and ♀ forewings, though whether the ♂ fork 5 is a true or false one is a moot point. In drawings of *A. senegalensis* and *berneri* males (Kimmins 1962a Figs 4 & 24) it could be a true fork 5 as Cu_2 does not join Cu_1 directly but ends in a cross-vein connecting Cu_1 and 1A with the anal margin. In other species, however, including *scottae*, the posterior branch of "fork 5" might represent Cu_1 , or $Cu_1 + Cu_2$ or Cu_2 alone. In females, however, there is a true fork 5 in the forewing as Cu_2 clearly ends in a cross-vein to the margin as does 1A, and Cu_1 has two branches.

BIOLOGY

Little is known of the biology of *Amphipsyche* larvae. Hickin (1955) described the larvae of *senegalensis* as inhabiting tough, whitish-grey silk-like tubes underneath stones and boulders a few metres into Lake Victoria, where the water was moving rapidly and they were extremely common, and on the banks of the Nile a couple of miles downstream from the Owen Falls. Their identity was confirmed by breeding some of the larvae to male imagos. Hickin suggested that they might be important predators of *Simulium* larvae. This was confirmed by Chutter (1968) in his search for predators of *Simulium* larvae. He found that *A. scottae* larvae possessed a moderately strongly toothed gizzard (though not as strongly so as *Macrostemum* larvae) and that their gut contents comprised mainly fragments of insect exoskeleton with some algae. They are thus predatory and omnivorous, possibly eating more insect than plant food, and are in all probability one of the hydropsychid predators of *Simulium*.

Amphipsyche larvae are also abundant in certain other African lakes particularly where the water is in constant motion, as is the case near the entry or exit of rivers (Marlier 1962b).

A. scottae may be numerous, with other hydropsychid larvae (notably *Macrostemum*, *Hydropsyche* and *Cheumatopsyche* species, with a few *Aethaloptera*), below dam outlets and barrages in rivers where they exploit the plentiful supply of food in the outflow.

In South Africa the imagos fly from August to April, most commonly in the summer months, and the larvae appear to be present throughout the year, there being a preponderance of younger instars in spring.

According to Corbet (1966), *Amphipsyche senegalensis* appears to be able to reproduce parthenogenetically, perhaps accounting partly for its wide distribution.

AFRICAN SPECIES OF AMPHIPSYCHE

A. africana Ulmer, 1905c: 48–50, pl. 1, figs 36–39. ♂. West Africa.

This species was removed to the genus *Protomacronema* by Kimmins (1962b: 99–101).

A. bernerii Kimmins, 1962a: 91–92, figs 24–28. ♂.

Distribution: Gold Coast (Volta River).

A. corbeti Kimmins, 1962a: 89–91, figs 19–23. ♂.

Distribution: Uganda (Victoria Nile).

A. curvinerve Navás, 1927: 214, fig. 10. ♀.

Ulmer 1963: 257, discussion of *curvinerve* and description of larvae which he ascribes to it. ♂ unknown.

Kimmins (1962a) suggested that Navás's *curvinerve*, described from the ♀ only, may prove to be the female of *senegalensis* (and see 'Remarks').

Distribution: Egypt.

A. fuscata Kimmins, 1962a: 128–129, figs 24–29. ♂.

Distribution: Ethiopia.

A. instabilis Kimmins, 1962a: 126–128, figs 15–23. ♂ ♀.

Distribution: Ethiopia, N. Rhodesia (Zambezi River).

- A. plicata* (Jacquemart), 1963a: 363–364, fig. 22A–F. ♂; as *Phanostoma*.
Distribution: S. Rhodesia (Victoria Falls).
- A. scottae* Kimmins, 1962a: 93–94, figs 29–37. ♂ ♀.
Scott 1975: 49–51, figs 35, 36, larva.
Distribution: South Africa: Transvaal, O.F.S., N. Cape, Natal.
- A. senegalensis* (Brauer), 1875: 71, as *Phanostoma*. ♂.
Kimmins 1962a: 85–89, figs 4–13, descriptions and figures of ♂, ♀.
Hickin 1955: 155–163, figs 10–14, larva.
Gibbs 1973: figs 89–91, pupa.
Marlier 1978a: 299–301, fig. 7, description of ♂ pupa.
Distribution: Senegal, Congo, S. & N. Rhodesia, Nyasaland, Uganda, Ethiopia, Sudan, Mozambique, Ghana, Togo, Tchad, also Madagascar.
- A. ulmeri* Kimmins, 1962a: 89, figs 14–18. ♂.
Distribution: Sudan (Sennar).

Genus *PROTOMACRONEMA* Ulmer 1904

Protomacronema Ulmer 1904b: 416–417.

Type species *Protomacronema pubescens* Ulmer 1904b: 417–419, figs 4–8. ♂. Kamerun.

Protomacronema Ulmer; Ulmer 1907d: 34 (and see col. pl. I figs 1, 3, for imagos with spread wings). ♂ ♀.

Generic diagnosis (based on Ulmer 1904b & 1907d):

Imago: tibial spurs 0.4.4, ♂ ♀. ♂ mid- and hind femora with a fuzz of long, white hair; tibiae of ♂ mid-legs weakly widened, in ♀ mid-tibiae and first tarsal segments very strongly so, fringed. Antennae with short bulbous scape, flagellum very long, slender; eyes not very large, dark. Head reminiscent of that of *Amphipsyche* but palpi well developed. Vertex with large, paired anterior warts, posterior warts not as large. Maxillary palpi long, sparsely setulose, basal segment very short, 2nd longer, 3rd longer than 2nd, 4th shorter than 2nd, 5th very slender, about 1½ times as long as rest together, clearly ringed. Labial palpi with 1st and 2nd segments short, 3rd longer than both together, ringed. Wings very similar in shape to those of *Amphipsyche*, but show little or no indentation at arculus (except in *P. splendens*); venation also resembles that in *Amphipsyche*. Forewing with brownish membrane, densely hairy, with hyaline mark at anastomosis: forks 1, 2, 3, 4 in ♂, 1, 2, 3, 4, 5 in ♀ discoidal cell open or absent, SC and R end in costa, a few indistinct costal veins present; in ♂ Cu₁, Cu₂ and 1A do not join margin directly but end in a curved cross-vein, hence the absence of fork 5. (Marlier, 1962b, regards this cross-vein as representing the two branches of Cu₁, in which case, of course, a rather peculiar fork 5 would be present.) Hind wing with forks 2, 3, 5 or 1, 2, 3, 5; hooked macrotrichia along costa, no discoidal cell; Sc and R₁ join apically just before joining RS; clear false costal veins present; wing much folded when at rest. ♂ forewing in known species 8–15 mm in length, ♀ smaller. ♂ genitalia simple, 10th tergum divided into a pair of lobes, copulatory organ may have spiniform processes of the endotheca (“parameres”); claspers slender, hairy, with long apical segment. Fifth abdominal sternum in ♂ bears a pair of small, knob-like organs. ♀ genitalia of usual hydropsychid type but I can find no description of one (see that given below).

The genus is endemic to the Afrotropical Region, particularly to tropical West Africa, from which seven species have been described; one of these has also been recorded from Madagascar, home, too, of an eighth species.

Protomacronema pubescens Ulmer

(Figs 137–156, Table XIII)

Protomacronema pubescens Ulmer 1904b: 417–419, figs 4–8 (δ palpi, wings & genitalia). Kamerun. δ .Lectotype δ and paralectotype δ in the Stockholm Museum, designated by Kimmins (1962b).*Protomacronema pubescens*, Ulmer 1907d: 36 (*partim*, Kamerun only, *nec* figs 28–30).*Protomacronema pubescens*, Ulmer 1912: 98, 99 (Kamerun only).? *Protomacronema pubescens*, Ulmer 1913: 191 (Zululand).*Protomacronema pubescens* Ulmer; Lestage 1919a: 303 (*partim*, Cameroon).? *Protomacronema pubescens* Ulmer; Barnard 1934: 370, figs 41a–e (Zululand).*Protomacronema pubescens* Ulmer; Kimmins 1962b: 99–101, figs 1, 2–4 (wing & δ genitalia), from a re-examination of the material gives the above synonymy and separates off *P. africana* (Ulmer). He gives the known distribution as Cameroons, Sierra Leone.*Protomacronema pubescens* Ulmer; Gibbs 1973: 389, 391, figs 73–76, 87, 88 (larva & pupa). Ghana.*Protomacronema pubescens* Ulmer; Scott 1975: figs 43, 44 (larva). Ghana.

Distribution: Cameroons, Sierra Leone, Ghana, Ivory Coast.

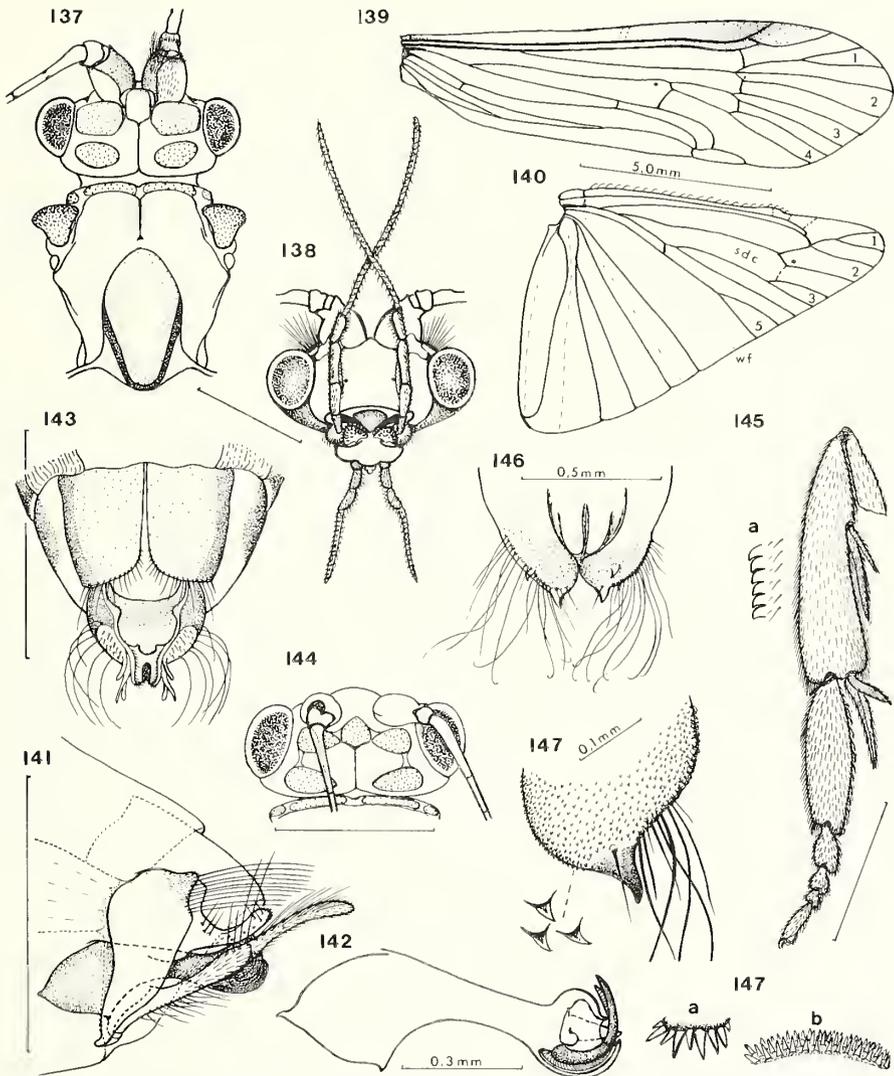
Material available comprises 1 δ from Ivory Coast, presented by Mr F. M. Gibon of O.R.S.T.O.M., also two larvae and part of a pupal skin from Ghana, given by Mr D. G. Gibbs, one δ and two larvae given by Dr B. Statzner and one η on loan from him, and a further δ and η received from Mr Gibon.

DESCRIPTION OF IMAGOS (Figs 137–145)

Imago (δ , in spirit, Figs 137–143): a fairly large, pale yellow caddisfly, vertex, thoracic nota and genitalia yellowish brown, warts pale, setae on anterior head warts fine, stiffly up-standing, on posterior head warts, pronotum and scapulae long, coarse, curly; anterior warts separated by an almost quadrangular raised "dorsal triangle". Antennae yellowish with narrow brown annulations, at least 3x length of forewings. Maxillary and labial palpi noticeably long and slender, mouthparts very clear (see Fig. 138): mandibles of usual hydropterygine type, meeting beneath labrum, laciniae with small denticles, stipites rounded, strongly setose, haustellum (in specimen drawn) expanded, small labial lobes visible below it (*cf.* Crichton 1957: 75, 76, fig. 43). Legs slender, pale yellow, with black spot at bases of femora. Wings as in generic description, forks 1, 2, 3, 4 in forewings (length 12.0 mm), 1, 2, 3, 5 in hind wings, which are noticeably short in the genus and much folded when at rest. Abdomen mauve-white dorsally, yellowish ventrally, genitalia brown, much retracted into VIII in this specimen.

Ulmer (1904b) described his specimens (dry material) as having red-brown head and thorax with yellowish-red setae, face and mouthparts reddish, apical segments of labial palpi dark brown. Legs reddish, hind legs yellowish red. Abdomen dorsally reddish with white shimmer, pleura clothed with white pubescence, ventral side whitish. Forewings pubescent, a golden yellow strip over the hyaline mark at the anastomosis, otherwise copper-red to copper-brown, two dark patches over the pterostigma. Hind wings hyaline, iridescent, with scattered brown setae in the apical cells. Antennae yellowish red ringed with brown at the joints.

Male genitalia with dorsal margin of 8th segment entire, 9th with slight median excision and setal fringe, 10th divided to form two lateral digitate lobes, upturned apically, bearing



Figs 137-147. MACRONEMATINAE: *Protomacronema pubescens*, ♂, ♀, ♂ pupa. 137. ♂: dorsal view of head & thoracic nota, 138. ♂: face showing maxillary & labial palpi and mouthparts, comprising: median labrum, lateral to that mandibles (black), paired lacinia (maxillary lobes), papillate or denticulate, median haustellum, below it minute median labial lobes (ligula)., 139, 140. ♂: fore & hind wings (right), wing folds indicated by broken lines, 141. ♂: lateral view of genitalia (abdominal segments VII, VIII shown partly by light broken lines, setae on IX drawn as if VIII omitted), 142. ♂: copulatory organ (lateral) showing paired spines ("parameres"), 143. ♀: genitalia (ventral), 144. ♀: dorsal view of head, 145. ♀: right mid-leg, 145a, same, portion of serrated inner margin of tibial spur, further enlarged, 146. ♂ pupa: apical part of exuviae (ventral), slightly twisted, setal fringe not marginal on right side, thus small dorsal spine visible; position of left dorsal spine indicated by inset circle, 147: ♂ pupa: apex of left appendage further enlarged, not all setae shown & some shortened; 3 denticles (shagreening) greatly enlarged, 147a, b, anterior & posterior dorsal sclerites from segment III, enlarged.

some long, erect setae; copulatory organ with slender stem and clavate apex, within which is a pair of claw-shaped spiniform processes ("parameres"). Claspers slender, to very slender, setose, with long apical segment.

Female imago (in spirit; Figs 143–145): similar in general appearance to male, though smaller, antennae shorter, and palpi smaller, very slender and inconspicuous. Forewings have forks 1, 2, 3, 4, 5. A notable difference is that the anterior head warts are smaller than the posterior in both available females instead of the reverse, and the head narrower from side to side, which makes the eyes appear relatively larger. Mid-legs much widened, fringed, tibial spurs 0.4.4. Abdominal sternum V without paired lateral knobs or slits, paired sternal plates of VIII separated for entire length, with apical fringe of setae, lateral margins more heavily sclerotized than rest; sterna of apical segments represented by median plate, XI with usual paired papilli and cerci, dorsal hood fringed with long curved setae.

DESCRIPTION OF LARVA (Figs 148–157, Table XIII)

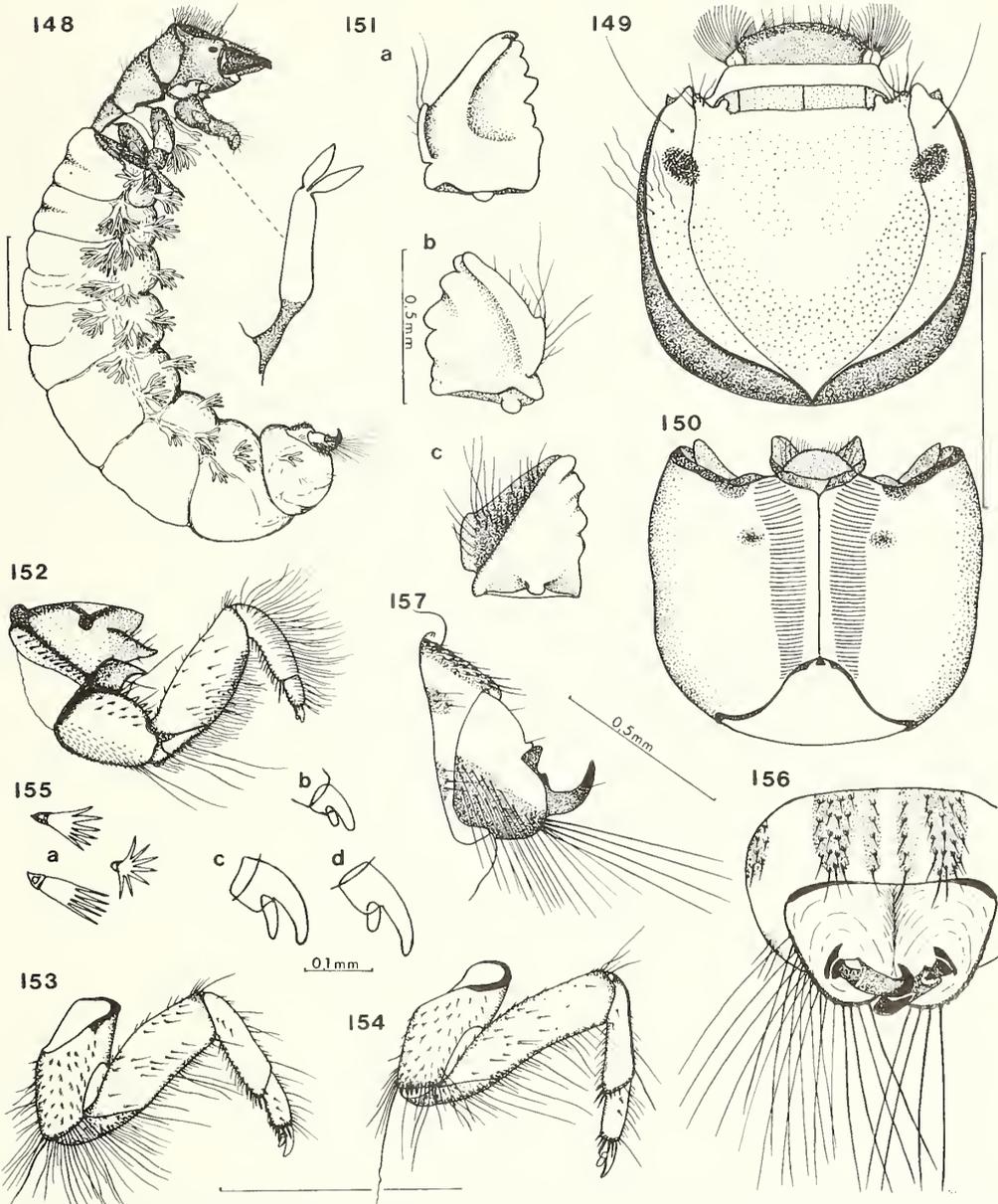
Protomacronema larvae are strongly reminiscent of *Amphipsyche* larvae in appearance, though smaller, with less conspicuous gills and with characteristic long, curly setae on their heads, in later instars of the only known species at least. There are also certain resemblances to *Macrostemum* larvae, such as shape of submentum, stridulatory files and mandibles.

Mature larva (in spirit, Figs 148–157, Table XIII): length about 7.0 mm. One of the specimens is commencing to pupate; the other is about the same size and evidently a mature larva, both come within the same head width range (head width at eyes 4.3 and 4.9 grid squares respectively), and are therefore presumably in the same instar, in spite of slight size and colour differences.

Head (Figs 148–150): rounded, with flat top and carina, frontoclypeal apotome longer than wide, a pair of small knobs on the anterior margin, apex acute, dividing carina, which runs alongside it almost to the posterior margin; colour described by Gibbs (1973) as follows: area within carina dark brown with orange-brown areas in centre and adjacent to eyes, head otherwise dark brown with orange-brown stridulatory files. Head within carina with long, curling setae arising from clear pits, anchor-shaped central area smooth. Eyes dark, placed well forward. Stridulatory files long, narrow, reaching to occipital foramen, a pair of small depressions lateral to them. Anterior ventral apotome brown, represented by a small sclerite with cleavage line on left side only; posterior ventral apotome minute, black. Head in available specimens retracted within pronotum.

Mouthparts (Figs 149–151): labrum brown, largely sclerotized, with membranous lateral lobes bearing tufts of silky setae, anterior margin with smaller tufts on ventral side, anteclypeus with four brown, sclerotized plates, of which the median ones are large, the lateral ones small and partly concealed by the anterior corners of the frontoclypeal apotome. Mandibles large, strong, subtriangular in section, with a number of setae on outer side, which is partially demarcated by a short, oblong lateral flange in both cases; left mandible with seven teeth, one flattened; right mandible with five teeth, no inner brushes. Submentum oval with setose margin, flanked by stipites, all brownish.

Thorax (Fig. 148): thoracic nota dark brown, with few, small setae; pronotum has paired sclerites with indented anterolateral corners and posterolateral black marginal thickenings. Meso- and metanota undivided, with slight black lateral thickening and large posteromedian black spots, lateral diagonal stripes only faintly indicated. Prosternal plate narrow, brown, without median sulcus. Meso- and metasterna membranous, mesosternum with one pair of coxal gills; these are very long and distinctive because the basal part is contracted and sclerotized, widening to form a soft stalk tipped with a single pair of leaf-like apical branches. Metasternum with two pairs of tufted gills. Propleuron also unusual, with pre-episternum set into



Figs 148–157. MACRONEMATINAE: *Protomacronema pubescens*, mature larva. 148. habitus, lateral (right appendages only shown) mesosternal gill shown further enlarged (same scale as legs). 149, 150. dorsal & ventral views of head, 151. a. left mandible, dorsal, b and c. right mandible; a. dorsal, b. ventral., 152, 153, 154. foreleg, mid- & hind legs (right), foreleg with pleural sclerites. 155. a. palmate setae from coxa, b, c, d. claws of foreleg, mid- & hind legs, all further enlarged, 156. ventral view of abdominal segment IX, with anal prolegs. 157. right anal proleg, lateral.

side of large 2nd pleural sclerite, epimeron narrow, bearing a row of small spine-like setae (see Fig. 152).

Legs (Figs 152–155): short, strong, subequal, yellowish brown to brown, forelegs as usual darker than rest, claws brown, legs with many secondary setae, particularly on and near posterior margin. Forelegs: coxa with high basal process which articulates with propleuron just below pre-episternum, a row of short spine-like setae along anterior margin and many small palmate setae as indicated; femur with small thumb-like basal projection on inner side, as in *Macrostemum*; tibia and tarsus with row of ventral spine-like setae and very weak brush of long setae; claws blunt with thick blunt basal spine. Mid- and hind legs also with palmate or feathered setae on coxae, both with stout spines at apices of tibiae and tarsi, claws larger but still blunt, with blunt basal spines.

Abdomen (Figs 148, 156, 157): smooth, not deeply segmented, few setae except along the transverse indented bands on segments I and II, which are set with minute hooked spinules as in *Macrostemum* and *Amphipsyche*. Tufted tracheal gills (rather small and inconspicuous, with fine branches), present in six rows on segments I–VI, four on VII and two on VIII. Gill filaments tend to form tufts towards apices of gill stalks. Segment IX bears a pair of fairly large but inconspicuous setose ventral plates, also smaller ventrolateral plates; paired dorsolateral plates present but almost concealed under VIII, each bears a few short setae. There are no such sclerites on VIII. Anal prolegs short, stout, with somewhat indistinct lateral sclerites, large anal claws and lateral fringe of long setae, no fan. Anal gills not seen.

TABLE XIII.

Number and position of tracheal gills in mature larva of *Protomacronema pubescens*

Segment	Mature larva		
Mesothorax	1 pair		
Metathorax	2 pairs		
Abdomen (right side)	DL	VL	V
I	1	1	1
II	2*	2	1
III	2	2	1
IV	2	2	1
V	2	2	1
VI	1	2	1
VII	1	2	—
VIII	—	1	—
IX	—	—	—

*Abdominal gills marked 2 have two main stems whose bases are contiguous but not joined.

DL = dorsolateral gill, these are not separated into pre- and postsegmental gills, but are, however, all presegmental in position whereas the ventrolateral gills are postsegmental. Gill branches range in number from 10–14 per gill stem on segment II to 4–6 per stem on V–VIII, and are always small and slender.

VL = ventrolateral gill.

V = ventral gill.

DESCRIPTION OF PUPA (Figs 144–147)

The only pupal material available is the middle and posterior (apical) part of the pupal skin of a ♂ pupa (see Figs 144–147). It has been mounted on a slide and from it the following facts could be ascertained:

Anal appendages short and stout compared with other genera so far described, each tipped with a large, sharp, sclerotized point, and fringed laterally (largely ventrally) with long, stout setae, some with curled tips, arising from prominent bases; between them, towards the dorsal side, there is a pair of smaller sclerotized points. The appendages are heavily shagreened (i.e. covered with scattered triangular points as in shark skin). Usual pockets for ♂ genitalia, smaller than in *Amphipsyche* or *Macrostemum*. Dorsal plates large, with long stout teeth; anterior plates apparently on segments III–VIII, posterior on III only. There were no gills on the material available, and as I have been unable to obtain any further pupal material it is not possible to provide a table showing gills or dorsal plates (of which only some are present).

REMARKS

Ulmer (1904b) made *Protomacronema pubescens* Ulmer the type species of his new genus, *Protomacronema*, from Kamerun. Shortly afterwards he described *Amphipsyche africana* from West Africa (Ulmer 1905c), but later decided that he had been mistaken, placing it in synonymy with his *Protomacronema pubescens* (Ulmer 1907d). This led to subsequent confusion in the identification of specimens and consequently in the literature. The position was later clarified by Kimmins (1962b) in a revision of these two species. He concluded that both were certainly *Protomacronema* but that *africana* was in fact a valid species, clearly different from *pubescens*, and gave new figures and descriptions of both species with their known distributions and synonymy. The parts relevant to *P. pubescens* are given above. Ulmer's record from Zululand (Ulmer 1913) is given with a query as Kimmins felt that from the description the specimens appeared to be intermediate between *pubescens* and *africana* and should be re-examined. Material from Rhodesia (Zambezi River) examined by Kimmins proved to be of *africana*. Jacquemart (1963a) figured a male from the Victoria Falls (Zambezi) as *pubescens*, however, his drawing clearly shows the U-shaped excision of *africana*, to which species it must be referred.

As will be seen from the list which follows, eight species have been described. Of these probably only four or five represent valid species, since three were described, with very poor figures, by Navás from females only.

Statzner (1981) had two kinds of *Protomacronema* larva from Ivory Coast, which he separated by differences in the submentum and the dorsal sclerites on abdominal segment IX.

BIOLOGY

Little is known of the biology of *Protomacronema* larvae. Gibbs' larvae and pupae were taken from the Black Volta River at New Bator, in an area where fast-flowing rapids linked by slow-flowing deeper parts occurred (Gibbs 1973; Petr 1970). The *Protomacronema* larvae were found where the current velocity exceeded 20 cm/sec, increasing in numbers with increased current speed, and making a contribution to the standing crop of, for example, 2 534.9 mg/sq. m out of a total of 42 957.9 mg/sq. m where the current speed was 140 cm/sec. The total Trichoptera contribution at that point was 30 835.2 mg/sq. m, of which the great majority were *Cheumatopsyche* species.

The substratum in the rapids consisted mainly of stones, often with deep crevices between them, the depth of water during the dry season being under 30 cm. During floods the current speed increased to 300 cm/sec at times.

AFRICAN SPECIES OF *PROTOMACRONEMA* (Endemic Genus)

- P. africana* (Ulmer) 1905c: 48–50, pl. 1, figs 36–39, as *Amphipsyche*. ♂. West Africa.
 Kimmins 1962b: 99–101, figs 5–9 (♂ genitalia), in a revision of the two species concerned, transferred *africana* from *Amphipsyche* to the genus *Protomacronema* as a species *sui generis*, removing it from the synonymy of *P. pubescens* (Ulmer) in which Ulmer had himself placed it (Ulmer 1907d), and giving the following synonymy:
Protomacronema pubescens Ulmer (*partim*), 1907d: 36, figs 28–30, Congo examples.
Protomacronema pubescens Ulmer, 1912: 98–99 (Congo examples).
Protomacronema pubescens Ulmer, Lestage, 1919: 303, (*partim*, West Africa).
 ? *Protomacronema pubescens* Ulmer, Navás 1930a: 329, Congo.
 ? *Protomacronema divisum* Navás 1930a: 329, Congo. ♀.
 ? *Protomacronema pubescens* Ulmer, Navás 1931c: 277 (Congo); 1931b: 141 (Congo).
 ? *Protomacronema pubescens* Ulmer, Mosely 1932: 5 (Zambezi).
Protomacronema pubescens Ulmer, Jacquemart, 1961b: 19, fig. 12 (Congo).
 Distribution: West Africa, Congo Rhodesia (Victoria Falls), ? Portuguese East Africa (Zambezi).
- P. divisum* Navás 1930a: 329–330, fig. 44. ♀. Belgian Congo.
 Kimmins 1962b: 101 places this in probable synonymy with *P. africana*.
 Distribution: Belgian Congo.
- P. hyalinum* Ulmer 1904a: 354–355, 359, fig. 1. ♂. French Congo.
 Ulmer 1905a: 27, figs 13, 14. ♀. Congo.
 Distribution: French Congo, Belgian Congo, Madagascar.
- P. pellucidum* Navás 1923: 26, fig. 37. ♀. Madagascar.
 Distribution: Madagascar.
- P. pubescens* Ulmer 1904b: 417–419, figs 4–8 (♂ palpi, wings & genitalia).
 Ulmer 1907d: 36 (*partim*, Kamerun only, *nec* figs 28–30).
 Ulmer 1912: 98, 99 (Kamerun only).
 ? Ulmer 1913: 191 (Zululand).
 Lestage 1919: 303 (*partim*, Cameroon).
 ? Barnard 1934: 370, figs 41a–e (Zululand).
 Distribution: Cameroons, Sierra Leone, Ghana, Ivory Coast.
- P. splendens* Ulmer 1905c: 65–67, pl. 3 fig. 106. ♂. Gabun.
 Ulmer 1907d: 34, 37, 38, fig. 31, col. pl. 1, fig. 3 (whole insect).
 Distribution: Gabun.
- P. tanganyikae* Jacquemart 1961c: 69–71, figs 7–10. ♂. Lake Tanganyika, Albertville.
 Distribution: Belgian Congo (Lake Tanganyika).
- P. testaceum* Navás 1934b: 91–92, fig. 57. ♀. French Guinea.
 Distribution: French Guinea.

Genus *LEPTONEMA* Guérin-Meneville 1843

Leptonema Guérin 1843: 165, 396.

Type species *pallida* (recte *pallidum*) Guérin 1843: 396. Brazil.

Location of type unknown; Type species currently unrecognizable, see Mosely 1933: 7–8.

Leptonema Guérin; Mosely 1933: 7–12.

Revision of the genus, with key to known species.

Leptonema Guérin; Ulmer 1957: 346–348, 352, 354, larval and pupal stages.

Leptonema Guérin-Méneville; Fischer 1947: 313–315.

Leptonema Wiggins 1977: 108, 109, figs 6. 7A–E.

Generic diagnosis (derived mainly from Mosely 1933: 9–10)

Imago: tibial spurs of ♂, ♀, 2.4.4 or 1.4.4, inner spurs longer than outer; mid-leg of ♀ not usually dilated; antennae very long, twice to three times length of forewing, scape short and thick, flagellum slender; maxillary palpi with basal segment short, second long, third shorter, fourth shorter still, fifth as long as or longer than the rest put together, ringed. Forewing usually with short, broad discoidal cell, forks 1, 2, 3, 4, 5 present, fork 1 with footstalk; hind wings broader and shorter than forewings, forks 1, 2, 3, 5 present. Wings semi-transparent or streaked with black pubescence or irrorated in American species, generally coloured or patterned in African and Madagascan species. Forewing length in ♂ 8–28 mm, in ♀ 10–19 mm (not many females known); where known ♀ usually larger than ♂. Male genitalia with tenth tergum divided, bearing simple or complex cerci; copulatory organ with or without spiniform processes. ♀ with sternal plates of VIII widely separated. ♂, ♀ both with paired fenestrae on fifth sternum.

To date over 40 species have been described from the Neotropical Region, extending as far north as Mexico and the Texan border, fourteen from Central and Southern Africa and Madagascar, and one each from the Mediterranean and India.

Leptonema natalense Mosely

(Figs 158–176, Tables XIV, XV)

Leptonema natalense Mosely, 1933: 24–25, figs 43–48 (forewing, ♂ genitalia). Natal, Kloof, 1 500'. ♂.

Holotype ♂ in British Museum (Natural History).

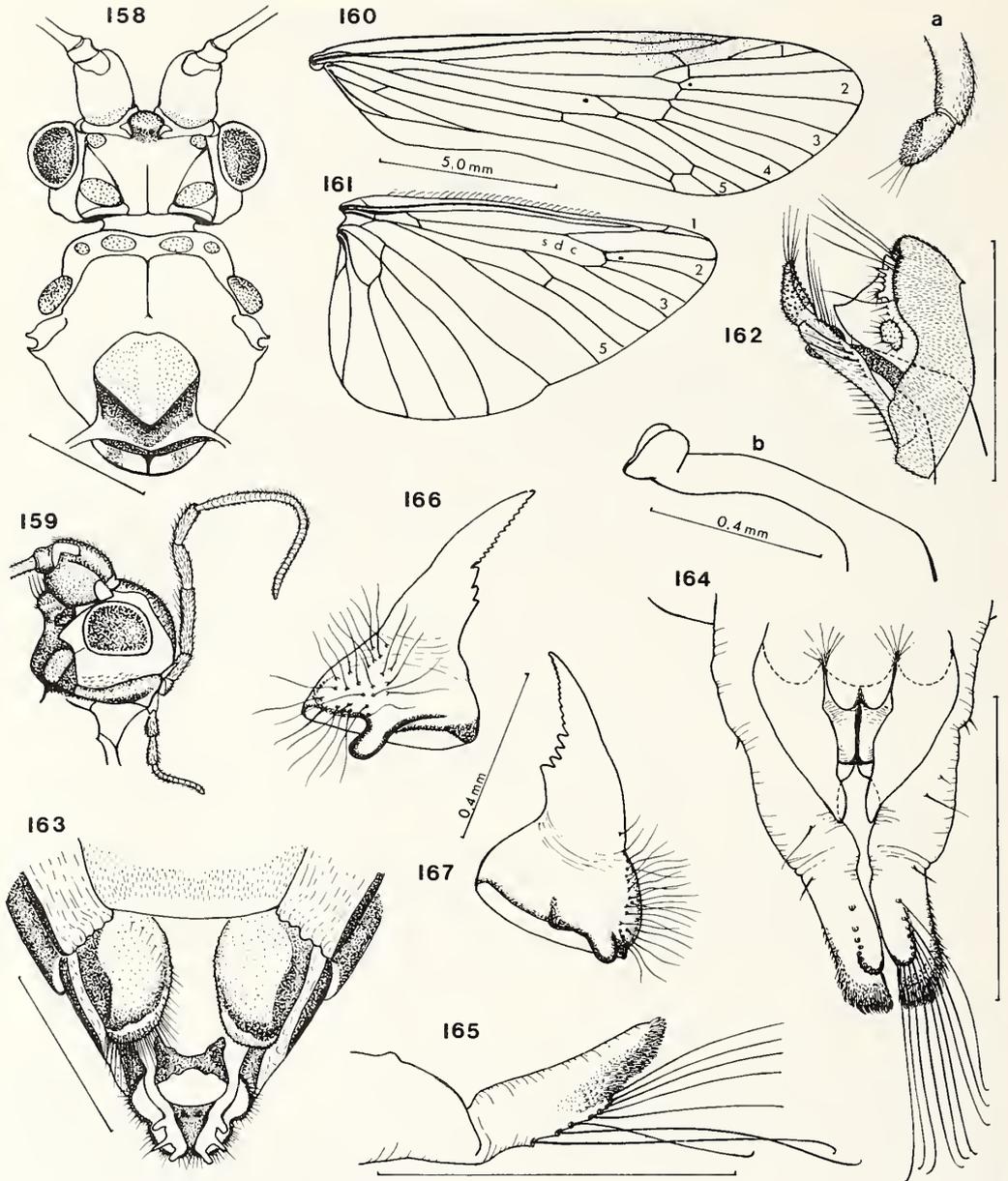
Leptonema natalense Mosely; Barnard 1934: 370, fig. 41f–h (wings, ♂ genitalia), as *L. occidentale* Ulmer; a mistaken identification which he later corrected (Barnard 1940).

Leptonema natalense Mosely; Marlier 1961: 159, 202–207, figs 23, 24. ♂, ♀, larva, pupa (♀ not described). Kivu.

Distribution: South Africa: Natal, Eastern Transvaal, Pondoland; Lesotho, Congo (Kivu).

DESCRIPTION OF IMAGOS (Figs 158–163)

Male imago (in spirit): a fairly large species, medium to dark brown in colour, forewings 11–13 mm long, pubescent, fuscous, hind wings hyaline, often iridescent, wide at base (folded at rest); legs yellowish, not noticeably widened, spurs 1.4.4 (2.4.4 in some Natal specimens, second spur on foretibia very small); eyes medium-sized, dark; antennae very long (*c* 35 mm), dark, scape enlarged, flagellum very slender; palpi well developed, finely pubescent; face rounded, with few setae; a single small, flat, median wart near antennal bases; vertex with two small warts at bases of antennae, a large protuberant median wart between them, all brown, posterior warts larger, cream-coloured, setae long. Thus in this genus the anterior warts on the



Figs 158–167. MACRONEMATINAE: *Leptonema natalense*, ♂, ♀, pupae. 158. ♂: dorsal view of head & thoracic nota, 159. ♂: head, lateral, with maxillary & labial palpi, 160, 161. ♂: fore & hind wings (right), 162. ♂: genitalia, right lateral: a. apex of left clasper, ventral, b. copulatory organ, right lateral., 163. ♀: genitalia, ventral view, 164. ♂ pupa: apical part of exuviae, ventral, 165. ♂ pupa: apex of left appendage, lateral, 166, 167. ♀ pupa: right & left mandibles, ventral.

vertex are, most unusually for Macronematinae, considerably smaller than the posterior ones. Pronotum with median division and two pairs of oval cream warts; mesonotum without warts, but mesoscutellum with large pair of poorly defined cream warts. Abdomen brown, with paired fenestrae on 5th sternum, genitalia brown, 9th tergum with margin rounded, entire, tenth divided to form a pair of triangular plates with basal setose processes, copulatory organ with small truncate apex flanked by wing like expansions; claspers with basal segment apically widened, apical segment short, broad, truncate in dorsal view, in lateral view bluntly pointed with short blunt spines and fine setae.

Mosely (1933) described the pinned male as having a black head, dark fuscous antennae with yellowish annulations, ochraceous palpi, black thorax, brown forewings with light brown pubescence and fuscous hind wings.

Female imago (in spirit): much same size as male (forewing 12.4 mm), antennae shorter, mid- and hind legs somewhat flattened, scarcely widened, not fringed; spurs 1.4.4 (only two females available). Pale fenestrae on V obvious; paired sternal plates of VIII widely separated, apical margins thickened, pale, setose, lateral margins darkened, sterna of apical segments represented by sclerotized median plates, usual apical papillae and cerci, dorsal hood fringed.

Material in the Albany Museum collection includes 20 males, 2 females, 32 larvae and 9 pupae, about half the specimens being in good condition. Amongst the pupae are mature males disclosing genitalia, also one good female bred out in the laboratory by Dr Chutter. In each case these are accompanied by the pupal case, larval sclerites and pupal exuviae, thus definitely linking both sexes of the species with their larval and pupal stages.

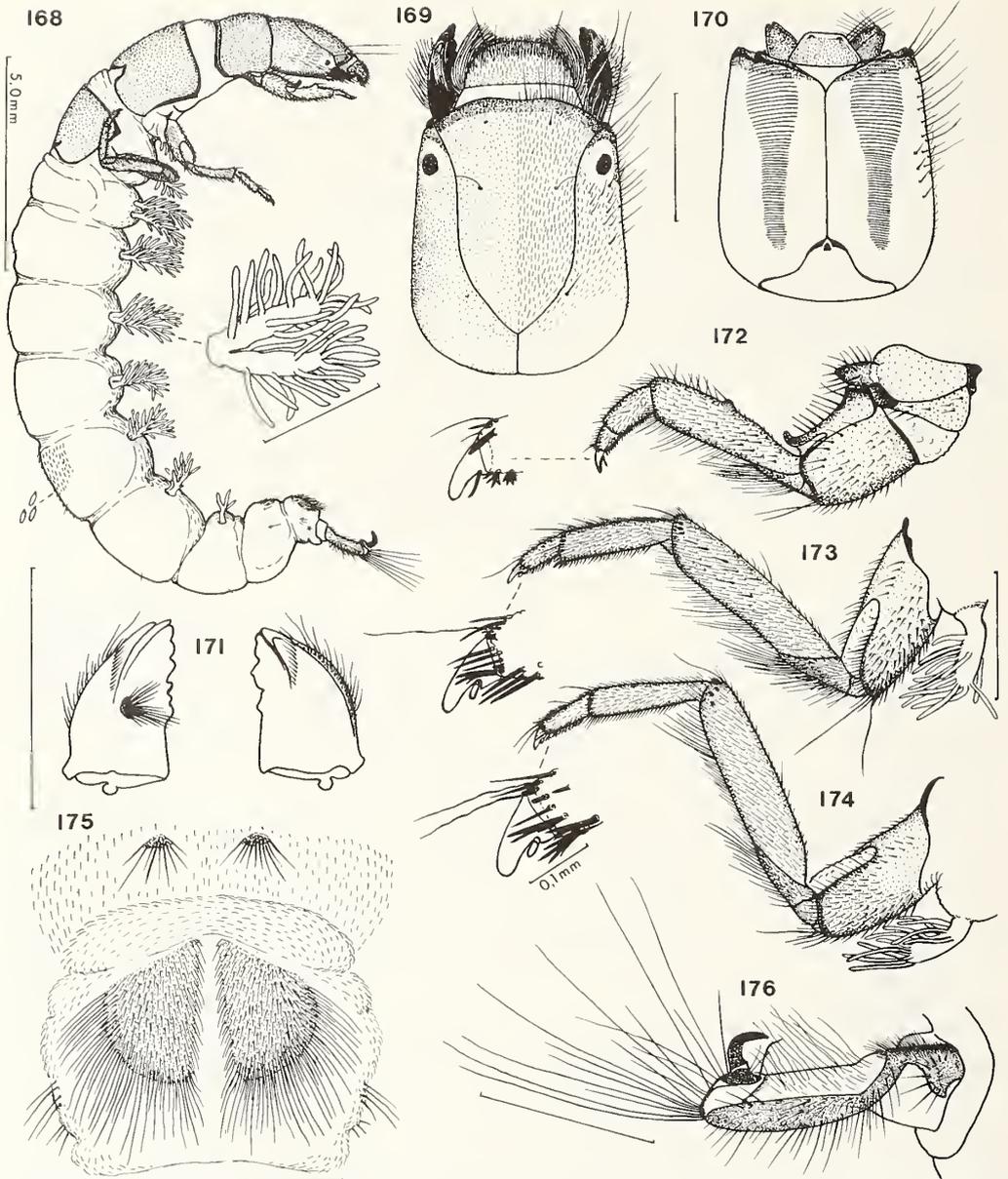
DESCRIPTION OF LARVA (Figs 168–176, Table XIV)

Mature larva (in spirit; Figs 168–176): length 22–23 mm, greatest width (abdomen) *c.* 3 mm. Large larvae, sclerotized parts amber to pale orange or brown in colour, abdomen cream to pale mauve, gills white. Mean head width of mature larvae examined, at eyes, 1.34 mm (mean of 18 mature larvae, range 1.21–1.53 mm). As these larvae are somewhat smaller than those described by Marlier (1961), I checked the size of the frontoclypeal apotome against that of the frontoclypeal sclerites found in the pupal cases, and found that they fell into the same range. I am therefore assuming that these are mature larvae.

Head (Figs 169, 170): almost oblong, widest near occipital foramen, rounded, without carina, nearer in shape to those of Hydropsychinae than Macronematine larvae; frontoclypeal apotome with slight median indentation in rounded anterior margin, head bright amber yellow to chestnut with a few obscure muscle marks, thickly set with short, fine setae and a few longer ones, ventral side paler. Eyes black, set in lighter areas, each beneath six small cuticular lenses. Antennae minute, at base of mandibles. Stridulatory files large, long, inconspicuous unless darkened. Anterior ventral apotome a shallow triangle, with sutures on both sides, posterior ventral apotome dark, minute.

Mouthparts (Figs 169–171): labrum large, retractile, setose, brownish, almost semicircular, with silky lateral brushes; anteclypeus pale, with shiny areas which may represent sclerites, but if so are scarcely distinguishable. Mandibles strong, red-brown, left one with two large apical teeth, in mature larvae usually worn down to appear a single broad, flat-topped curved tooth, dorsal to which is a smaller tooth bearing a row of white setulae, five smaller, less prominent teeth along cutting edge, mandible hollowed with inner brush of setae. Right mandible with two apical teeth, a smaller dorsal tooth with row of setulae, three irregularly shaped teeth on cutting edge, mandibles triangular in section, outer faces setose. Maxillary palpi short, thick, 5-segmented, longer than maxillary lobes; labium short, thick, palpi minute. Submentum a truncated triangle, brown, as are stipites.

Thorax (Fig. 168): terga bright amber yellow to chestnut, unpatterned, with many small setae and a few longer ones, most margins narrowly black or brown; pronotal sclerites paired



Figs 168–176. MACRONEMATINAE: *Leptonema natalense*, mature larva. 168. habitus, lateral (right appendages only shown), paired gills from abdominal segment II (left) further enlarged, 169, 170. dorsal & ventral views of head, 171. right & left mandibles, dorsal, 172, 173, 174. foreleg, mid- & hind legs (left); foreleg shown with pleural sclerites, mid- and hind legs with attached coxal gill; in each case tarsal claw & adjacent setae shown further enlarged, 175. ventral view of abdominal segments IX & part of VIII, showing ventral sclerites, 176. left anal proleg, lateral.

with narrow posterior division, mesonotum with a conspicuous black M-shaped mark, centrally placed near posterior margin, metanotum with a much smaller crescent. Prosternum with large, deep, flanged sclerite, attached laterally to the pronotum by muscles & epidermis; a pair of smaller sclerites lie behind it, along the posterior border of the mesonotum, sometimes partially obscured by an epidermal fold. Pre-episternum unbranched, conical, set with stout setae as is the epimeron; episternum glabrous. One pair of branched mesosternal gills present, two pairs of branched metasternal gills (see Figs 173, 174).

Legs (Figs 172–174): slender, brownish yellow to yellow, forelegs as usual darkest, thickly set with setae, mainly small, inconspicuous, except marginally. Foreleg with strong thumb-like process on upper distal margin of coxa and line of strong setae, trochanter divided, femur with usual protuberance (scrapers of stridulator) on anterior margin, tibia and tarsus with ventral band of multifid or plumose setae, the latter also mingled with strong spine-like setae on the other joints; claw blunt with slender basal spine. Mid- and hind legs subequal, tibiae and tarsi with marginal belt of strong spine-like setae, in hind leg mingled with long pinnate setae, which also occur on femur, tibia and tarsus of both legs; claws small, stout, blunt, with single short thick spine near base.

Abdomen (Figs 168, 175, 176): thickly covered with small, narrow scale-like setae, pale and hard to see unless larva comes from turbid water. Abdominal tracheal gills: two pairs on segment I, one pair on II–VII (see Table XIV), gills on segments II–VII each with two stems and 12–20 filaments per stem on the more anterior gills, fewer on the posterior ones. On eighth sternum a small pair of triangular setose sclerites, on ninth a large pair; no dorsal or lateral sclerites on VIII or IX, but four small clumps of lateral setae on IX. Anal appendages fairly long, setose, with strong yellow lateral sclerites, claws stout, no anal brush. Anal gills present, only three seen but according to Ulmer (1957) there are five.

Earlier instars:

Only one identifiable younger larva was found in the material available, and this was apparently very recently ecdysed (many gills still in cuticle of earlier instar). Head width at eyes 0,9 mm; gill count as in mature larva, all double gills already present, but filaments only 1–4 in number per gill stem. Posterior prosternal sclerites present but very pale and inconspicuous, otherwise as mature larva in general appearance, only paler and smaller. Assuming that *Leptonema* has six larval instars as in the other Macronematinae studied, this one would appear to be in the fourth instar.

There were in addition five probable early instar larvae, of which brief descriptions follow, but it was not possible to be certain of their identity, though they were clearly separable from early Hydropsychine larvae present in the same samples, and do appear to be of *Leptonema*.

Probable second instar larvae: large head relative to body, width at eyes 0,23–0,26 mm (three larvae), head setae few, long, no stridulatory files as yet; mandibles strong, labrum large, setose. Gills absent. All three thoracic nota well sclerotized with fine brown lines demarcating most edges, a few long setae; pre-episternum present, simple, with one seta. Legs: foreleg with two long feathered setae on tarsus, claw long, stout, with two long basal setae, one shorter one and a small spine. Long plumose setae also present on coxa and tibia; coxa with anterior row of about three long setae but no thumb-like process as yet. Abdomen smooth with a row of very long setae, IX with two long ventral plumose setae but no ventral sclerites as in older larvae. Anal prolegs long, claw strong, curved, a few long setae.

Probable third instar: head width at eyes 0,35 and 0,36 mm (two larvae); setae over whole larva shorter and much more abundant, stridulatory files present on ventral side of head. Lateral margins of thoracic nota darker, one pair of simple gills on mesothorax, two pairs on metathorax, pre-episterna with four setae. Forelegs: coxae still lack thumb-like process, femora with scrapers; all limb claws with a single long basal spine-like seta and a small basal spine. Abdomen hairy, now with many small scale-like setae; patches of long setae on eighth and

ninth sterna. One pair of simple gills, each with a single filament, on segments II–VII, no double stems as yet. No gills bear a seta, as in third instars of *Macrostemum* and *Amphipsyche*, but this is to be expected as *Leptonema* does not have ventral gills.

TABLE XIV.

Number and position of tracheal gills in mature larva of *Leptonema natalense*

Mesothorax	1 pair		
Metathorax	2 pairs		
Abdomen (right side)	L	VL	V
I	—	1	1
II	—	2*	—
III	—	2	—
IV	—	2	—
V	—	2	—
VI	—	2	—
VII	—	2	—
VIII	—	—	—

*Gill with 2 main stems arising from a common base.

L = lateral gill.

VL = ventrolateral gill.

V = ventral gill.

DESCRIPTION OF PUPA (Figs 164–167, Table XV)

Nine pupae were available, including one good, mature male pupa with case and larval sclerites from Lesotho, and one good male from Natal (Inkomba stream), also six male and female pupae in very poor condition from the Ingeli Forest and from the Inkomba stream, Natal. In each case they were associated with larvae and identifiable as *Leptonema natalense*. There was also a female imago from the Inkomba stream which had been correlated in the laboratory, together with its associated case, pupal pelt and larval sclerites.

Male pupa (in spirit; Figs 164, 165): pupa still within pupal pelt, length 12 mm; head similar to that of imago, eyes, head and thoracic warts and palpi clearly visible. Labrum small, rounded, a few setae along upper margin and near antennal bases; above labrum paired clumps of long, hooked brown setae. Mandibles as in ♀ (Figs 166, 167), with inflated bases, outer faces set with setae; left mandible with apical and four lateral teeth, right with apical and three lateral teeth, inner margins between apical and lateral teeth serrated. Palpi long, well developed. Antennae very long, slender, each terminating in $2\frac{1}{2}$ coils round apex of abdomen. Forewing cases brownish, hind wing cases cream, reaching anterior end of segments VI and V respectively. Mesoscutum shows wide, paired median bands of pubescence through pelt. Legs cream with small brown spots at apices of trochanters and tibiae, spurs 1.4.4. Abdomen: segment III with a pair of tapering unbranched lateral gills, IV–VII with two such gills each side; II–VII also with paired ventral tufted gills, each with two main stems and numerous filaments. Paired dorsal plates as in Table XV; presegmental plates on segments II–VIII, postsegmental

plates (wide strips with many teeth) on III only. Shagreening practically absent; a belt of long setae on IV and a number of hairs on V. Anal appendages of medium length, plump, strongly curved dorsad, contracting abruptly to form short finger-like apices densely fringed with small spine-like setae. Proximal to the apex the appendage is fringed with eight to ten long stout setae with curved tips. Male genitalia enclosed in pockets as usual.

Female pupa (in spirit; Figs 166, 167): general appearance as male, but larger, antennae shorter, abdomen stouter; female genitalia not in pockets; anal appendages much as in male, but somewhat stouter.

Pupal case: about 15 mm in length, almost completely covered with large stones or rock fragments, interstices filled with small sand grains. Pupa within a complete sac-like silken lining, closed at both ends, which are formed from a fine meshwork of strands, allowing for passage of water. Ventral side of case adpressed to rock, of silk only; larval sclerites packed into posterior end of case as usual.

TABLE XV.

Number and position of branchial gills, dorsal plates etc. of ♂ pupa of *Leptonema natalense* Mosely.

Abdominal segment	Tracheal gills (right side)		Dorsal plates (paired)	Setae
	L.	V.		
I	—	—	—	
II	—	2	Presegmental	
III	(1)	2	Presegmental Postsegmental	
IV	(2)	2	Presegmental	Belt of hairs
V	(2)	2	Presegmental	Scattered hairs
VI	(2)	2	Presegmental	
VII	(2)	2	Presegmental	
VIII			Presegmental	

L. = lateral gills; these are conical pouch-like gills, either single (1), or double, lying one above the other (2).
V. = ventral gills; these are branched gills, each with 2 main stems arising from a common base.

REMARKS

The larvae and pupae described above are definitely those of *L. natalense* Mosely, correlation with the imagos having been reliably established.

Marlier (1961) described larvae of *L. natalense* from Kivu. These show small differences in patterning from the larvae described above, due perhaps to a certain amount of geographical variation. There are also slight differences in mandibular teeth. Marlier described the gills as "two pairs per segment", but presumably meant one pair of double gills per segment, except on segment I, as is the case in all Afrotropical specimens that I have seen.

Gibbs (1973) described the larvae of three species of *Leptonema* from Ghana: *normale* Banks, *guineense* Gibbs, and a third uncorrelated species near to *natalense* but showing some

differences in head pattern and structural details. He stated that the larvae of all three species had one pair of two-branched gills with many filaments on segments II–VI, however, his diagram shows in addition two pairs of single gills on segment I and a pair of two-branched gills on VII as in *natalense*.

It is somewhat more difficult to reconcile the gill position in *natalense* (and other known African species) with that in the American *Leptonema* sp. larva from Mexico, beautifully delineated in Wiggins' book (1977, Fig. 6.7A). In the latter species the pairs of double gills are present though slightly separated basally but there are in addition single gills in a presegmental position on segments II–VI (presumably also paired), so that the gill count would be two pairs on segments I and VII and three pairs on II–VI. However, Dr O. S. Flint, Jr. (in litt. 4.viii.1982) has very kindly informed me that there are two groups of *Leptonema* species represented in the Americas, one of which being that which includes the African species and the other being entirely American. All Flint's associated larvae belong to species in the second group and all have the additional ventral gills, as figured by Wiggins (1977). When next in the Neotropics Dr Flint will endeavour to collect larvae of the first group. Should these resemble known African larvae in gill arrangement, it may prove necessary to reconsider the generic status of the two groups.

There is a surprisingly wide variation in the coxal armature in *Leptonema* species, in African species at any rate. In *L. normale* the fore-coxa ("anterior femur" of Gibbs) has its anterior margin produced into a flat flange-like plate fringed with heavy sword-like setae, in *guineense* the coxa is bordered with a row of long stiff spine-like setae, and in *natalense* and Gibbs' unknown species it bears an anterior thumb-like process and a few stiff spine-like setae. Wiggins' Mexican species also possesses such an apical coxal process (Wiggins 1977, Fig. 6.7B). In species known to me the easiest characters to use in separation are the coxal armature and the shape of the stridulatory files. Statzner (1981) in addition uses the abdominal setae in separating his three species.

The Angolan larvae that were kindly lent to me as *Protomacronema* sp. by Drs de Barros Machado and Carvalho of the Museo do Dundo (see Marlier 1965/66) proved to be either *Leptonema normale* Banks, as described by Gibbs (1973), or a similar species. They differed from *natalense* not only in coxal structure but also in having narrower stridulatory files and two thin stiff anal gills as well as three normal ones (thus making up the usual five).

The most interesting features of *Leptonema* larvae, however, lie in their many similarities to Hydropsychine and Diplectronine larvae, particularly those of *Cheumatopsyche* and *Diplectronella*, for which they may easily be mistaken unless closely examined. Resemblances include the rounded head, mandibular structure, hairy appearance and possession of setose ventral plates on both VIII and IX. Nonetheless, *Leptonema* larvae have the usual main Macronematine characters such as simple pre-episterna, entire labium, frontoclypeal apotome not widely expanded behind eyes, minute posterior ventral apotome and meso- and metanota without transverse sutures (Scott 1975). It is possible that these wide differences and similarities in larval structure may be due to differences and similarities in larval biology, currently not well known.

BIOLOGY

Leptonema larvae inhabit flowing water, usually living beneath stones or on rocks in current or in cascades. There they construct typical hydropsychid retreats covered with sand grains, rock fragments or plant material, rather more rigidly constructed than is the case in *Hydropsyche* and provided with a simple net for catching food, which appears to include insects and plant material. In Kivu *Leptonema* larvae were common in high altitude streams (2 000–3 000 m) with acid or neutral water, often slightly peaty. In Ghana they were found

both in highlying forest streams and also in streams in cultivated lowlands. (See Marlier 1961, Gibbs 1973, Wiggins 1977.)

South African specimens in the Albany Museum collection (all *L. natalense*) came from streams. The larvae were collected from stones in current and the imagos were either bred out in the laboratory or taken in the field on riverine vegetation or at light. They appeared to be present throughout the year.

AFRICAN SPECIES OF *LEPTONEMA*

- L. affine* Ulmer, 1905a: 27–28. ♂ ♀.
 Ulmer, 1907d: 57, 58, fig. 60 (♂ wings) & pl. II fig. 8 (col. fig. of imago).
 Mosely 1933: 27, figs 54–56 (♂ genitalia).
 Distribution: Madagascar.
- L. alatum* Marlier, 1961: 159, 199–200, fig. 22 (wings). ♂ ♀.
 Distribution: Kivu.
- L. displicens* (Navas), 1935: 73–74, fig. 34. ♂, as *Macronema*.
 Sýkora, 1964: 281, figs 13–16 (♂ genitalia), as *Leptonema*.
 Distribution: Madagascar.
- L. guineense* Gibbs, 1973: 385–386, figs 56–59 (♂ genitalia), 66–68 (larva), 80–82 (pupa). ♂ ♀ larva pupa.
 Distribution: Ghana.
- L. latipenne* Marlier, 1947: 31–32, figs 1, 2 (genitalia). ♂ ♀.
 Distribution: Ivory Coast.
- L. machadoi* Marlier, 1965/66: 22, 44–45, fig. 15 (wings). ♂.
 Distribution: Angola.
- L. madagascariense* Ulmer, 1905b: 81, fig. 50 (wings). ♂.
 Ulmer 1907d: 58, figs 61, 62 (wings, ♂ genitalia).
 Mosely 1933: 28, figs 57–59 (♂ genitalia).
 Distribution: Madagascar.
- L. milae* Sýkora, 1964: 279–291, figs 5–9 (♂ genitalia). ♂.
 Distribution: Madagascar.
- L. natalense* Mosely, 1933: 24, 43–48 (♂ genitalia & forewing). ♂.
 Barnard, 1934: 340, figs 4lf-i (wings, ♂ genitalia), as *occidentale*.
 Marlier, 1961: 159, 202–207, figs 23, 24 (larval & pupal parts).
 Distribution: South Africa: Natal (type locality), Pondoland, East Transvaal; Belgian Congo (Lake Kivu); Basutoland.
- L. normale* Banks, 1920: 357, t. 7, fig. 108, as *L. normalis*. Sex not stated in text, but figure given is of ♂.
 Mosely, 1933: 64, regarded *normale* as an unrecognizable species.
 Gibbs, 1973: 383–385, figs 53–55 (♂ genitalia), 63–65 (larvae), 83 (pupal appendages). ♂ ♀ larva pupa. Ghana.
 Distribution: Cameroons, Ghana. Larvae are similar to those described by Marlier (1965/66) from Angola as *Protomacronema*, so distribution could extend south to Angola.

- L. occidentale* Ulmer, 1907c: 57, 58, fig. 87 (wings). ♂ ♀ (♀ undescribed). Cameroons.
 Ulmer, 1913: 191, Barberton, Transvaal. I have examined this material, which proved to be *L. natalense* Mosely.
 Mosely, 1933: 23, figs 38–42 (♂ genitalia). Gives probable synonymy of *L. vanderysti* Navás with this species.
 Marlier, 1961: 159, 201, 202. Description of ♂ pupa. Urundi.
 Distribution: Cameroons, Urundi, Zaïre.
- L. tholloni* Navás, (1922) 1923: 48, 49. Gabun. ♂.
 Mosely, 1933: 30, figs 65–68 (♂ genitalia). ♂.
 Distribution: French Gabun.
- L. vanderysti* Navás, 1930a: 330–331, fig. 45 (wing fragments). ♀.
 Mosely, 1933: 66 states that this is possibly the ♀ of *occidentale*.
 Distribution: Belgian Congo.
- L. zahradniki* Sýkora, 1964: 277–279, figs 1–4 (♂ genitalia). ♂.
 Distribution: Madagascar.

Note:

- Leptonema tridens* Mosely, 1933: 10, 17–18, figs 17–21. ♂. Brazil.
 Ross, 1967: 195, stated that *tridens* also occurred in Africa.
 Flint (in litt. 14.ix.1979), however, corrected this as being a mistaken reference, *L. agraphum* Kolenati being the Brazilian species in Ross's mind, and being a species closely related to *L. tholloni* from Gabun. *L. tridens* is thus confined to South America, and should not be placed on the African list.

Genus POLYMORPHANISUS Walker 1852

Polymorphanisus Walker 1852: 78 (under Leptoceridae).

Type species *Polymorphanisus nigricornis* Walker 1852: 79. North India.

Oestropsis Brauer 1868: 263, 407.

Type species *Oestropsis semperi* Brauer 1868: 264–265, pl. 2A f, 1–1d, ♂ ♀. Philippines. Synonymy established by Ulmer 1905a: 24, 25.

Polymorphanisus Walker; Ulmer 1907b: 14, 19, 20, figs 4–9.

Polymorphanisus Walker; K. H. Barnard 1934: 369.

Polymorphanisus Walker; P. C. Barnard 1980: 78, 79, generic diagnosis, comment and key to known species.

Generic diagnosis (based on P. C. Barnard 1980, K. H. Barnard 1934 & Ulmer 1907b, checked against specimens in Albany Museum collection):

Imago: tibial spurs of ♂, ♀, 1.3.2, 1.3.3 or 2.3.3, spurs, particularly of foretibia in some species, may be very small; tibiae and tarsi of mid-legs of ♂ slightly broadened, of ♀ very strongly so, forming swimming legs with fringe of stiff setae. Antennae (♂ ♀) up to twice forewing length, scape rounded, less than half head length. Vertex with one pair large anterior warts, behind these a transverse ridge interrupted by the mid-cranial sulcus; posterior head warts inconspicuous or absent. Palpi vestigial. Face glabrous, subquadrangular. Wings pruinose, appearing naked, sometimes with several lines of setae in apical cells of forewings. These are the largest African Hydropsychidae, forewing length 13–25 mm. Forewings long, narrow, widest near arculus, apical border in ♂ may be sinuous and more strongly produced than in ♀; discoidal cell closed, short, broad, median cell larger, additional costal cross-veins present; wing forks 1, 2, 3, 4, 5 (♂ ♀). Hind wing much broader and shorter than forewing, subtriangu-

lar, with forks 1, 2, 3, 5 or 2, 3, 5; no true discoidal or median cells, anterior margin with two rows curved macrotrichia for wing coupling. Insects dark green to yellowish brown or whitish, wings colourless to pale green, in African species unmarked except in *guttatus* and *similis*, which have brown patches; some species with a conspicuous pair of dark spots on mesoscutellum; fifth sternite (δ ♀) with paired oval apertures.

P. C. Barnard (1980) has revised the genus, giving key, full descriptions and figures of the 19 known species, and dividing it into two species-groups, the *nigricornis* group, with small eyes and often with dark spots on the mesoscutellum, and the *ocularis* group, with large-eyed males and lacking dark spots on thorax. Barnard suggests that these two groups may prove to warrant separate generic status, but is leaving them as species-groups for the present. Composition of the two groups in Africa is indicated in the species list pertaining to this genus.

The genus *Polymorphanisus* has been recorded from the Afrotropical Region, including Madagascar, from the Oriental Region from India through South-east Asia to Indonesia, and from the Philippines and Borneo. Of the 19 known species, seven are Afrotropical, one (*P. guttatus*) being endemic to Madagascar, while the rest are all from the Afrotropical mainland.

Polymorphanisus bipunctatus (Brauer)

(Figs 177–191, Tables XVI, XVII)

Oestropsis bipunctata Brauer, 1875: 73. ♀. Blue Nile.

Lectotype ♀, designated by P. C. Barnard (1980:81), in Naturhistorisches Museum, Vienna.

Polymorphanisus bipunctatus (Brauer); Ulmer 1907b: 20–22, figs 4, 6–9. ♂ ♀. Natal.

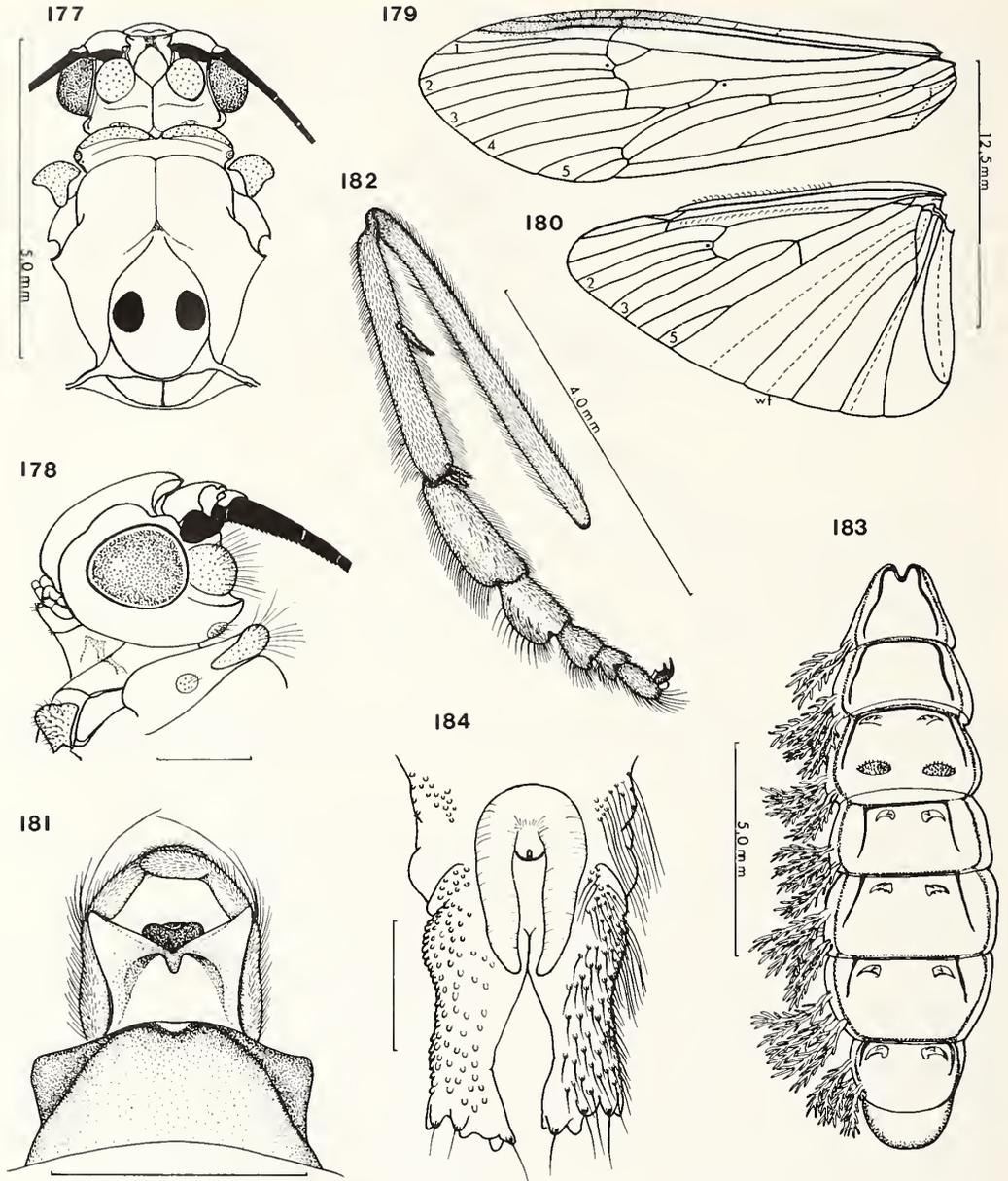
Polymorphanisus bipunctatus (Brauer); P. C. Barnard, 1980:81, figs 47–53 (♀ wings, head, thorax, genitalia).

Distribution: Sudan (type locality Beni Sciangul, Blue Nile); widely spread in the Afrotropical Region from the Sudan through Ethiopia and Kenya in the north, to Angola, Zimbabwe and South Africa (Natal, Transvaal) in the south.

DESCRIPTION OF IMAGOS (Figs 177–182)

P. bipunctatus appears to be the largest of the Afrotropical species, body length about 22 mm, forewing 22–26 mm in ♂, up to 28 mm in ♀; description below taken from pinned specimens in this collection, checked against others in spirit; colour from dry specimens.

Male imagos (see Figs 181, 182): cream-coloured insects with black eyes and a pair of large, rounded black spots on mesoscutellum. Antennae very long (up to 40 mm), slender, scape and pedicel yellowish-brown, flagellum brown with darker annulations at joints. Head: face smooth, shining, without warts; vertex with usual pair of large anterior setose warts, between these a prominent raised dorsal triangle, posterior to them a transverse ridge; posterior warts represented by a small pair of setose patches, clearly demarcated in some specimens, scarcely visible in others. Palpi rudimentary. Pronotum high, narrow, collarlike, with deep median division, a pair of long, narrow median warts and a smaller pair of lateral warts, all strongly hairy. Meso- and metanota without warts, largely smooth, shining, but with some long, pale anterior and posterior setae, particularly on metanotum; mesoscutellum with pair of large black spots and fringe of pale setae. Wings apparently naked, pruinose, covered with microtrichia, in life pale green, in dry specimens cream to pale brown. Legs yellowish, darkening distally to orange-yellow, a small dark spot at apices of tibial and tarsal joints; forelegs slender, mid-legs somewhat widened, fringed, oarlike, hind legs not widened, but tibiae and tarsi with short fringe of stiff setae. Tibial spurs 1.3.3 or 2.3.3. Abdomen cream with purplish



Figs 177-184. MACRONEMATINAE: *Polymorphanius bipunctatus*, ♀, ♂ pupa (mature). 177. ♀: dorsal view of head, pro- & mesonota, 178. ♀: head, lateral, note vestigial palpi, 179, 180. ♀ fore & hind wings (left), 181. ♂ pupa: genitalia, dorsal, 182. ♂ pupa: mid-leg, pupal exuviae removed, 183. ♂ pupa: abdomen, dorsal (genitalia and apical part of exuviae removed), 184. ♂ pupa: apical part of exuviae, ventral.

marks, darkening in dry specimens, a pair of inconspicuous oval apertures on sternum of V, small lateral segmental processes present, possibly remains of pupal gills. Genitalia brown; terminal segment of claspers short, wide, ninth segment relatively broad ventrally, rounded dorsally.

Females resemble males in colouring and general appearance, excepting that mid-legs are very strongly widened and antennae have scape and pedicel cream above, black beneath, 3rd to 6th segments blackish, rest of flagellum yellowish to brownish cream with brown annulations, paling distally. ♀ genitalia have sternal plates of VIII widely separated to base, inner margins reflected and strongly setose; tenth segment forms an apically setose dorsal hood and has a median ventral sclerite; XI bears the usual pair of cerci and two pairs of small lobes. (See Figs 177–180, which also apply largely to males, though the wings differ slightly in details and the antennae in colour.)

The large size of the imagos, and the conspicuous black spots on the mesoscutellum, make recognition of this species easy.

DESCRIPTION OF LARVA (Figs 185–191, Table XVI)

As *Polymorphanius bipunctatus* is the only species that has been recorded from Southern Africa, the larvae described here have been taken as belonging to it, particularly as all the larvae examined, both from the Eastern Transvaal and from Natal, evidently represent a single species. The only available pupa, though bred out in the laboratory, was not associated with any larval sclerites.

Mature larva (in spirit; Figs 188–191, Table XVI; Figs 185–187, of a fifth instar larva, may also be used for comparison): a very large, powerful larva, length of present specimens up to 42 mm, greatest width (abdomen) 5 mm. Sclerotized parts smooth, shining, rich chestnut brown to mahogany in colour, head and thoracic nota strongly patterned with paler brown to yellowish markings; abdomen pinkish buff to mauve (blue-green in life).

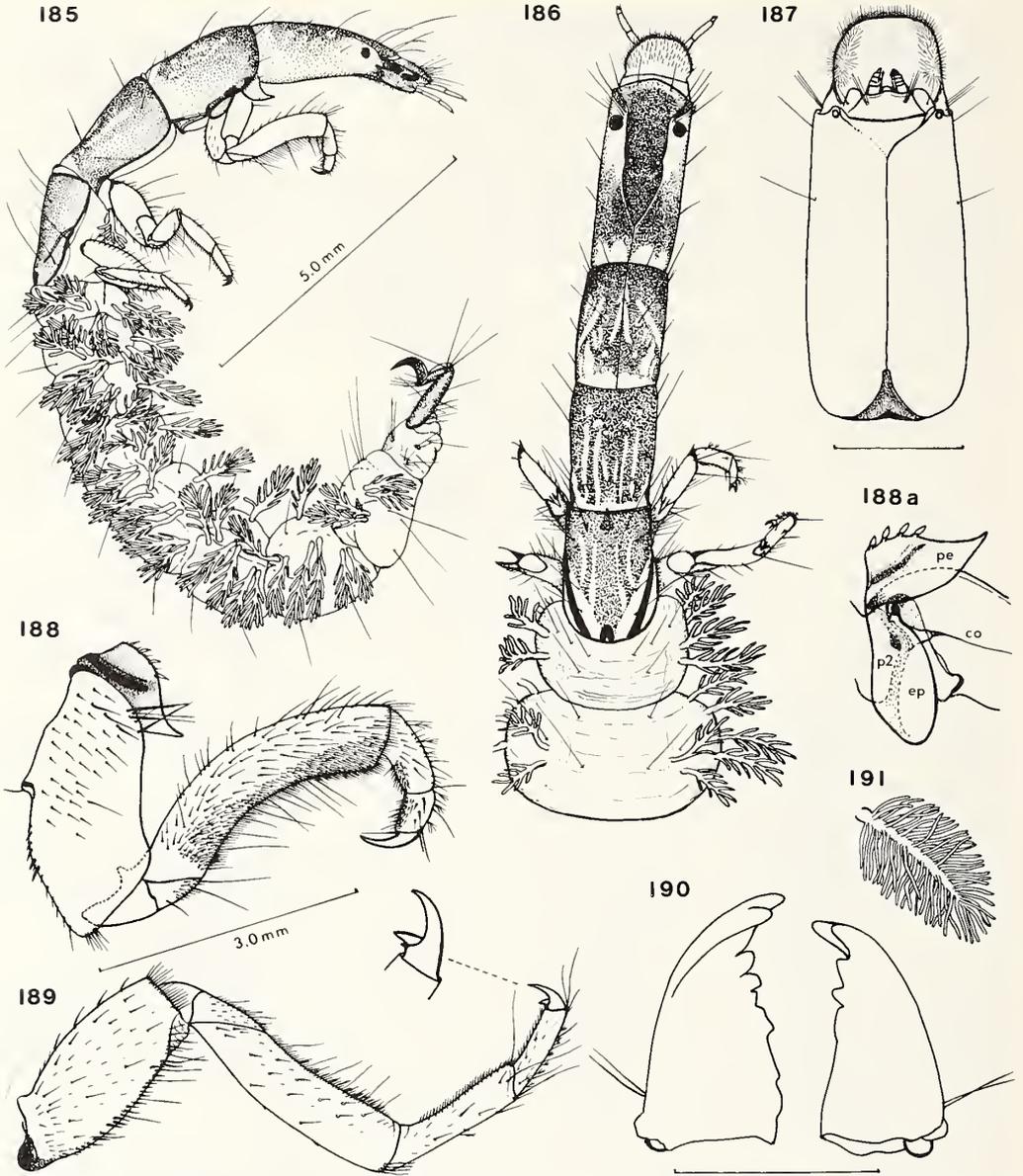
Head: (*cf.* Figs 185–187): long, slender, without carina, frontoclypeal apotome narrow, widening anteriorly, anteclypeus membranous; eyes medium-sized, black, placed well forward; antennae minute, at base of mandibles; anterior ventral apotome triangular, with suture on left side only; posterior ventral apotome and stridulatory files absent.

Mouthparts (Fig. 190 & *cf.* Figs 185–187): labrum large, rounded, without lateral expansions but with numerous small setae on dorsum and forming cushions under lateral margins; mandibles strong, blackish, with narrow apices, each with two large, blunt apical teeth and several small lateral teeth, the proximal ones poorly defined, no brushes or rows of setulae, outer side rounded, not keeled, bearing two or three long setae; maxillary palpi five-jointed, extensible, very long when extended, labial palpi minute; submentum subquadrangular.

Thorax (*cf.* Figs 185, 186, 188a): segments very long and slender compared with abdomen, patterned as indicated; prosternum with narrow transverse sclerotized plate, anteriorly flanged, articulated laterally with pronotum, behind it a second median sclerite concealed beneath the integument; pre-episternum collarlike, with anterior point, row of flattened setae and inner strengthening ridge, second pleural sclerite and epimeron large, conspicuous, glabrous. Mesosternum with one pair of tracheal gills, metasternum with two.

Legs (Figs 188, 189): foreleg with stout coxa, trochanter divided, femur strongly bent, with dense band of setae along inner side and ventral margin, this is continued narrowly along tibia and tarsus and on distal part of trochanter; claw stout, with long, slender basal bristle. Mid- and hind legs more slender, with thin marginal fringe of setae, claws smaller, with stout basal spine and small point. Legs subequal in length, foreleg slightly shortest.

Abdomen (Fig. 191 & *cf.* Figs 185, 186): tough, leathery, eight rows of tufted gills present on segments I–VII, four on segment VIII (see Table XVI). Gills have straight main stem and



Figs 185-191. MACRONEMATINAE: *Polymorphanisus bipunctatus*, larvae. 185. 5th (penultimate) instar larva: habitus, lateral (right appendages only shown), note absence of ventral sclerites on IX. 186. dorsal view of head, thorax & abdomen I, II of same, 187. ventral view of head of same. 188, 189. mature larva: foreleg & hind leg (left, median view); hind claw further enlarged, 188a. outer view of pleural sclerites of right foreleg (stippled areas indicate sclerotized structures shown by transparency), 190. mature larva: left & right mandibles, dorsal, 191. Gill from abdominal segment IV (mature larva).

many slender filiform branches (40–50 per gill stem anteriorly, fewer posteriorly), but appear small in comparison with large size of larva; most lateral and ventrolateral gills have two main stems set so far apart that they almost appear to represent separate gills. No ventral sclerites on VIII, but several long setae; ventral sclerites on IX represented by a patch of pubescence and a few longer setae; two minute lateral seta-bearing sclerites present. Anal appendages fairly long, slender, with stout lateral sclerites and simple, strongly curved anal claw with few setae, no anal brush. Anal gills not visible on available specimens, but probably five in number since *Aethaloptera*, the other genus in this Tribe, has five.

Earlier instars: the 17 larvae available were measured as before (width of head capsules at eyes) and other features studied. On this basis they were tentatively sorted as follows, number of specimens in each case given in brackets (see also Table XVI). The instars have been taken as being six in number as in the other Macronematinae studied, but this may of course prove to have been an erroneous assumption should a large amount of material become available.

Third instar (3 larvae): head width 0.38–0.43 mm. Gills as in Table XVI, all gills simple, unbranched, each gill ending in a single filament; ventral gills each bear a seta (*cf.* Fig. 99a); no gills with double stems as yet. Body setae very long; colour pattern not yet distinguishable, but frontoclypeal apotome and anterior margin of thoracic nota darkened.

Fourth instar (3 larvae): head width 0.63–0.64 mm. Gill numbers and arrangement as in the mature larva (Table XVI), but each stem with only 3–6 filaments; all gills which will have two main stems now have them, arising from a common base. Colour pattern just distinguishable.

TABLE XVI:

Number and position of tracheal gills in 3rd to 6th larval instars of
Polymorphanisus bipunctatus

Segment	3rd instar				4th, 5th, 6th instars			
Mesothorax Metathorax	1 pair		2 pairs		1 pair		2 pairs	
Abdomen (right side)	L	Post.	Pre.	V	L	Post.	Pre.	V
I	1	1	1	1	2*	1	1	1
II	1	1	1	1	2	2	2	1
III	1	1	1	1	2	2	2	1
IV	1	1	1	1	2	2	2	1
V	1	1	1	1	2	2	2	1
VI	1	1	1	1	2	2	2	1
VII	1	1	1	—	2	2	2	1
VIII	—	1	1	—	—	2	2	—

* Abdominal gills marked "2" each have two main stems, in instars 4–6 usually separated more or less widely at base.

On segment I the post- and pre-segmental gills are alongside one another and could be branches of the same gill.

L = lateral gill.

Post = postsegmental ventrolateral gill.

Pre = presegmental ventrolateral gill.

V = ventral gill.

Fifth instar (6 larvae) (Figs 185–187): head width 1.0–1.2 mm. Gill stems with 15–22 filaments; where gill stems are double the bases may already be widely separated. Colour pattern reasonably clear, but not as strong as in mature larva. No ventral setose plates on VIII or IX, only small patches of long setae. The paired lateral setae on IX arise from very small sclerites. (Figs 185–187 were made from a fifth instar larva owing to the difficulties posed by the size of the mature larva.)

Sixth instar (mature larva, 5 specimens) (Figs 188–191): head width 1.5–1.9 mm. Gills very bushy, each stem with 40–50 filiform branches. Ventral setae on VIII and IX much as in fifth instar, also minute paired setose lateral sclerites on IX; no ventral plates. Colour pattern fully developed (as in Fig. 185 but darker).

DESCRIPTION OF PUPA (Figs 183, 184, Table XVII)

A single good male pupa from Natal was available in the collection. This is described below.

Male pupa (in spirit; Figs 183, 184, Table XVII): very large, length c. 23 mm, head rounded, two pairs of small setae on vertex; antennae more than twice body length; labrum small, transversely oblong, with thick fringe of marginal setae; mandibles lacking, maxillary palpi vestigial, labial palpi absent. Paired dorsal plates present as follows: presegmental plates on segments III–VII, each with a single very large hook bearing 1–3 very small ones, hooks increasing in size aborally. Postsegmental plates on segment III large, oval, with many small hooks, no postsegmental plates on IV as recorded by Marlier (1962) for specimens from Lake Tanganyika (later identified as probably *P. elizabethae* by P. C. Barnard, 1980). Small paired patches of setae occur on segments II–VII, on III situated between the posterior plates. Paired tracheal

TABLE XVII:

Tracheal gills and dorsal plates of ♂ pupa of *Polymorphanisus bipunctatus*

Abdominal segment	Tracheal gills			Dorsal plates (paired)
	DL	VL	V	
I	—	2	—	
II	2*	2	2	
III	2	2	2	Presegmental plates Postsegmental plates
IV	2	2	2	Presegmental plates
V	2	2	2	Presegmental plates
VI	2	2	2	Presegmental plates
VII	2	2	2	Presegmental plates
VIII	—	—	—	—

* Gills marked "2" are each represented by two main stems, in a few cases arising from a common base, otherwise well separated. The dorsolateral and ventrolateral gills are so placed that they are, respectively, presegmental and postsegmental in position. All are tufted branchial gills and none has an inflated base.

DL = dorsolateral gill.

VL = ventrolateral gill.

V = ventral gill.

gills occur on segments I–VII, in three rows on each side except on segment I (see Table XVII). The dorsolateral and ventrolateral gills usually lie close together, in post- and presegmental positions. Gills have paired stems, each forming a long, feathery branch which is easily broken off. None of them have pouch-like bases. Anal appendages large, apically widened, each terminating in several strong blunt points; on ventrolateral surface many setiferous tubercles, increasing in size towards apex of appendage. Usual ventral pockets enclosing male genitalia. Tibial spurs 1.3.3. Mid-legs widened and fringed.

Pupal case: no case has to my knowledge been described, but see comments under Biology below.

REMARKS

P. C. Barnard in his 'Revision of the Old World Polymorphanisini' (1980) has sorted out the nomenclatural problems of the species of *Polymorphanisus* and reference should be made to his paper when African specimens have to be identified. As mentioned earlier on, he has divided the genus into two species-groups, the *nigricornis*-group and the *ocularis*-group, the composition of which as far as African species are concerned is reflected in the species list given below.

All material collected to date in South Africa falls into *bipunctatus*, a very widely distributed species belonging to the *nigricornis*-group. Barnard retains *bipunctatus* as a valid species separate from the Oriental species *nigricornis* to which it is closely allied. Of the other three African members of this group, *elizabethae* includes specimens with a wide variety of black mesoscutellar markings whereas two new species, *hargreavesi* and *marlieri*, lack such spots. Those two species known only in the female sex differ from one another in antennal colour.

African members of the *ocularis*-group include *angustipennis*, *similis* (of which *bisignatus* is a synonym) and *guttatus*, all of which lack dark markings on the mesoscutellum.

The three colour varieties of *P. bipunctatus*, described by Marlier (1965/66) as *Forma A*, *Forma B* and *Forma incolor*, are referred by P. C. Barnard to *P. elizabethae* (as is also *P. pupillatus* Navás). Those specimens of *Forma incolor* which entirely lack the typical black spots would, however, belong to one of the species lacking mesoscutellar spots but as all are females it is not clear which. Marlier and Botosaneanu's (1968) '*Polymorphanisus cf. similis*' has proved to be *P. angustipennis* (Barnard 1980).

A larva (as "Macronematinae Larva C") and pupa of *Polymorphanisus* were first described by Marlier (1943c: 85–88, fig. 13) who later (1961) identified the larva as *P. bipunctatus*, commented briefly on both stages and gave some biological notes. Barnard (1980), however, commented that the larvae were probably of *elizabethae* as the adults collected at the same time were *elizabethae*. This explains the small discrepancies between the South African larvae and pupa of *bipunctatus* and those described by Marlier, mentioned below, which would thus indicate species differences.

Marlier's pupa from Tanganyika had a single gill stem in three places where the South African one has two; he also found small postsegmental dorsal plates on segment IV in addition to those on III. Apart from those differences the pupae seem to be very similar. *Aethaloptera*, the other African genus in the Polymorphanisini, also has postsegmental plates on III only.

BIOLOGY

Marlier (1958, 1961) has published observations on the biology of larvae found in Lakes Tumba and Kivu. Very young larvae were often found in the floating sudd where they mined the older grass stems. Mature larvae inhabited galleries in rotting submerged wood, often using pre-existing crevices, and spun fine longitudinal nets within the gallery in which micro-organisms (bacteria and algae) were trapped for food. Marlier was able to watch their activities in

glass tubes, closed at one end, in the laboratory aquaria. He noted that the net was fastened to the sides of the tube but was incomplete basally so that the larva retained space to pass it. The larva usually remained curled in a U-shape with head and thorax to one side of the net and abdomen and anal prolegs to the other. Constant undulations of the abdomen kept the water circulating assisting both with respiration and in food capture. Marlier could not see whether the larvae collected food from the net or ate the net at intervals but did note that their guts were filled with microscopic green algae. The feeding habits of *Polymorphanisus* larvae are thus closer to those of some species of *Macrostemum* than to those of the other Macronematinae.

Marlier found *Polymorphanisus* larvae in lakes, large rivers and torrents. He considered that in its mining habits the genus was comparable with the mayfly *Povilla adusta*. The larvae in the Albany Museum Collection all came from stones in current in small rivers. Their habits there are unknown although the blue-green colour of the abdomen may well indicate that microscopic algae form their main food supply. Imagos in the Albany Museum collection were taken in early summer (October—December) and larvae in various months, probably being present all the year round.

It seems probable that the larvae may pupate in the larval dwelling tubes simply plugging the opening loosely with debris. Wiggins (1960) in a study of Phryganeidae, the pupae of which lack mandibles, concluded that such pupae have no need for mandibles as they do not have to cut their way out of the pupal cases but merely have to push out a loosely inserted plug. *Polymorphanisus* pupae are included in Wiggins' discussion.

AFRICAN SPECIES OF *POLYMPHANISUS*

A. *P. nigricornis*-group (eyes small, well separated ventrally)

For other characters and comments see P. C. Barnard, 1980: 78, 79; he also gives keys, descriptions of species and drawings.

P. bipunctatus (Brauer), 1875: 73, as *Oestropsis*. ♀. Ethiopia.

P. C. Barnard, 1980: 81, figs 47–53 (♂, ♀ wings, ♀ head, thorax, ♂, ♀ genitalia), map (fig. 72). He places *P. bipunctatus pupillatus* Navás (1931b: 139, fig. 75), in synonymy with *P. elizabethae* Navás, and considers Marlier's material of "*bipunctatus*" (1961: 208; 1965/1966: 40) to be in fact *P. elizabethae*.

Distribution: Sudan, Ethiopia, Kenya, Angola, Zimbabwe, South Africa (Natal, Transvaal).

P. elizabethae Navás, 1931b: 140, fig. 76. ♂.

P. C. Barnard, 1980: 81, 84, figs 54–71 (♂, ♀ wings, genitalia, variations in mesoscutellar spots), also map (fig. 72). Barnard synonymizes *P. bipunctatus pupillatus* Navás (1931b: 139, ♂, Zaïre) with *elizabethae*; this synonymy naturally includes *P. pupillatus* Navás, erected to generic status by Marlier (1965/66: 22, 77).

Distribution: Sierra Leone, Ghana, Nigeria, Cameroun, Congo, Zaïre, Uganda, Zambia, Zimbabwe, Angola.

P. hargreavesi P. C. Barnard, 1980: 87, figs 74–76 (♀ wings, head, genitalia), map (fig. 73). ♀.

Distribution: Sierra Leone, Zaïre, Zambia, Zimbabwe.

P. marlieri P. C. Barnard, 1980: 64, 87, figs 77, 78 (♀ wings, 8th sternite). ♀.

Distribution: Zaïre.

P. nigricornis Walker, 1852: 79. ♂. Not African: see note below.

P. pupillatus Navás, 1931b: 139, fig. 75. ♂.

Marlier (1965/66: 22, 77) raised this to generic status and described ♀.

P. C. Barnard (1980: 81) places it in synonymy with *P. elizabethae* Navás.

Distribution: former Belgian Congo, Angola.

Note:

- P. nigricornis* Walker, 1852: 79. ♂. North India.
Brauer 1875 recorded this species from Central Africa and India.
Betten & Mosely (1940) suggested that *P. nigricornis* and *P. bipunctatus* were almost certainly synonymous.
- P. C. Barnard, 1980: 90, figs 91–93 (♂ thorax & genitalia), corrects earlier erroneous descriptions and misidentifications of these two species, concluding that *nigricornis* is much rarer and more restricted than thought earlier, and that although it is very similar to *bipunctatus*, there are differences in the ♂ and ♀ genitalia which, together with the widely separated distributions, suggest that the two species should be kept distinct.
- Distribution: India, Vietnam, Sumatra, Java.
- B. *P. ocularis*-group (eyes of male large, almost meeting ventrally)
For other characters and comments see P. C. Barnard, 1980: 78, 79, 98.
- P. angustipennis* Ulmer, 1912: 97, fig. 21. ♂.
P. C. Barnard, 1980: 98, figs 120–124 (♂ wings, head, genitalia), figs 125–128 (♀ wings, head, 8th sternite).
Distribution: Ghana, Nigeria, Cameroun, Sudan, Uganda.
- P. bisignatus* Navás, 1931c: 276, fig. 61. ♀. Belgian Congo.
P. C. Barnard (1980) places this in synonymy with *P. similis* Ulmer.
- P. guttatus* Navás, 1935: 71, 72, fig. 32. ♀.
P. C. Barnard, 1980: 98, 99, figs 133, 134 (♀ wings & 8th sternite).
Distribution: Madagascar.
- P. similis* Ulmer, 1912: 96–97, figs 19, 20. ♂.
Marlier (1961: 159, 211, 212, fig. 26) description of ♀.
P. C. Barnard, 1980: 103, figs 129–132 (♂ genitalia, ♀ wing & 8th sternite). Barnard places *P. bisignatus* Navás in synonymy with *similis*, and points out that Marlier & Botosaneanu's (1968) "*Polymorphanisus cf. similis*" is actually *P. angustipennis*.
Distribution: Sierra Leone, Nigeria, Cameroun, Zaïre, Uganda.

Genus AETHALOPTERA Brauer 1875

- Aethaloptera* Brauer, 1875: 71–72.
Type-species *Aethaloptera dispar* Brauer, 1875: 72. ♂. Senegal.
- Chloropsyche* McLachlan, 1880: 1xix, pl. Lvii, 5 figs.
Type-species *Chloropsyche evanescens* McLachlan, 1880: 69. ♂.
Synonymized by Kimmins, 1962a: 96.
- Primerenca* Navás, 1915: 181, fig. 6. ♂.
Type-species *Primerenca maesi* Navás, 1915: 182, figs 6a-c. ♂.
Synonymized by Lestage, 1919a: 293.
- Aethaloptera* Brauer; Kimmins 1962a: 94, figs 43–63, synonymy and discussion.
- Paraethaloptera* Martynov, 1935: 193. ♀ only.
Type species *Paraethaloptera gracilis* Martynov, 1935.
Synonymized by P. C. Barnard, 1980: 66.
- Aethaloptera* Brauer; P. C. Barnard, 1980: 66, 68, generic description, remarks and key to species.
- Aethaloptera* Brauer; Lepneva 1964 (1970): 617–627, description of larva of *A. rossica* Martynov.

Generic diagnosis (derived from P. C. Barnard, 1980, with additions from Ulmer 1907d, Marlier 1962b, and study of available material):

Imago: tibial spurs of ♂, ♀, 0.2.2 or 0.3.2. Sub-apical spur of mid-tibia near base at outer side; spurs small, unequal. Legs slender in ♂, mid-tibiae slightly dilated; in ♀ tibiae and tarsi of mid-legs greatly dilated, fringed. Antennae of ♂ three to four times as long as forewing, of ♀ little longer than wing; scape almost as long as head, flagellum very long, slender. Eyes small, blackish, not meeting ventrally, slightly larger in ♀. Vertex with two pairs of setose warts, the anterior larger than the posterior, latter weakly developed in ♀. Palpi absent or rudimentary. ♂ forewings long, basal half narrow, apical half widened along postcostal border; several false cross-veins between C and Sc, discoidal cell absent, but a false discal cell enclosing the corneous spot, formed by R₄ and R₅ rejoining shortly after separating; apical forks 1–5 present, though 5 may be a false fork between Cu_{1a} and Cu₂; median cell large, bent. Hind wing subtriangular, very wide basally, with forks 1, 2, 3, 5; discoidal cell absent. ♀ wings shorter, forewing wider, hind narrower than in ♂. Wings glabrous, unpatterned, greenish to brownish or colourless. ♂ forewing 10–18 mm, of ♀ 8–10 mm.

The genus occurs throughout most of the Afrotropical Region, Egypt, India, Sri Lanka, South-east Asia and Indonesia, to Northern Australia, with one species in the U.S.S.R.

Aethaloptera maxima Ulmer

(Figs 192–293, Tables XVIII, XIX, Fig. 214D)

Aethaloptera maxima Ulmer, 1906: 62, fig. 66 ♂. Orange Free State.

Holotype ♂ was in Hamburg Museum; later destroyed (Weidner 1964: 66). Type locality Bothaville, Orange Free State, South Africa, 25. III. 1899.

Neotype ♂, South Africa: Waterval River, National Road between Standerton and Greylingstad, 12. I. 1959; in Zoologisches Museum, Hamburg; designated by P. C. Barnard, 1980: 72.

Chloropsyche maxima (Ulmer), 1907d: 17, fig. 2. ♂. Orange Free State.

Chloropsyche maxima (Ulmer); K. H. Barnard 1934: 368, figs 40 b–g, also suggested larva from Natal (fig. 40 h–l); this however proved to be of *Macrostemum capense*.

Aethaloptera maxima Ulmer; Kimmins 1962a: 100, figs 40, 41, 45, 47, 56–59, 62, 63 (♂, ♀ wings, mid-legs, genitalia).

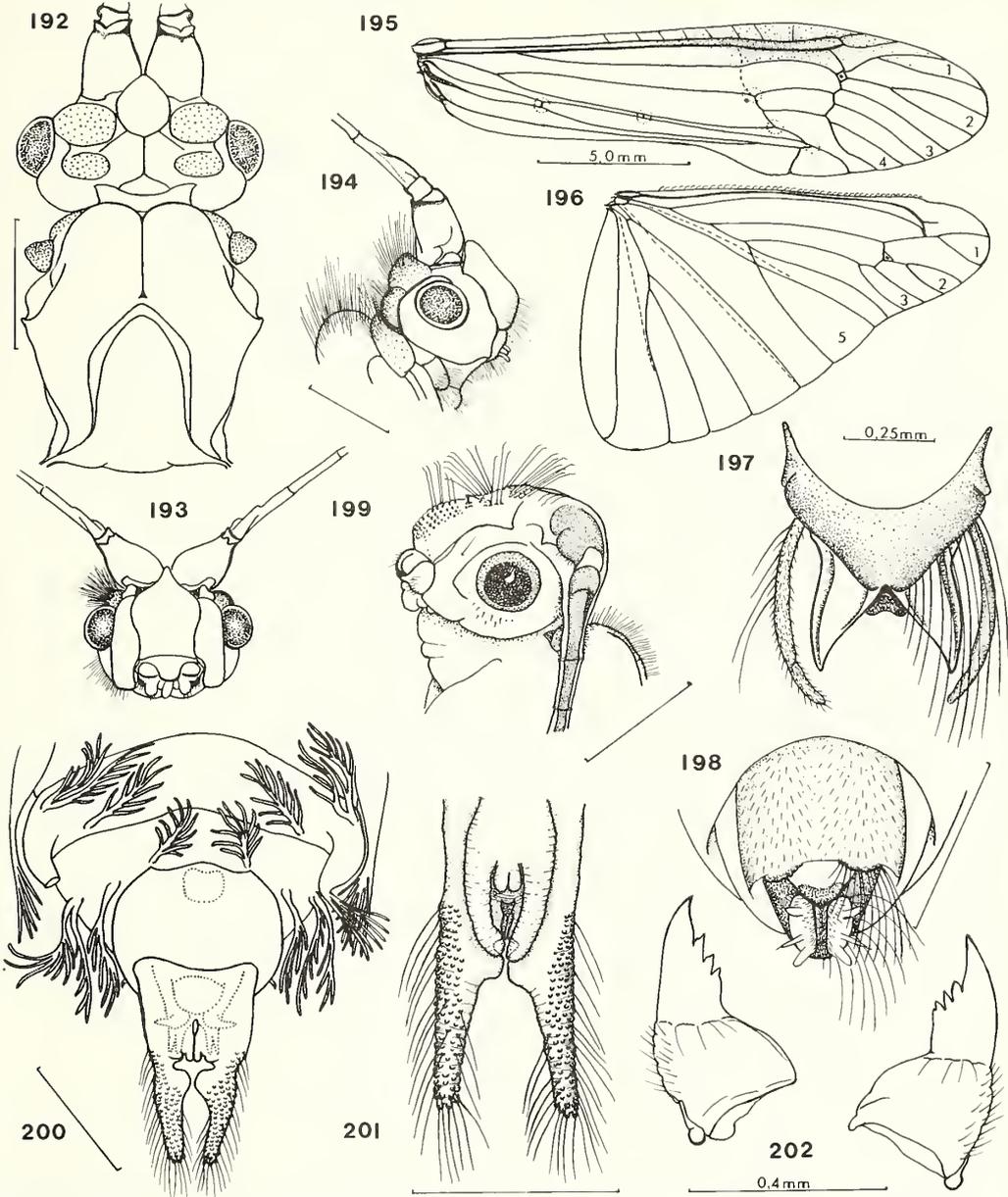
Aethaloptera maxima Ulmer; P. C. Barnard 1980: 72, figs 29–34 (♂, ♀ wings & genitalia), also distribution map (fig. 28).

Distribution: South Africa (Orange Free State, Transvaal, Northern Cape, Natal), South West Africa, Mozambique, Zimbabwe, Zambia. There is much material in the Albany Museum, including males, females, larvae and pupae; this is mainly from South Africa, but five imagos come from Zimbabwe.

DESCRIPTION OF IMAGOS (Figs 192–198)

Imagos (in spirit): fairly large, tawny yellow insects with cream to purplish abdomen, forewings almost hairless, slightly milky, membrane covered with microtrichia, a few scattered setae present, mainly along veins, several dark marks on most cross-veins (see Fig. 195); hind wing iridescent, with fork 2 stalked (sessile in *A. dispar*). Legs yellowish with dark apical spot on mid-tibia, tibial spurs 0.2.2. Males have plain brownish antennae, and a fuzz of soft, fine, white hairs on sternum, proximal end of mesoscutum and upper parts of legs. Females differ somewhat in appearance, having strongly striped antennae (segments proximally white, distally brown), and lacking the soft white hairs. Both sexes are heavy-bodied, with stout thorax and fairly stout abdomen; genitalia are small, those of male with slender claspers and large-ended

SCOTT: HYDROPSYCHIDAE (TRICHOPTERA) OF SOUTHERN AFRICA WITH KEYS



Figs 192–202. MACRONEMATINAE: *Aethaloptera maxima*, ♂, ♀, mature ♂ & ♀ pupae. 192. ♂: dorsal view of head, pro- and mesonota, 193, 194. ♂: frontal & lateral views of head, note vestigial palpi, 195, 196. ♂: fore & hind wings (right), 197. ♂ genitalia, dorsal (VIII removed to show IX, retracted within it), 198. ♀ genitalia, ventral, 199. ♀ pupa: head, left lateral, 200. ♀ pupa: apical part of abdomen with pupal appendages, ventral, 201. ♂ pupa: pupal appendages from exuviae, ventral, 202. ♂ pupa: left & right mandibles from exuviae, dorsal.

copulatory organ, those of female with sternal plates of IX apparently not separated medially (see Fig. 198 and also figs 60–63, Kimmins 1962a). Length of male forewings 14–18 mm, of female 9–13 mm.

DESCRIPTION OF LARVA (Figs 203–213, Table XVIII, Fig. 214D)

The 89 available larvae include at least four, possibly five or six, instars. Instars 3–6 were clearly *Aethaloptera* and easily recognizable as such. Of the very young larvae, there were three that looked as though they might belong to *Aethaloptera*, but as they were colourless and transparent it was difficult to be certain. They have, however, been included with a query.

Mature larva (Figs 203–213, Table XVIII): length up to 15 mm, width of abdomen up to 3 mm, all sclerotized parts pale yellow to brownish, largely transparent (muscles etc. show through).

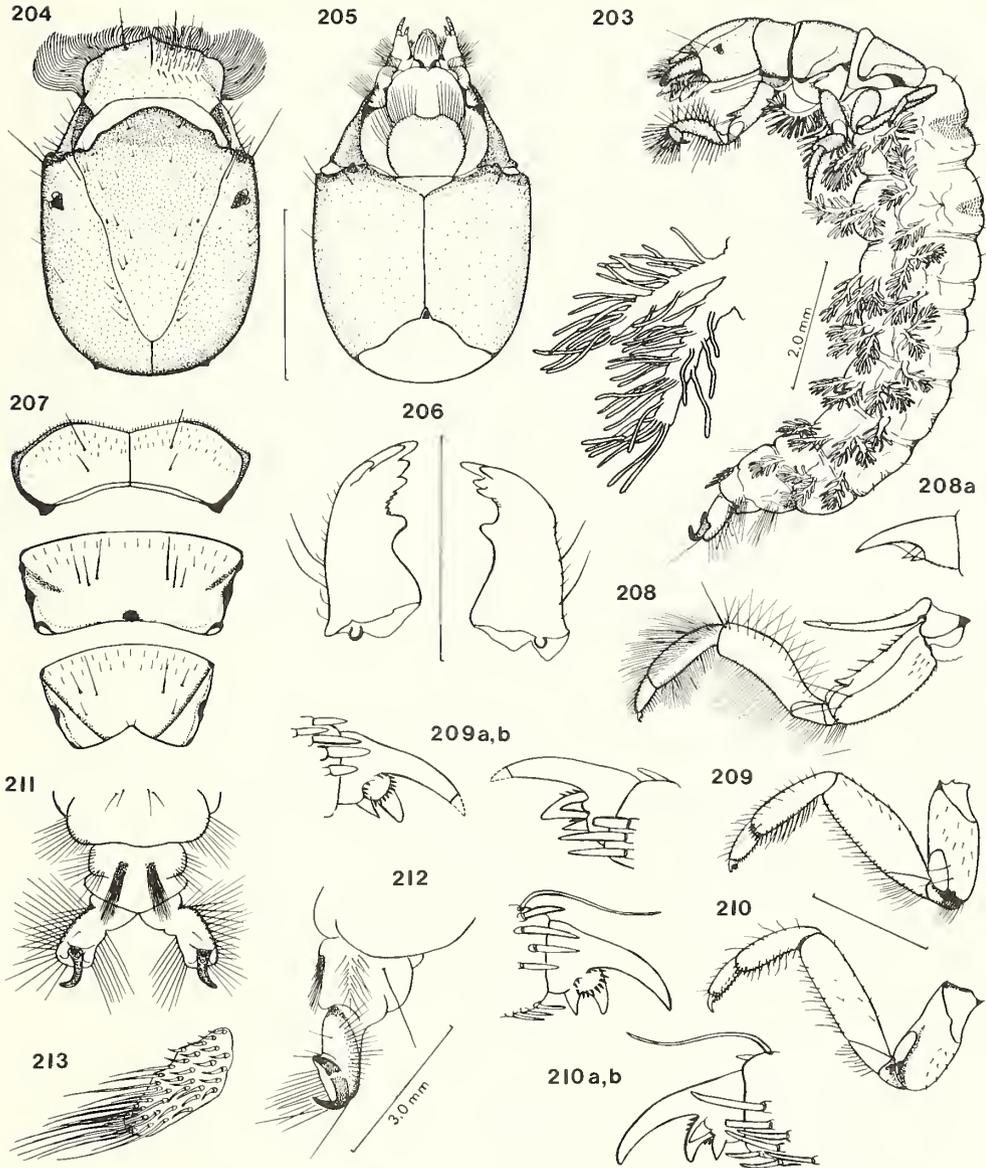
Head (Figs 203–205), broadly oval, dorsally rounded, without carina; frontoclypeal apotome triangular with two pairs of very slight lateral indentations, anterior margin strongly convex, with paired lateral emarginations; anteclypeus membranous; eyes black, medium-sized, situated well forward within a paler area; antennae minute, near base of mandibles. Anterior ventral apotome small, triangular, clearly demarcated on left side only; posterior ventral apotome minute; no stridulatory files.

Mouthparts (Figs 204–206): labrum large, retractile, lightly sclerotized, with partial median sulcus, and membranous lateral expansions fringed anteriorly and laterally with long, silky setae, dorsal surface with two long brown setae and a number of shorter colourless ones; maxillary palpi five-segmented, galeae small, palpifers with large tufts of lateral setae, labium stout, labial palpi minute, submentum a truncated oval, distal end concave, without setae, lateral margins setose. Mandibles (Fig. 206), large, strong, left one with five terminal teeth, right with four, each mandible with one lateral tooth situated midway along inner edge; no inner brushes or rows of setulae, scattered setae along outer rounded margin.

Thorax (Figs 203, 207): thoracic segments short, wide, pale yellowish brown, anterior and lateral margins darkened, the latter with black thickenings, pronotum with transverse sulcus near posterior margin; mesonotum with faint brown diagonal stripes extending half way across shield and central black spot on posterior border; metanotum with darker brown diagonal stripes extending right across shield, no median black spot. Pre-episternum long, slender, dagger-shaped, as long as coxa. Prosternal plate sclerotized, yellowish, with wide anterior and narrow posterior parts.

Legs (Figs 208–210): sub-equal in length, pale yellowish brown with slight darkening at joints. Foreleg with distal spine on anterior surface of coxa; trochanter divided; long setae fringing trochanter and femur, fairly thick brush on tibia and tarsus. Mid- and hind legs with relatively few setae apart from a thin fringe along posterior border of tibia and tarsus, which also have larger bladellike apical bristles. Claws small, shown enlarged, of unusual structure; anterior tarsal claw with two sharp basal spines, those of mid- and hind tarsi each with three basal spines and a "cushion" edged with spinules (the third spine and "cushion" are only clearly visible under a compound microscope, see Figs 208a, 209a, b, 210a, b).

Abdomen (Figs 203, 211–213): smooth, bare, except for two transverse areas on segments I and II respectively, which are grooved and covered with minute hooked spinules as in *Amphipsyche*. Tufted tracheal gills (15–20 filaments per stem) present on mesosternum, metasternum and abdominal segments as shown in Table XVIII and Fig. 203. Thoracic gills have filaments at tip and along one side only; abdominal gills have a more ring-like arrangement but filaments tend to bunch. Certain gills have two main stems; in these the bases may be contiguous, but as the abdomen of a mature larva increases in size they usually become quite widely separated. Abdominal gill count as follows: six rows on segments I and VII, eight rows on segments II to VI, none on segment VIII. Sternum of IX with two sub-ovate sclerites bearing



Figs 203–213. MACRONEMATINAE: *Aethaloptera maxima*, mature larva. 203. habitus, left lateral (right appendages only shown), pair of abdominal gills shown further enlarged, 204, 205. dorsal & ventral views of head, 206. left & right mandibles, dorsal, 207. pro-, meso & metanota, dorsal, 208. left foreleg with pleural sclerites, 208a. claw of same, further enlarged, 209. left mid-leg, 209a, b. claw of same, inner & outer views, further enlarged, 210. left hind leg, 210a, b. claw of same, further enlarged, inner & outer views, 211. abdominal segments VIII & IX and anal prolegs, ventral, 212. left anal proleg, further enlarged, lateral, 213. ventral plate from IX, further enlarged.

bladeliike setae, also paired lateral patches of setae (no dorsal or dorsolateral sclerites, and no ventral sclerites on VIII). Anal prolegs fairly long and stout with long setae on lateral sclerites and inner side; lateral sclerites very lightly sclerotized, scarcely visible); anal hooks smooth, plain, sharply curved; five anal gills present.

Earlier instars: comments on earlier instars follow, assuming that there are six altogether as in *Macrostemum* and *Amphipsyche*, as will be the case if instars 1 and 2 definitely prove to belong to this genus (see Fig. 214D).

Probable first instar (2 larvae): head width 0,15 mm; head large, rounded, labrum large, mandibles with several small teeth along margin; pre-episternum present, comparatively large, which is unusual in first instar larvae, sub-ovate, with downturned blunt apical point; tarsal claw of foreleg with three basal spines, graduated in length; mid- and hind claws appear to be similar, though longer basal spines are not in same plane. Gills absent. Anal claw large, clear. Setae long, sparse, two to three long ventral setae on VIII and IX.

Probable second instar (1 larva): head width 0,22 mm; head large, rounded, labrum large, frontoclypeal apotome with rounded anterior margin, mandibles large, solid, with about five apical and lateral teeth and a median lateral projection; pre-episternum longer, with thick base tapering to pointed apex; fore claw with two basal spines, mid- and hind claws unclear. Simple gills present. Setae shorter, more numerous.

Third instar (4 larvae): head width 0,35–0,37 mm; pale but easily recognizable as *Aethaloptera*, head shape and mandibles typical, also dagger-shaped pre-episternum, now two-thirds length of fore-coxa, with lateral seta, fore-coxa with distal spine present, apparently basally articulated with fore-coxa. Gills now bear a single filament (branch), the ventral ones carrying a seta (cf. *Macrostemum*, Fig. 99a); same number of gills as in later instars, but each has only one main stem. Foreclaw with two short basal spines, mid- and hind claws each have a single stout basal spine and ring of smaller spinules.

TABLE XVIII:

Tracheal gills of mature larva of *Aethaloptera maxima*

	Mesothorax	1 pair			
	Metathorax	2 pairs			
Abdomen (right side)		Post	Pre	VI	V
I		—	—	2*	1
II		1	2	2	1
III		1	2	2	1
IV		1	2	2	1
V		1	2	1	1
VI		1	2	1	1
VII		1	2	1	—
VIII		—	—	—	—

* The figure 2 denotes that the gill in question has two main stems, either arising from a common base or separately.

Post = postsegmental lateral gill.

Pre = presegmental lateral gill.

VL = ventrolateral gill.

V = ventral gill.

Fourth instar (2 larvae): head width 0,55–0,65 mm; in foreleg coxal spine is short, fused to coxa, and carries a stout basal seta. Most gills bear two to three filaments, some ventral gills still have a terminal seta and some gills now have double stems. Foreleg with thin brush, fore-claw with two basal spines, mid- and hind claws with two stout basal spines (one larger than the other) and small “cushion” surrounded by spinules (i.e. basically the same as in the mature larva). Claw structure can only be clearly seen under compound microscope $\times 400$.

Fifth instar (17 larvae): head width 0,87–1,0 mm; these resemble final instar larvae but have fewer gill filaments (usually 6–12), none of which bears a seta.

Mature larvae, i.e. sixth instar (many larvae): head width 1,27–1,54 mm. These have been described above.

DESCRIPTION OF PUPA (Figs 199–202, Table XIX)

Pupae available included mature males and females, in a few cases complete with pupal cases and larval sclerites, thus affording correlation between larvae and imagos.

Male pupa—pharate imago—in spirit, Figs 201, 202, & cf. Figs 199, 200, ♀, Table XIX): 3 specimens, length c. 9 mm. Head yellowish, vertex rounded with four flattened groups of pale setae, each of the two anterior groups situated above a small corneous projection, setae with bent tips. Eyes medium-sized, dark; antennae very long, slender, brownish, forming a coil on posterodorsal side of abdomen (four turns of each antenna in coil). Labrum somewhat bulbous, a few small, colourless setae and several long ones with bent tips centrally placed, rows of setate tubercles giving a transversely striated appearance to labrum. Mandibles small, narrow, very similar, each with bulbous base and an apical and three lateral teeth, maxillary and

TABLE XIX:

Branchial gills, dorsal plates etc., of ♀ pupa of *Aethaloptera maxima*

Abdominal segment no.	Tufted gills (right side)			Dorsal plates	Setae (shagreening scarcely visible)
	DI	VI	V		
I	—	—	—	—	1 pair setae
II	1	2*	2	1 ant. pair	few short setae
III	(1)	2	2	1 ant. pair 1 post pair (strips)	few short setae
IV	(1)	2	2	1 ant. pair	2 scattered areas of long setae
V	(1)	2	1	1 ant. pair	few short setae
VI	(1)	2	1	1 ant. pair	few short setae
VII	2	1	1	1 ant. pair	few short setae
VIII	—	—	—	1 ant. pair	few short setae

* The figure 2 denotes that the gill in question has 2 main stems.

DI = dorsolateral gills; brackets indicate that the gill in question has a broad pouch-like base.

VI = ventrolateral gills; these have been bracketed with the dorsolateral gills when they arise at virtually the same place.

V = ventral gills.

labial palpi rudimentary. Fore and hind leg small, slender; mid-legs longest, broader, flattened, with swimming fringes; tibial spurs 0.2.2. Tufted gills and dorsal plates present on abdomen as shown in Table XIX. All anterior dorsal plates with two points only; posterior plates long narrow strips with many minute points; few setae on abdominal tergites, shagreening almost invisible. Anal appendages of medium length, blunt-ended, curved dorsad, bearing strong ventrolateral and apical setae set on papillae; pockets for male genitalia present as usual.

Female pupa (in spirit, Figs 199, 200, Table XIX): very similar to male, but mid-legs more expanded, antennae shorter, equally slender, not coiled but curled round; gill count as in male, gills very clear: dorsal plates as in ♂, anal appendages very similar to those of ♂ but smaller and without pockets for genitalia. Two specimens, length c. 10 mm.

Pupal case: oval, examples incomplete, but evidently made from variously sized sand grains, mainly either very large or very small, completely lined with silk except at ends; head end with neat cap of stones overlying a silken meshwork, these stones being attached to the meshwork round rim of lid only; lid partially surrounded by a raised flange of stones (probably originally forming a complete ring); larval sclerites packed into posterior part of inner lining as usual.

REMARKS

Kimmins (1962a) discussed the genus *Aethaloptera* and concluded that there were only two doubtfully distinct species in Africa, *A. dispar* Brauer (1875) and *A. maxima* Ulmer (1906), the former having a more northerly distribution than the latter. P. C. Barnard (1980) regards *dispar* as a widespread and variable species and considers *maxima* to be a valid species, separable from *dispar* by hind wing venation and tibial spur formula. He further considers that the two species meet at the Victoria Falls, as shown on his distribution map (1980 fig. 28). In the Albany Museum collection there are adults from the Victoria Falls of which several are *maxima* but one, which differs from them in colour and certain other features, proved to be *dispar* (P. C. Barnard det.). All South African imagos are of *maxima*.

Various larvae have been ascribed in the literature to *Aethaloptera* (see Ulmer 1957), however, of these the only valid ones appear to be those of *A. rossica* Martynov, described by Lepneva (1964 (1970): 617-627, figs 762-773), and *A. dispar*, described by Gibbs (1973: 391, figs 77-79). The larva figured by K. H. Barnard (1934: 368, figs 40h-l) as ? *Chloropsyche* is in fact a *Macrostemum*. The larval and pupal stages of *A. maxima* have not, to my knowledge, been described previously.

The *maxima* larvae are on the whole very similar to those of *rossica* and *dispar* but there are distinct differences in mandibular teeth, anterior margin of frontoclypeal apotome, submentum and setation. The limb claws have a similar though not identical arrangement of basal spines (spinelike setae) and they and the long, slender pre-episternum probably represent valid generic characters, as does the type of mandible. Statzner (1981) in his comparison of *dispar* with another species also used the margin of the frontoclypeal apotome, submentum and setation, together with comparison of the ventral sclerites on IX.

Gibbs (1973; Figs 92-94) figured the pupa of *dispar* (evidently ♀), but without description. I can find no description of *Aethaloptera* pupae in the literature. The anal appendages as figured by Gibbs are similar to those of *maxima*, however, the mandibular teeth do show differences. The absence of palpi is characteristic of the Polymorphanisini, to which Tribe *Aethaloptera* belongs.

BIOLOGY

Statzner (1981), who observed *A. dispar* larvae in streams in Ivory Coast, noted that they built tubes which protruded into the current, somewhat altering the character of the substratum. They were not able to survive dry periods without flow and were killed by the application

of the insecticide Chlorphoxim. They took some months to repopulate, presumably by imagos from the nearest water, some 80 km distant. Instar distribution suggested a long larval life, similar to that shown by the *Cheumatopsyche* species observed.

Aethaloptera maxima, like *Amphipsyche scottae*, is found in the Vaal River and its tributaries, always amongst stones in current, and in similar habitats in Natal, South West Africa and Zimbabwe as far north as the Zambezi River. It particularly favours localities below dam outlets or barrages where there is a good food supply. The retreats have not been seen, but may well be similar to those of *dispar*. Larvae have been recorded from October to April, most commonly in summer, and imagos over much the same period. Dissection showed gut content to be very finely divided material, possibly indicating a diet of microseston as in some species of *Macrostemum*.

AFRICAN SPECIES OF *AETHALOPTERA*

A. dispar Brauer, 1875: 72, pl. iv, figs 4a-c, ♂ ♀.

Lectotype ♂, Senegal, near Taoué, xi.1869; in Naturhistorisches Museum, Vienna. Designated by P. C. Barnard, 1980: 68.

Primerenca maesi Navás, 1915: 182. Holotype ♀, Zaïre. Synonymy by Lestage, 1919: 293, 294.

Primerenca maerina Navás, 1916: 242 (unjustified emendation).

K. H. Barnard, 1934: 366–368, fig. 40a (♂ wings).

Kimmins, 1962a: 98–100, figs 38, 39, 43, 46, 48–55, 60, 61, ♂ ♀.

P. C. Barnard, 1980: 68–72, figs 19–27 & fig. 28 (distribution map); revision of genus and redescription of species with synonymy.

Marlier, 1965/66: 22, figs 11a, b, recorded two new forms of *dispar*, from Angola, namely Forma A and Forma B, both from females, of which Forma A is in fact *A. maxima*, Forma B *A. dispar* (Barnard 1980).

Distribution: Senegal, Sierra Leone, Ivory Coast, Ghana, Nigeria, Zaïre, Sudan, Uganda, Tanzania, Angola, Zambia, Malawi, Zimbabwe. P. C. Barnard considers that *dispar* and *maxima* meet only at the Victoria Falls, so that the Transvaal and Madagascar records need confirmation.

A. maxima Ulmer, 1906: 62, fig. 66. ♂.

Neotype ♂, South Africa, Waterval River, 12.i.1959, in Zoologisches Museum, Hamburg, designated by P. C. Barnard, 1980: 72.

Marlier, 1965/66: 40, *A. dispar* Forma A, misidentification of *maxima*.

Scott, 1975: 49, fig. 37, larva. (For other references see above under *A. maxima*.)

Distribution: South Africa (Orange Free State, Transvaal, Natal, Northern Cape), South West Africa, Zimbabwe, Zambia, Angola.

A. sexpunctata (Kolenati), 1859: 226, pl. III. Not African, see Note below.

Note:

Ulmer, 1912: 95, recorded *A. sexpunctata* from the Cameroons with a query, since it is an East Indian species. Navás (1932a: 288 & 1934b: 90), probably following Ulmer, recorded *sexpunctata* from the Belgian Congo and the Zambezi River. Kimmins (1962a: 100), suggested that the above records probably refer to *dispar*, possibly to *maxima*, but not to *sexpunctata*.

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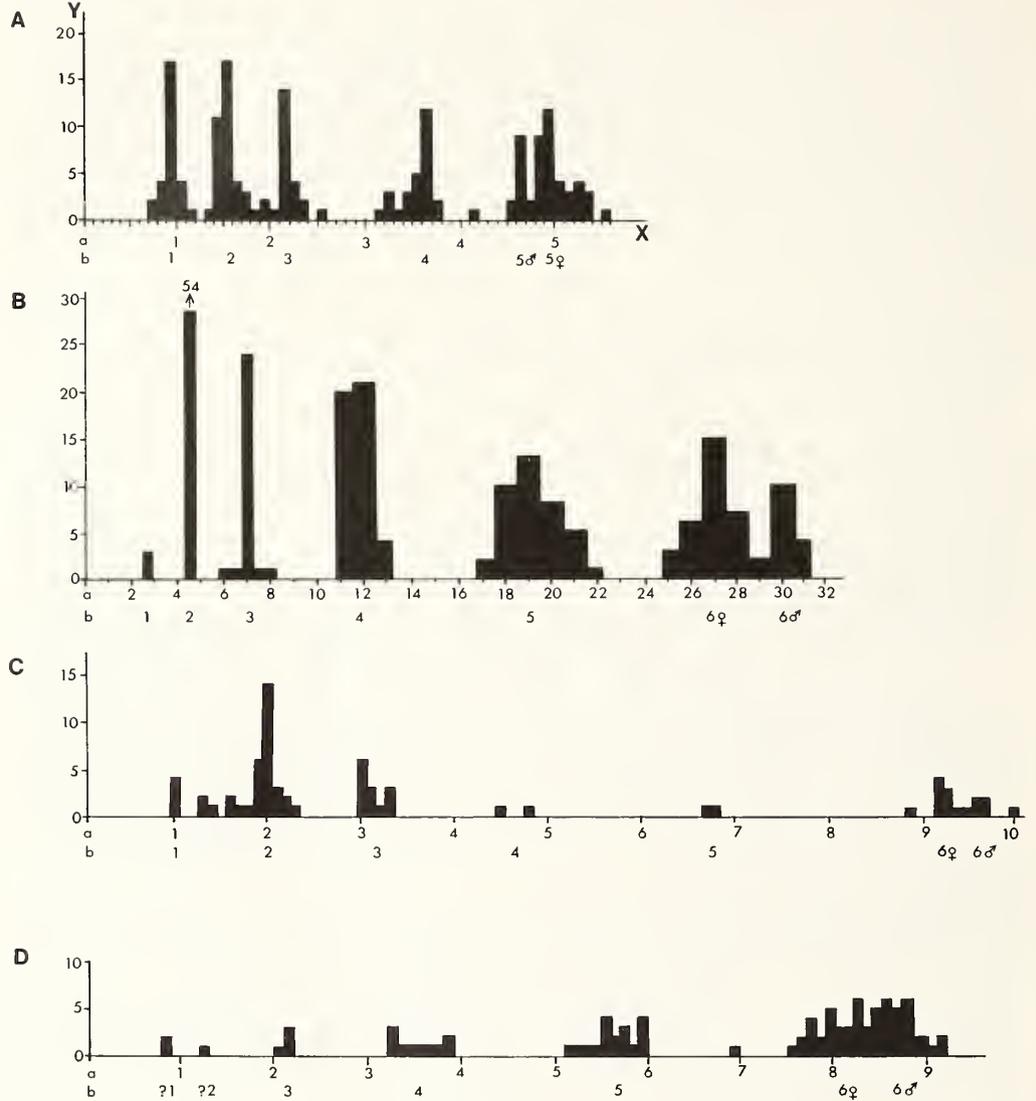


Fig. 214 A-D. Larval instars of certain Hydropsychidae shown as block histograms, based on head width at eyes. A: *Cheumatopsyche thomasseti*, B: *Macrostemum capense*, C: *Amphipsyche scottae*, D: *Aethaloptera maxima*, Y axes: number of individuals, X axes: a = head width at eyes in micrometer unit scale (6,0 units = 1 mm) (actual head widths in mm given in text), b = instar number.

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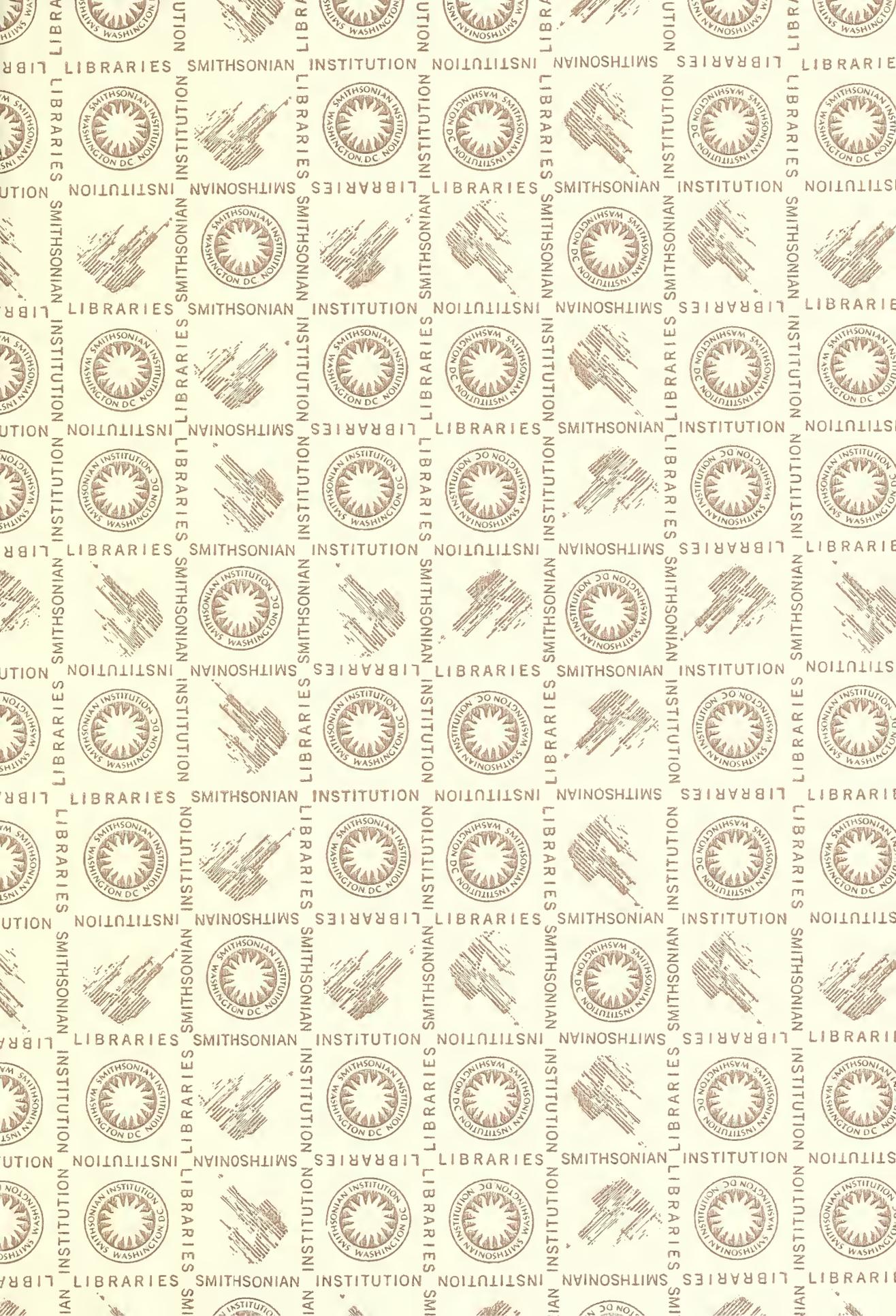
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