A REVISION OF THE SCORPION GENUS *HADOGENES* KRAEPELIN 1894 (ARACHNIDA: SCORPIONIDAE) WITH A CHECKLIST AND KEY TO THE SPECIES.

by

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Thesis submitted in partial fulfilment of the requirements for the degree of Magister Scientiae in the Faculty of Science, at the Potchefstroom University for C.H.E.

January 1980

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ABSTRACT

This thesis presents the results of a re-examination of the scorpion genus *Hadogenes* Kraepelin 1894 (Scorpiones; Ischnurinae) in Africa. For the first time in Africa, modern techniques such as chromosome studies and electrophoresis of the venom proteins have been utilized in conjunction with the morphological features of the species to obtain more meaningful results. Also for the first time ever, collective accurate distributional records of each species have been compiled in terms of geographical co-ordinates and plotted on maps. These distributional records are based upon all the acceptable literature records to-date, all the specimens housed in the major museums of the world and upon extensive field work during the course of the study. Each species is fully described and keys provided to enable the non-specialist to identify any of the fourteen species currently accepted. A detailed account of the scorpions anatomy is included which will enable the non-specialist to comprehend the taxonomic sections of this study. Besides the synonomising of several subspecies, one subspecies is errected to full specific status (*H. zuluanus* Lawrence) and a new species (*H. zumpti*) formally described. A photograph of each species is included.

UITTREKSEL

Hierdie verhandeling bied die resultate aan van 'n nadere ondersoek van die skerpioengenus, *Hadogenes* Kraepelin 1894 (Scorpiones; Ischnurinae), in Afrika. Vir die eerste keer is moderne tegnieke, soos chromosoomstudies en elektroforesis van die gifproteines aangewend tesame met die morfologiese kenmerke van die spesies teneinde meer betekenisvolle resultate te verkry. Daar is ook vir die eerste keer gebruik gemaak van gesamentlike akkurate distribusierekords van elke spesie wat saamgestel is in terme van geografiese koördinate en gekarteer is op kaarte. Hierdie distribusie rekords is gebaseer op alle huidige beskikbare literatuur; alle eksemplare wat bewaar word in die belangrikste museums van die wêreld; en op ekstensiewe veldwerk gedurende die tydperk van die studie. 'n Uitvoerige weergawe, van die anatomie van die genus, word gegee waardeur die taksonomie in die werk verstaan kan word, en verder is elke spesie tenvolle beskryf, en sleutels word voorsien teneinde die niespesialis instaat te stel, om enige van die veertien spesies, tans aanvaar, te identifiseer. Afgesien van die sinonimie van verskeie subspesies, is een subspesie verhef tot volle spesie status (*H. zuluanus* Lawrence) en 'n nuwe spesie (*H.zumpti*) formeel beskryf. Fotos van elke spesie is ingesluit.

DEDICATION

This thesis is dedicated to my late father
who's untimely death prevented him from
seeing the completed work.

CONTENTS

1. INTRODUCTION

1.1 The problem and how it was approached in the past

Scorpions of the genus *Hadogenes* Kraepelin 1894, commonly known as rock scorpions, are restricted to the southern half of the Afrotropical Region where they are widespread and fairly common. It is thus unfortunate that these scorpions cannot be identified satisfactorily by means of the existing keys to the species. Reference to the original species descriptions does not assist much in most cases as these descriptions are often very brief and of virtually no diagnostic value. To complicate the matter further, the taxonomic status of many of the fourteen species and eleven subspecies currently accepted are suspect. When confronted with probably conspecific species, the policy of some local taxonomists in the past appears to have been to reduce the status of the suspect species to the subspecies level in order to avoid sinking species. On the other hand at least one of the forms described as a variety or subspecies over the past sixty-five years is clearly deserving of full specific status.

Since Kraepelin erected the genus in 1894, four checklists and keys to the species have been published, viz Kraepelin 1899, Hewitt 1918, Lawrence 1955 and Newlands 1972. Kraepelin's 1899 checklist and key only dealt with three African species he recognised. Both Hewitt's 1918 and Lawrence's 1955 keys employed the degree of curvature of the carapace anterior margin to subdivide the genus into three species groups. Newlands (1970) demonstrated that the degree of curvature of the carapace anterior margin was both relative and extremely variable within even a given species population. Thus the keys of Hewitt and Lawrence cannot be regarded as a valid means of identifying species of the genus. The checklist and key of Newlands (1972a) was devised solely

for the fauna of South West Africa and is thus of limited application and is in need of revision. Besides these shortcomings, the revisions of the past were based upon small collections and in many cases the type specimens of dubious species were not consulted, which reduced deductions concerning these species to the conjectural level. Furthermore, basic ecological factors in understanding gene flow possibilities between populations were not taken into account when deciding species status and validity.

There are two subfamilies of the family Scorpionidae in the Afrotropical Region, viz Scorpioninae and Ischnurinae. Three southern African genera are contained within the Ischnurinae, *Hadogenes* Kraepelin, *Cheloctonus* Pocock and *Opisthacanthus* Peters. Morphologically, *Opisthacanthus* species are the closest relatives of *Hadogenes* species in southern Africa but certain genera from East Africa, Madagascar and Asia are more closely related. On morphological grounds, the closest relative of *Hadogenes* species are species of the genus *Iomachus* Pocock which occur in East Africa and Asia. However, if we accept that the number and position of pedipalpal trichobothria serve as suitable generic markers as proposed by Vachon (1973) then *Iomachus* species and *Hadogenes* species could not be considered congeneric for the trichobothrial patterns of these genera differ very considerably. Species of *Hadogenes* have the highest number and most complex trichobothrial arrangement of all known scorpion species. Similarly, the Asian genus *Chiromachetes* Pocock and the Malagasian genus *Heteroscorpion* are structurally very similar to *Hadogenes* but differ considerably with regard to the trichobothria. In fact, species of *Hadogenes* and *Heteroscorpion opisthacanthoides* are so similar in appearance that Kraepelin (1899) originally included *H. opisthacanthoides* in the genus *Hadogenes*. While these scorpions resemble each other structurally, the

trichobothrial arrangements are widely different. It seems probable that species of the genera *Chiromachetes*, *Heteroscorpion* and *Hadogenes* had a common ancestor in Gondwanaland, the ancestral populations became isolated and over the millions of years that followed, evolved into the three present-day genera. There is no question of these genera being regarded as congeneric at the present time. Species of the African genus *Ischnurus* Koch are also related to the species of *Hadogenes* but their general shape and trichobothrial pattern allies them more with the genus *Opisthacanthus* than with *Hadogenes* species. I believe that the genera *Opisthacanthus* and *Ischnurus* might prove to be congeneric, for the only morphological feature which separates these genera at present is the presence of bristle-like setae on the ventral tarsal surfaces in *Ischnurus* species and the presence of spines on the tarsal surfaces of *Opisthacanthus* species. Structurally there is very little difference apart from shape between these tarsal spines and bristles and as this is a character which varies continuously according to habitat in species of the genus *Opisthophthalmus*, it seems a very weak character with which to separate genera. A hypothetical phenogram showing the generic relationships based upon a simple comparison of specimens and as interpreted by myself is seen in fig. 1.

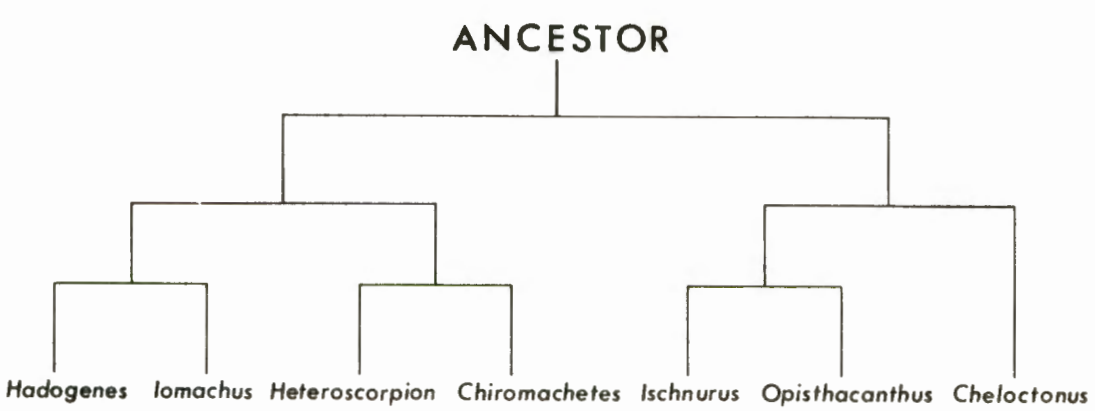


Fig. 1. Hypothetical phenogram showing the generic relationships within the subfamily Ischnurinae.

1.2 Conceptual background to the present study

Zoologically and biogeographically, *Hadogenes* is a most interesting scorpion genus. The genus houses some of the smaller southern African scorpionids as well as the largest. The longest scorpion on record in the world is a male *Hadogenes troglodytes* (Peters) from the Zoutpansberg district in the northern Transvaal which measures 210mm from the carapace to the tip of the sting. Although species of the genus have the highest number of trichobothria of all known scorpions the reason for this is not known. Ecologically, species of the genus are interesting in that they all have the same habitat requirements which is probably why they are very rarely found sympatrically.

In my opinion the genus is very old and existing species have evolved allopatrically as a result of population isolation caused by changing geomorphological and ecological factors. For example, the gradual erosion of a mountain reduces the elevation of the range with the formation of peneplains. The resistant rocks erode more slowly and give rise to inselbergs and short ridges on the resultant peneplain. If the pre-erosion ridge was inhabited by a single species, erosion causing the formation of inselbergs and short ridges will result in population isolates no longer interconnected by gene flow. Gene flow is interrupted as soon as there are no longer rocky outcrops on the peneplains between adjacent inselbergs or ridges. Field observations suggest that often, very narrow valleys or plains can interrupt gene flow between adjacent populations. An example of a narrow valley effectively isolating two species is seen in Pretoria where *H. gunningi* Purcell occupies the Magaliesberg and ranges to the south thereof while in the series of low hills just north of the Magaliesberg, *H. gracilis* Hewitt occurs. Although these ranges are less than three kilometres apart, no mixing of

the species occurs and hybrid forms have never been found in spite of extensive collecting. The valley between these ranges is filled with sandy loam soils and is free of rocky outcrops. The minimum width a valley would have to be to act as an ecological barrier to the scorpions is not known.

In arid regions, parts of mountain ranges can be isolated by the invasion of wind blown sand. For example, the Hauchab Mountains of the southern Namib have been cut off from the inland plateau by a narrow belt of sand which blew in from the coast. King (1951) believes that the Namib sands are coastal sands which have been carried inland by wind action over a period of millions of years. It is thought that the isolation of the Hauchab Mountains from the inland plateau probably took place during the Pliocene which started about eleven million years ago and lasted ten million years. Thus it seems as if the *Hadogenes* species population of the Hauchab Mountains have been isolated from the inland plateau populations for at least one million years. In this period, the isolated population on the Hauchab Mountains have evolved into a morphologically distinct species, *H. lawrencei* Newlands (1972a). The reason for the sand forming a positive ecological barrier to the species of the genus is that their tarsi are adapted to providing grip on rock surfaces (Newlands, 1972b). In laboratory observations, it is evident that species of *Hadogenes* experience great difficulty in walking over soft sand. Psammophilous scorpions have long setae on the tarsi which serve to increase the effective surface area of the tarsi and thus enabling these species to move over soft sand with great ease. It is unlikely that a specimen of *Hadogenes lawrencei* could move more than a few hundred metres over soft sand in a night and the sun would certainly kill these heat sensitive scorpions unless cover could be found during the day. As there are no rocks in the area between the Hauchab

Mountains and the inland plateau the 26km stretch of soft dune sand provides an insurmountable barrier to these scorpions.

As to how the speciation events took place once geomorphological factors had broken a parent population into a series of geographic isolates is a matter of pure speculation at the present time. Several models of speciation events have been proposed over the years and in discussing the problem, Paterson (1978) states that only two of these models have attained general acceptance, viz speciation by reinforcement and speciation in allopatry. Because of gene flow interruption by geomorphological processes such as peneplaination it seems reasonable to assume that speciation events in the genus *Hadogenes* have generally taken place in allopatry. By what mechanism the population isolates speciated is not clear. Carson (1971) in reviewing the "founder principle" suggests that in some species, a single founder individual, for example, a fertilized female, is a pre-condition for speciation. This might be feasible in the event of unpopulated inselbergs being colonized by individuals of a population in the vicinity. Alternatively, if a population crash occurs on an inselberg such that only a few individuals survive, any mutation with selective advantage would stand a good chance of becoming established. As Paterson (1978) has pointed out, in a large population the rarer chromosome arrangements (mutants) will be eliminated by selection. Thus, it would seem that small numbers of isolated individuals are the most likely candidates for speciation. It is not possible to say whether or not species of *Hadogenes* resulted from founder individuals or if some other less likely principle such as gradual change under the selective pressure of natural selection was responsible.

However intellectually exciting the concepts and mechanisms

of speciation may be, the task of the taxonomist is to define each species such that it can be recognised by other workers. Darwin stated that a species is what a competent taxonomist considers it to be and while modern taxonomists disagree with this vehemently, in practise, this is often the case. This is especially true of animals like scorpions which do not lend themselves to even simple investigations such as tests for hybrid sterility. For example, in the case of *Hadogenes* species, to test F1 hybrids for sterility would take at least 10 years under ideal conditions. Having successfully mated the species under test, the F1 hybrids would be born about a year later. For these young to reach sexual maturity would take approximately eight years. To test the F1 generation for sterility, one would have to wait the duration of a second gestation period to see if viable young are produced. These estimates are based on laboratory observations of specimens at all nymphal and adult stages with regard to ecdysis frequency and gestation period and are probably conservative estimates. Accordingly, the taxonomist has to turn to morphological and biochemical differences to assess species status. In some cases, chromosome numbers assist but obviously different species need not have different chromosome numbers.

Numerous species definitions have been advanced since Darwin published his *The Origin of Species* in 1859. Two definitions which satisfy the demands of a biological species concept have been adopted for the purposes of this study and are as follows. Merrell (1962) defined a species as a natural biological unit tied together by bonds of mating and sharing a common gene pool. A simpler definition which is in effect essentially the same is that advanced by Paterson (1978) in which he defines a species as a group of organisms which share a common specific mate recognition system (SMRS). Although Paterson's definition might appear to be an over simplification at first, it satisfies all the demands of a

species definition. The SMRS concept ensures that correct partners mate and accordingly that genes are only exchanged between members of the same species. The gene pool is thus kept species specific. Furthermore, the SMRS would act as a stabilizing element in that any individual departing from the norm would probably not find a mate and there is therefore a good chance that aberrant genetic material would be prevented from entering the gene pool.

The morphological differences which separate the various species of *Hadogenes* are relatively minor and this can possibly be accounted for in terms of two considerations. All species of the genus occupy virtually identical ecological niches and there is accordingly very little differential selective pressure upon the species with regard to habitat fit. Secondly all the species have poor eye sight and are of nocturnal habit. It follows that sight probably plays little or no role in specific mate recognition. Observations of the courtship and mating of *Hadogenes* species have led me to believe that the SMRS of these scorpions probably involves a contact pheromone.

For the purpose of this study I have attempted to delimit species of the genus *Hadogenes* into a series of reproductively isolated populations, each of which displays morphological and other differences, which I have regarded as specific. Alternative interpretations are never-the-less plausible. For example, some would regard the fact that with very few exceptions, no two species occur sympatrically as evidence for clines involving a few polymorphic species distributed over a very wide range. Obviously, where chromosome differences occur, the cline concept is untenable. Workers such as Ehrlich and Raven (1969) regard gene flow as less important in securing the integrity of a species than has been hitherto believed. To uphold this view, Ehrlich points to cases such as the warm water marine faunas which

occur as undifferentiated "twin species" on either side of the Isthmus of Panama. These isolated organisms have not exchanged genes for at least two million generations according to Ehrlich. In actual fact all this seems to prove is that in the absence of environmental pressure successful species will probably change very little. The findings of Ehrlich are based solely on morphological comparisons and his "twin species" might well prove to be sibling species if investigated cytogenetically. In most cases where gene flow has been interrupted by population fragmentation caused by changed geomorphological features over lengthy periods of time, speciation has occured in this genus.

A rather unique feature of gene flow in some *Hadogenes* species which would tend to emphasize cline formation is caused by the linear distribution of each species along rocky outcrops. Often the rocky outcrops and mountain ranges are considerably less than a kilometre wide and many hundreds of kilometres in length. In these cases, exchange of genetic material between individuals of the opposing extremities must be minimal. Species which inhabit mountain ranges over hundreds of kilometres such as *H. troglodytes* (Peters) do display clinal characteristics. This was never appreciated by taxonomists in the past who randomly sampled populations at various points along the cline and proceeded to describe their aliquots as new species and subspecies. When one looks at the distributional ranges of species such as *H. troglodytes* the linear nature of the distribution pattern is not immediately apparent and a more spatial distribution is seen. However, when these distributional ranges are superimposed on maps showing mountain ranges, it is clear that the distribution follows the range and when the range bifurcates so does the scorpion's distribution. Where branches of mountain ranges have subsequently become isolated from the main range complex by erosion, the populations have

become isolated and gene flow interrupted. In some such cases, speciation has occurred as in the case of *H. gracilis* which is clearly related to *H. troglodytes* and *H. gunningi* which is in turn closely related to *H. bicolor*.

It is now clear that far from solving the problem, the full extent of the problem has in fact been exposed for the first time. Speciation in the genus is complex and it is evident that a great many sibling species exist. It is clear that the traditional morphological approach of the past has been simplistic and an example of a species complex which has been unearthed by elementary chromosome and electrophoretic studies is provided by the *H. tityrus* group.

2. MATERIALS AND METHODS

2.1 Collecting specimens in the field

Collection of specimens in the field involved microhabitat location (see section 4.0), capture and storage. Unlike most scorpions *Hadogenes* species seldom leave their rock shelters and this behavioural characteristic renders the setting of pitfall traps and specimen location by means of ultra-violet light at night ineffective. All scorpions fluoresce in the presence of ultra-violet light radiations (Lawrence, 1954) and this affords a convenient method of locating specimens at night, provided the scorpions are out of their shelters (Honetschlager, 1965; Stahnke, 1972). Pitfall traps set by S. Endrody-Younga to collect terrestrial Coleoptera in the Namib Desert and Richtersveld captured over a thousand scorpions during a one year period but not a single specimen of the genus *Hadogenes* (personal communication).

Virtually all specimens found in the field were under large rock masses weighing between about 100kg and several tons. For the lone field-worker, the capture of these specimens is a difficult task and alternative methods to lifting the rock mass above specimens were tried. Pungent and irritating chemicals used in an attempt to drive the scorpions from their rock shelters included ethyl acetate, chloroform, ether and ammonia, but these only served to drive the scorpion deeper into its shelter. A mechanical method tried was a noose made from thin nylon fishing line and attached to a stout wire holder. This met with very limited success mainly because the only appendage one can safely grasp with a noose is the pedipalp. As the pedipalp is richly endowed with sensory setae, any attempt to move the opened noose over the pedipalp simply alerts the scorpion who then retreats deeper into the rock cavity.

The only satisfactory method of capture proved to be lifting the rock mass above the scorpion carefully by means of a builders crow-bar at least 75cm long. The rock is moved a little at a time and wedges or stones forced into the widening crack at each advance. An *Estwing* all steel geological pick proved to be a very satisfactory wedge in the initial stages of opening the rock cracks. Actual capture of the specimen was done with 20 to 30cm surgical forceps. The specimen was grasped by one of the pedipalps and lifted off the substrate in one swift flowing movement. If this operation was not done positively and rapidly, the specimen would be able to adopt a defensive stance and latch onto the rock substrate by the tarsal locking mechanism (Newlands, 1972b). Alerted scorpions move at great speed and are difficult to pull off the rock without damage. Under no circumstances should capture be attempted by grasping the delicate metasoma with the forceps.

Captured specimens were placed in disposable petri-dishes (10cm diameter) and taped closed with pressure sensitive masking tape. Relevant details of each specimen were written on the petri-dish lid with a felt-tipped permanent marking pen. The sealed petri-dishes were placed in bags (15x30cm) made from *Thermos* space blankets such that the aluminumised surface was outermost. Each bag was equipped with a draw-string at its mouth to facilitate sealing in the field. Space blankets are lightweight insulating blankets and the storage bags were made from this material to keep the captured scorpions as cool as possible for lethal temperatures can easily be reached in canvass rucksacks exposed to the sun during the average day's collecting. At the end of each day, the sealed space blanket bags were transferred from the rucksack used in the field to wooden boxes. The specimens received no further attention for the duration of the field work and very few deaths (less than 3%) occured using this method. On early

field work trips specimens were placed in wide mouthed petroleum jelly jars 10cm wide by 10cm high. These proved very bulky and at least 10% of the specimens died in transit. The space blanket bags also provided a measure of shock absorption while travelling over rough terrain with the four-wheel drive vehicle used.

2.2 Preparation of museum specimens for taxonomic study

Specimens intended for taxonomic study should be well preserved, flexible and properly labelled. Williams (1968) and Newlands (1969) have described methods for the preparation of scorpion specimens for scientific study and display. These methods were found to be unnecessarily complicated and the following simplified method was adopted.

2.2.1 Killing specimens

Williams (1968) and Newlands (1969) advocated killing specimens by dropping them into hot water (over 90^{o}C) for 10-60 seconds. This method appeared to render the inter-segmental membranes more prone to damage subsequently and was abandoned. Specimens were killed by placing them in a conveniently sized wide mouthed jar with a cotton wool pad soaked in chloroform. Specimens were left in the chloroform atmosphere for several minutes longer than was necessary to anaesthetise them. Anaesthetised specimens were pithed by inserting a pointed scalpel blade into the supraoesophageal ganglion below the median ocelli. The blade was inserted through the intersegmental membrane between the carapace and the first tergite. Specimens killed in this way were relaxed provided they were not left in the chloroform for very long periods.

2.2.2 Fixation and preservation

Specimens were fixed by injecting formal saline (4% formalin made up to contain 0,9% sodium chloride) into the haemocoel of the prosoma and mesosoma. In large specimens longitudinal cuts were made in the pleural membranes to facilitate replacement of the haemolymph with fixative. Injected specimens were then soaked in 4% formal saline for 6-16 hours, depending upon the size of the specimen. If specimens are over fixed they become very brittle and unsuitable for taxonomic study and the appendages and metasoma generally break off when the specimen is handled. Once fixed, the fixative is removed by washing the specimens in running water for several hours. The specimens were then labelled and transferred to 1 litre canning bottles filled with 70% ethanol.

2.2.3 Cataloguing and labelling of specimens

An accession catalogue was kept for all scorpions received during the study. Each specimen received was entered in the catalogue listing the species, collector's name, date of collection, precise locality in terms of the place name and degrees of latitude and longitude. The place names were given as listed on the official 1:250 000 topocadastral map series. When the locality was a farm, the official farm name, number and magisterial district were entered in the catalogue. A label of laundry tag paper (obtainable from most printers) which retains its strength when wet, was attached to the left pedipalp of each specimen. This label listed the catalogue accession number, locality and co-ordinates, collector and date of collection. The information was written on the label with a *Rotring* 0,2mm drawing pen charged with *Pelikan* india ink. Locally produced india inks were found to wash off when the specimens were stored in 70% alcohol. The labels were always tied to the

left pedipalp as the right pedipalp was used for the trichobothrial studies. With the label tied to the specimen there is no chance that specimens can be separated from their data. In many museums such as the British Museum (Natural History) labels are not attached to the specimens and it is thus possible to inadvertently mix specimens and labels when material is being compared. Furthermore, when labels are not attached to the specimens, the specimens have to be stored individually in glass containers.

In cases where the paraxial organs of the male were dissected out for morphological study, these were stored in individual glass vials measuring 10x50mm. The vials contained a label with full specimen particulars, were filled with 70% ethanol and capped with a tight-fitting cotton wool plug. The vials were stored in wide mouthed glass bottles filled with 70% ethanol.

Labels were never stuck on the external surface of bottles containing specimens as these labels can become detached or fade. Good quality light card was used for specimen jar labels and the necessary particulars were written with india ink. The labels were placed in the jars such that they could be read from the outside.

2.2.4 Paraxial organ removal and preparation

When adult males were available, the right paraxial organ (see 3.2.1) was dissected out for morphological examination. If the dissection is done neatly, the incision in the intersegmental membranes is barely visible. In specimens which had been opened for the removal of the gonads (see 2.6) the paraxial organs could be reached from above. Fine dissecting scissors were used to cut the paraxial organ as near as possible to its junction with the gonotreme. The paraxial organ was then pulled free of the body cavity using

fine forceps. In the case of museum specimens which had not previously been opened, the right paraxial organ was removed by carefully cutting the ventral intersegmental membrane just posterior to the coxae of legs IV with very fine scissors. The cut was made through the entire width of the scorpion and passed just anterior to the genital operculum mesially. It was then possible to fold the sternite including the genital operculum and pectines ventro-posteriorly. The paraxial organ could then be grasped near its base by forceps inserted into the incision and extracted by gently pulling it ventro-anteriorly. With the paraxial organ extracted, the sternites were pushed back into position to expose the characters used for taxonomic study, the soft membranous sheath covering the sclerotised components of the paraxial organ were removed by carefully dissecting them away with two pairs of watchmakers fine forceps. The dissection was done under 70% alcohol.

2.3 Morphological examination and mensuration

Morphological examinations of specimens were conducted using a Wild M5 stereo microscope fitted with 8X oculars and a drawing tube. A separate pair of 20X oculars, one of which contained a graticule, was used for measurements through the microscope. Measurements taken with the graticule could be converted into millimetres by multiplying by factors which were computed for each magnification. The factors were established by measuring standard scales with the graticule. All low power observations (6-50X) were done using the incident light source supplied with the microscope.

Counting trichobothria proved to be the most difficult and time consuming task, taking up to an hour or more per specimen. The trichobothria of each pedipalpal surface were sketched with the aid of the camera lucida drawing

tube at a magnification of 12X. As it was very difficult to distinguish between trichobothria and other setae at this magnification, the drawing was checked carefully with the microscope set at a higher magnification. Trichobothria were represented by a small circle on the sketches. In the case of old specimens which had lost many of the setae on their pedipalps, great difficulty was often experienced in distinguishing trichobothria pits from those of other setae. Specimens were held in an appropriate position during mounting and drawing by being pressed lightly into balls of adhesive putty.

In scorpions as large as most *Hadogenes* species, it is physically impractical to take most of the measurements through the microscope. The majority of measurements were made with an engineers vernier calliper which enabled measurements to be made to 0,05mm and as most of the measurements taken were between 5 and 100mm, this accuracy was perfectly adequate.

In the case of articulating segments, the length of the segment was always taken between the articulation points. The height, and width of a segment was taken at the greatest diameter unless otherwise stated. In the case of sclerites, the maximum length or width was taken.

2.3.1 Colour determination

Newlands (1969, 1972) first used soil colour charts based upon the Munsell system to describe scorpion colouration in a simple and objective manner. In the Munsell system colour is described in terms of hue, value and chroma (Oyama and Takehara, 1970). To determine the colour of a specific surface, it is simply matched to the appropriate colour chip in the colour chart. Colour matching is best done in fairly bright diffused sunlight. Stahnke (1970)

was of the opinion that the most effective method of describing colours is the simplistic and advocates the use of "primary colours in a variable manner" as being the most precise. This seems irrational to me as is his condemnation of colour charts because of "variation in surface conditions and the reflectivity of light".

The "Revised Standard Soil Colour Charts" of Oyama and Takehara (1970) which are based upon the Munsell system were used for colour determinations in the present study.

2.4 Laboratory maintenance of scorpion colonies

For electrophoretic, cytogenetical and behaviour studies, it was necessary to maintain laboratory colonies of live specimens. Specimens were kept in a small room maintained at 27°C by means of a thermostatically controlled heater. Specimens were kept individually in wide mouthed petroleum jelly jars measuring 10cm wide by 10cm deep. Each jar was fitted with a metal screw-cap. Smaller specimens were often kept in the petri-dishes they were placed in when caught initially (see 2.1). No holes were made in the lids of the petri-dishes or the jars and specimens were kept for up to two years under these conditions. Laboratory specimens were fed every two weeks with either Coleoptera larvae, *Tenebrio molitor* Koch (meal worms) or cockroaches. The meal worms were originally obtained from the Transvaal Museum in Pretoria and were placed in bins 40x80x20cm filled to a depth of 15cm with bran. Occasionally, lettuce leaves, carrots or oranges were added to the bins. The complete life cycle of the beetles continued under these conditions and ensured a constant supply of larvae. The cockroaches were obtained from the Entomology Section of the South African Bureau of Standards in Pretoria. The adults were maintained in 5 litre plastic buckets fitted with gauze lids. They were given water and ground dog-food weekly and survived well under these conditions.

Alexander (1959) found that species of *Hadogenes* refused all food in captivity. While most specimens fed readily on the meal worms and cockroaches, there were individuals who persistently refused to feed. Generally these specimens could be encouraged to eat by decapitating the food item and pushing it into the prebuccal cavity as far as possible. Body fluids from the decapitated prey entered the mouth parts and seemed to stimulate feeding. Specimens were given water weekly.

2.5 Milking scorpions

Electrophoretic patterns of the venom proteins were used as a taxonomic aid. Venom aliquots were obtained by electrical stimulation in the following manner. Specimens were held firmly in a clamp which was specially designed for this purpose (fig. 2). This clamp was made as methods described in the literature, a modified mouse-trap (Whittemore *et al*, 1963) and a petri-dish (Deoras, 1967), proved unsuitable for handling the large and relatively delicate species of *Hadogenes*. Components of the clamp are an immovable, polished chassis to which a high density foam rubber strip was glued to form the lower jaw. A polished surface was used for the lower jaw or chassis to prevent the scorpion from being able to grip the surface. The upper jaw was equipped with a high density foam strip above that of the lower jaw and a pressure pad. The pressure pad was half of an elastic ankle-support bandage as sold by sports equipment dealers and pharmacists. The upper and lower jaws were kept closed by the spring which was positioned over the joint pin. The joint pin was welded to the chassis piece so that the upper jaw only could move when the device was clamped in a retort stand by the protruding portion of the joint pin on one side.

For milking, 20V AC supplied by a mains step-down transformer

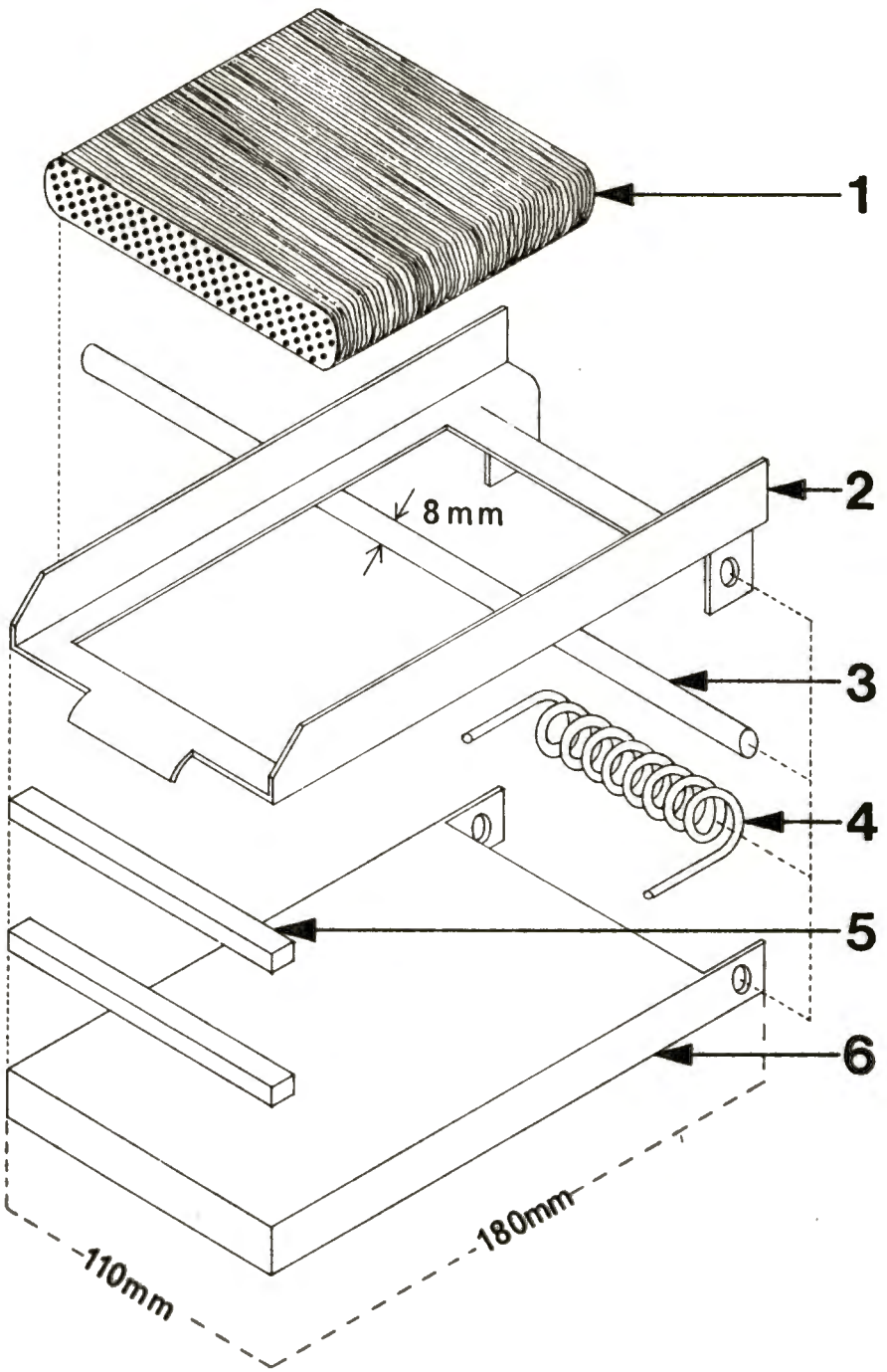


Fig. 2. An exploded view diagram in isometric projection showing constructional details of a scorpion clamp. The components include an elastic pressure pad (1), upper clamping jaw (2), joint pin (3), clamping spring (4), high density foam rubber strips (5) and polished stainless steel chasis (6).

was applied to the proximal and distal intersegment membranes of the 5th metasomatic segment by means of electrodes. The electrodes were formed by removing about 7mm of insulation from the end of two household electric cables. The bared copper strands were twisted tightly to prevent fraying. In use, these electrodes were moistened with 1-5% sodium chloride solution to improve current flow through the intersegmental membranes. Venom was collected in disposable pasteur pipettes.

2.6 Electrophoresis of the venoms

Initially, disc gel electrophoresis was tried but it was soon evident that subtle differences in component mobility between two aliquots could not be detected with certainty. Disc gel electrophoresis was thus abandoned in favour of slab gel electrophoresis which enabled accurate comparison of component mobilities for up to 12 samples per run. In order to reduce variables to a minimum, the venom samples were taken up in a splitting solution containing sodium dodecylsulphate (SDS). The splitting solution neutralizes all the charges of the protein molecules and the subsequent electrophoretic mobility is solely a function of molecular size. Advantages of this system are that the samples are stabilized and can be stored for long periods of time and small pH changes of the buffer systems employed do not affect electrophoretic mobility. The method used was adapted from Shapiro, Vinuela and Maizel (1967) who described the use of SDS in polyacrylamide gel electrophoresis. This method was in turn based on the original methods described for disc gel electrophoresis by Ornstein (1964) and Davis (1964).

2.6.1 Materials

Dodecyl hydrogen sulphate, sodium salt $C_{12}H_{25}NaO_4S$ (SDS) was

recrystallized from a 5% solution in 95% ethyl alcohol. The fraction crystallizing out between 20°C and 5°C was filtered off with a vacuum pump in buchner funnels and dried over phosphorus pentoxide under vacuum. A 20% yield was obtained.

Acrylamide (CH_2:$CHCONH_2$) and N,N,N',N'-tetramethylethylenediamine (TEMED), $(CH_3)_2$. $NCH_2.CH_2.N(CH_3)_2$ were purchased from Fluka A.G., N,N'-methylene-bisacrylamide (BIS) was obtained from Pleuger, 2-mercapto-ethanol from Merck, and Coomassie Brilliant Blue R-250 from ICI. All other chemicals were of AR grade obtained locally.

An Ortec, model 4010/4011 slab gel electrophoresis system with two vertical cells, each with a 12 aliquot capacity was employed in conjunction with a constant current pulsed power supply.

2.6.2 Sample preparation

The venom collected in the pasteur pipette (section 2.5 above) was transferred to a $2cm^3$ serology tube containing $0,5cm^3$ of splitting solution (8M urea in distilled water containing 1% SDS and 1% 2-mercapto-ethanol) mixed thoroughly and heated in a boiling water bath for 60 seconds. Samples were then stored below 4°C until required.

2.6.3 Slab gel preparation and sample application

Gel slabs were prepared as recommended by the manufacturer of the equipment. The Ortec vertical running cells were sealed below with parafilm and clamped in the gel forming stand mounted on a perfectly leveled adjustable base-plate. To prepare the four gel layers of the slab, the following solutions were prepared:

Solution A: 20g polyacrylamide plus 0,5g BIS in 100cm^3 distilled water.
Solution B: 0,2g SDS in 10cm^3 0,1 M sodium phosphate buffer at pH 7,2.
Solution C: 10cm^3 0,03 M sodium phosphate buffer at pH 7,2 containing 0,1% SDS and 50mg ammonium persulphate.
Solution D: 24cm^3 solution B plus 60cm^3 TEMED.
Solution E: 4,8g polyacrylamide plus 0,12g BIS in 15cm^3 distilled water.
Solution F: 0,105% ammonium persulphate in distilled water.
Solution G: 0,21% ammonium persulphate in distilled water.
Solution H: 20cm^3 solution D plus 0,19cm^3 TEMED.

Each slab gel was comprised of four layers. The main layer was a 9,5% polyacrylamide separating gel in which the sample components were separated from each other during electrophoresis. This gel was capped with a 4,7% polyacrylamide stacking gel which allowed the sample to pass through it rapidly and compact on the higher density separating gel. The object of the stacking gel was thus to sharpen the sample component bands in the separating gel. A well forming gel was cast above the stacking gel to receive the samples. The wells were formed by introducing a special Teflon comb-like well forming mould before the gel set. When the gel had set, the Teflon comb was extracted and the wells were ready for introduction of the samples. Samples were introduced into the wells by means of siliconized Biotip micropipettes. The fourth gel was a capping gel which was overlaid carefully into the loaded sample wells to stabilize the samples and prevent them mixing when the reservoir was added. Each gel layer was prepared as follows:

Separating gel layer

Aliquotes of 9,5cm^3 of each of solutions A and B (above) were added to 1cm^3 of solution C and 10cm^3 of TEMED in a

1 litre Buchner filter flask. The resultant solution was degassed under vacuum for 30 seconds, poured into the gel cell, overlaid with distilled water and allowed to polymerize. The gel was formed under distilled water to prevent air bubble formation between the cell walls and the gel slab.

Stacking gel layer.

The stacking gel was prepared by mixing 0,8cm^3 of solution D with 0,45cm^3 of solution E, 1,6cm^3 of solution F and 0,35cm^3 distilled water. This gel was layered between the polymerized separating gel and distilled water overlay and allowed to polymerize for 20 minutes. At the end of this period the water was poured off and the gel dried with a paper tissue.

Well-forming gel layer.

This layer was prepared by mixing 1,0cm^3 of solution E with 2,0cm^3 solution G and 1,0cm^3 of solution H. The well-forming layer was cast on top of the stacking gel and the well-forming Teflon comb inserted. After 10 minutes the Teflon comb was removed, the formed wells washed out with distilled water and dried very carefully with a paper tissue. The samples were then pipetted into the wells.

Capping gel layer.

The capping gel was prepared by mixing 1,0cm^3 of solution H with 1,0cm^3 solution E and 2,0cm^3 of solution F. This solution was then poured over the loaded wells taking care to prevent trapping air bubbles in the wells. Polymerization time for this gel is about 10 minutes.

2.6.4 Electrophoretic run

A 0.03M sodium phosphate buffer adjusted to pH 7,2 containing

0.1% purified SDS and 0.1% 2-mercapto-ethanol was used as a reservoir buffer.

The apparatus was assembled according to instructions given in the Ortec operations manual and run for two hours at 325 volts, 115 milliamperes and 300 pulses per second.

After two hours of running time, the gels were removed from the cells by gently inserting a 15cm cannula (blunt hypodermic syringe needle) connected to a cold water tap and by means of the water jet, detaching the gel from the cell walls. Much care was needed to prevent gel damage. The extracted gel was fixed in 20% trichloroacetic acid for at least an hour, after which time, it was washed in running tap water for a few seconds. Once fixed, the gel was stained in a 0,0125% CBBR-250 solution dissolved in methanol-water-acetic acid-glycerol mixture in the proportions 16:21:2:1 respectively. Destaining was performed in open trays with frequent changes of 7% acetic acid solution containing 10% methanol. Once destained, the gels were photographed (see section 2.82). Gels could be stored immersed in the destaining solution. Plastic lunch boxes with air-tight lids were found to be suitable containers for storing the gels.

2.7 Chromosome preparations

Chromosome spreads were prepared from testicular tissue as far as possible but somatic cell division was also studied for comparative purposes. Scorpions of the genus *Hadogenes* develop and grow extremely slowly, the gestation period being at least twelve months and the period from birth to maturity between six and eight years. Possibly for this reason, cell division is rarely seen in spreads made from various organs of developing scorpions. Testicular tissue proved the best source of chromosomes but occasional spreads were obtained from developing embryos.

Adult males and gravid females intended for chromosomal study were well fed and kept at 27°C day and night. About five hours before sacrifice the scorpion was injected with 0,2 to 0,5cm^3 (depending upon size) of a mixture of phytohaemagglutin (Wellcome Reagent HA15) and colchicine (Sigma Chemicals). Wellcome phytohaemagglutin (PHA) is only supplied as a freeze-dried deposit in sterile bottles and reconstitution is accomplished by injecting 5cm^3 sterile distilled water into the bottle through the rubber cap by means of a disposable, sterile hypodermic syringe. For use the PHA solution was mixed with an equal volume of colchicine solution (20mg per 100cm^3). A 1cm^3 disposable syringe with 26 gauge needle was used to inject the mixture subcuticularly into the haemocoel of the mesosoma. PHA is a mitogenic agent and colchicine arrests cell division at metaphase. Significantly better results were obtained when the PHA-colchicine mixture was administered.

Animals were sacrificed by anaesthetising with an overdose of chloroform and pithing. The gonads were reached by slitting the pleural membrane of the mesosoma through its entire length on one side. Severing of the dorso-ventral mesosomatic muscles enabled the tergites to be folded over so as to expose the systemic organs. Dissecting was done under 0,5% sodium citrate solution using fine watchmakers forceps (number 5). The excised gonads were transferred to fresh 0,5% sodium citrate solution and allowed to stand for 20 minutes. After 20 minutes in the hypotonic citrate solution the testicles were placed in Carnoy's fixative (methanol-acetic acid; 3:1) for at least 16 hours at 4°C. The hypotonic solution used by other invertebrate cytogenetists (Crozier 1968, Fontana 1976 and Igarashi and Kondo 1977) was a 1% sodium citrate solution but this did not appear to swell the cells. As it was not possible to determine the osmolarity of scorpion haemolymph, experiments were performed using various concentrations of sodium citrate to determine

which concentrations were hypotonic. The best cell swelling results were obtained with the 0,5% sodium citrate solution. Experiments were also conducted with the perfusion fluid devised by Padmanabhanaidu (1967) at various dilutions but this offered no advantage over the 0,5% sodium citrate. This technique of swelling cells in a hypotonic solution has never been used in the study of scorpion chromosomes previously.

Spreads were prepared by transferring about 4mm of testicle or a small fraction of an embryo to a drop of 60% acetic acid on a precleaned microscope slide and macerating the tissue with a pair of sharpened tungsten needles or fine forceps. With the tissue broken up into fine fragments, two or three drops of the methanol-acetic acid (3:1) mixture were dropped onto the slide and allowed to spread while passing the slide through a spirit burner flame so as to dry the tissue suspension. When dry the slides were stained in 10% Giemsa stain in pH 7,3 buffer for 1 hour. After staining the slides were thoroughly rinsed in distilled water, dried and mounted in Entellan (E. Merck). Slides were scanned and suitable spreads photographed. (see 2.8).

2.8 Photography of specimens, electrophoresis gels and chromosomes.

2.8.1 Macrophotography of specimens

All type and other important specimens examined were photographed for record purposes. In each case a dorsal and ventral view of the whole scorpion was recorded together with a scale and specimen label. Details of particular interest on certain specimens were also photographed. The camera used for most of this work was a Rolleiflex SL66. A Carl Zeiss 120mm 4 S-Planar lens was used as it is a flat field high resolution objective specially corrected for macro-photography. Agfapan 100 film (Agfa Gevaert) was used.

To avoid background shadows, specimens were supported on a sheet of 3mm window glass supported on three sides by a wooden frame. The frame was constructed of 12mm wood panels such that the 30x24cm glass sheet was supported 10cm above the background. The inside surfaces of the frame were painted matt white and the background was a sheet of white bond typing paper. To lighten the shadows on the specimen a white card was placed on the shadow side (fig. 3). The camera was supported in a coping stand and illumination provided by a single 500W Philips Argaphoto lamp with built-in reflector, at a distance of approximately 1 metre from the specimen. Exposure was determined with Gossen Lunar-six exposure metre by the incident method.

2.8.2 Macrophotography of electrophoretic gels.

Electrophoretic gels were photographed with the same equipment as outlined above (2.8.1) but with the following modifications. The wet gels were placed on the glass sheet and gently pressed to expel all trapped air between the glass plate and the gel. Photography was done in a darkened room by transmitted light which was achieved by placing a black card on the glass stage between the gel and light source such that no direct incident light fell on the gel. The gel was thus evenly illuminated by diffuse transmitted light reflected off the white background (fig. 3). Exposure was determined without the diffusing cone on the lightmeter.

The 120mm S-Planar lens was always used to photograph gels to reduce the parallax error in bands near the edges of the gel. As the bands are about three millimetres deep it follows that if they are not on the optical axis of the lens, they will appear wider in a photograph than they are. This effect is enhanced with short focal length lenses (i.e. wide-angle lenses). The 120mm lens used appeared to overcome this problem satisfactorily (fig. 4).

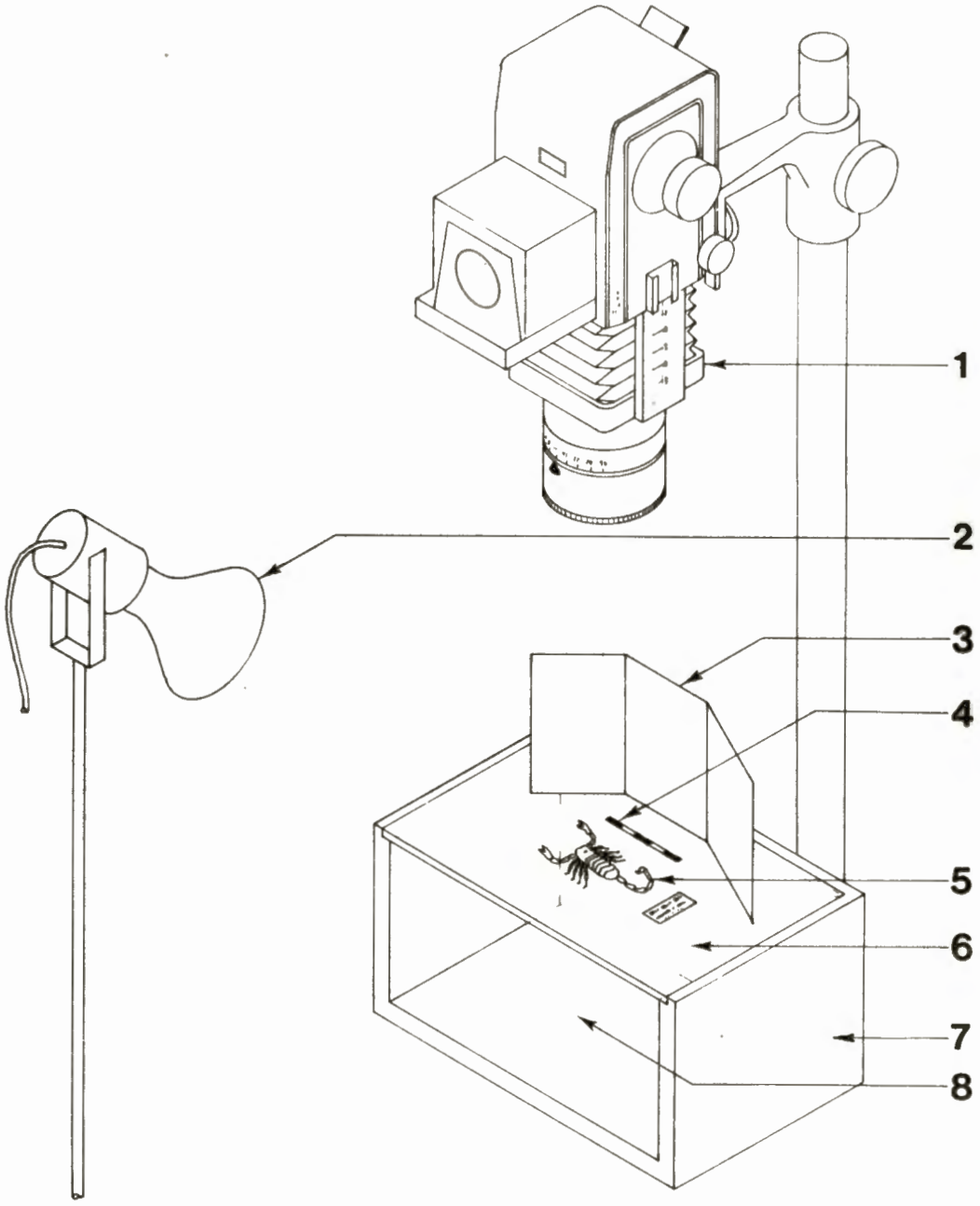


Fig. 3. Arrangement used to photograph museum specimens: 1. Camera. 2. Photoflood lamp. 3. White reflector card. 4. Scale. 5. Specimen. 6. Glass specimen support. 7. Wooden frame open on one side. 8. White background paper.

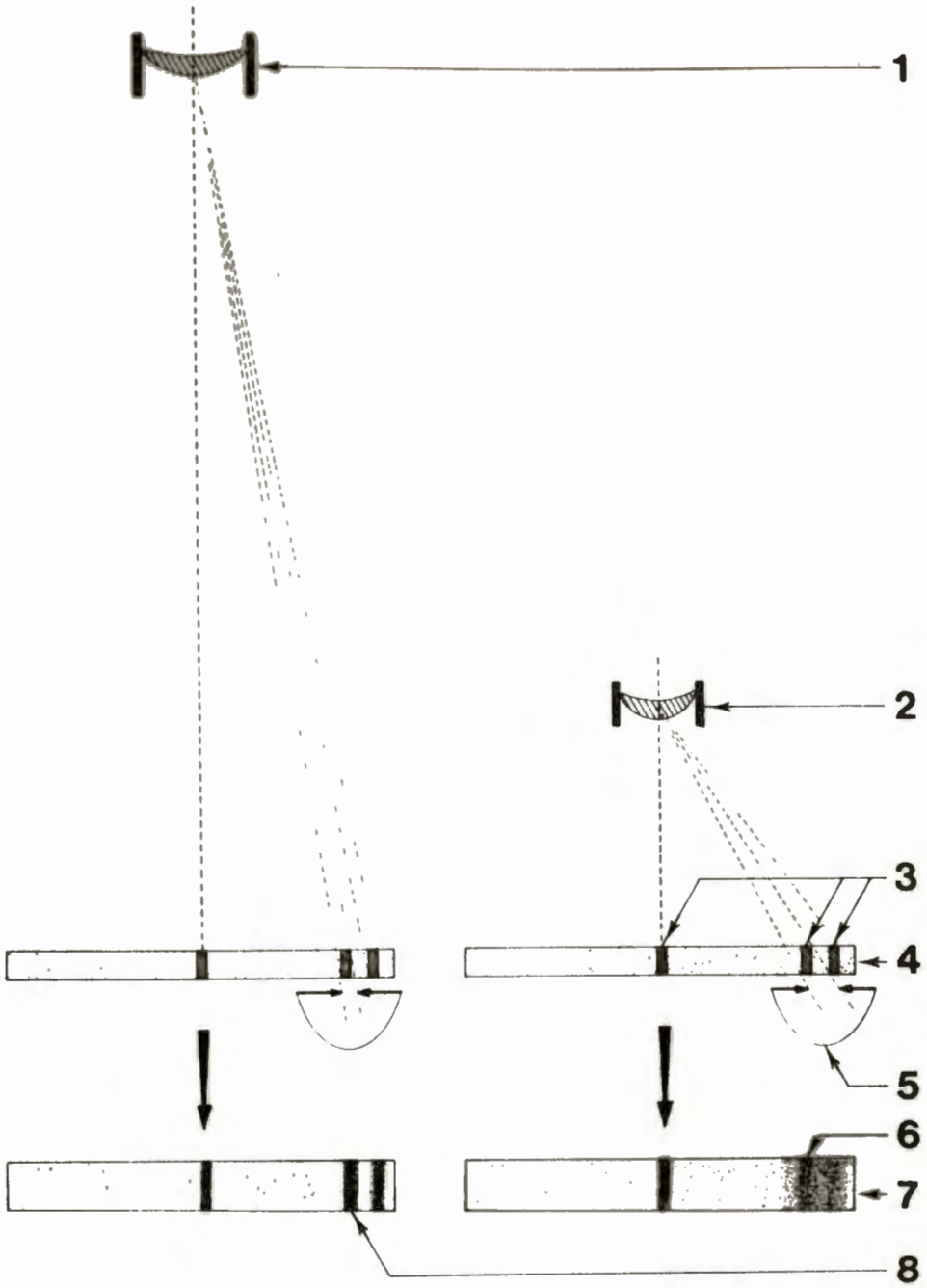


Fig. 4. Diagram showing why bands not on the optical axis of the lens appear wider than they are, especially when photographed with lenses of short focal length. In the diagram 1 represents a long focal length lens, 2 a short focal length lens, 3 component bands and 4 the gel. In the case of the short focal length lens the bands will widen as shown at 5 and lose definition and contrast as in 6 on the resultant photograph 7. In the case of the long focal length lens this parallax effect is minimal and the bands appear sharp as shown at 8 in the resultant photograph.

Many of the bands on the gels were very faint. As the bands were stained blue, a medium yellow filter was placed over the camera lens to enhance the contrast slightly.

2.8.3 Photomicrography of chromosomes

All the chromosomes photographed were prepared with a Zeiss Winkel Research compound microscope fitted with a Zeiss three way deflector prism, the binocular head being fitted to a side outlet and the camera to the top outlet. The camera was fitted to a monocular tube giving a tube length of 160mm by means of a standard microscope adaptor. All spreads were photographed with a N.A. 1.25, 100X planachromat objective in conjunction with Kpl oculars, the magnification factors of which were 8, 10, 12.5 and 20X times. The ocular was chosen so as to fill the photographic format. A dark green filter was used and the Köhler illumination principle was always used (Lawson, 1972). Scanning of the slides to locate the spreads was done with a N.A. 0.25, 10X achromatic objective and 10X compensating ocular.

In order to reduce vibrations caused by the camera shutter, vibration dampers were attached to the camera and base. Three aluminium rods, 10mm in diameter and 60cm long were capped with a 4-6cm diameter ball of adhesive putty at each end. The adhesive putty is in fact a sealing compound marketed under the name "Presstick" and is available at most stationers. In use a damper rod was pressed against one side of the camera housing and to the bench such that it is at an angle of about 60° to the bench. The process was repeated with two other sides of the camera housing. The large balls of putty enable considerable movement of the camera for focusing but hold the microscope absolutely steady, even when the reflex camera's shutter and mirror were released (fig. 5). Without these damping rods very noticeable camera shake is clearly evident when the shutter

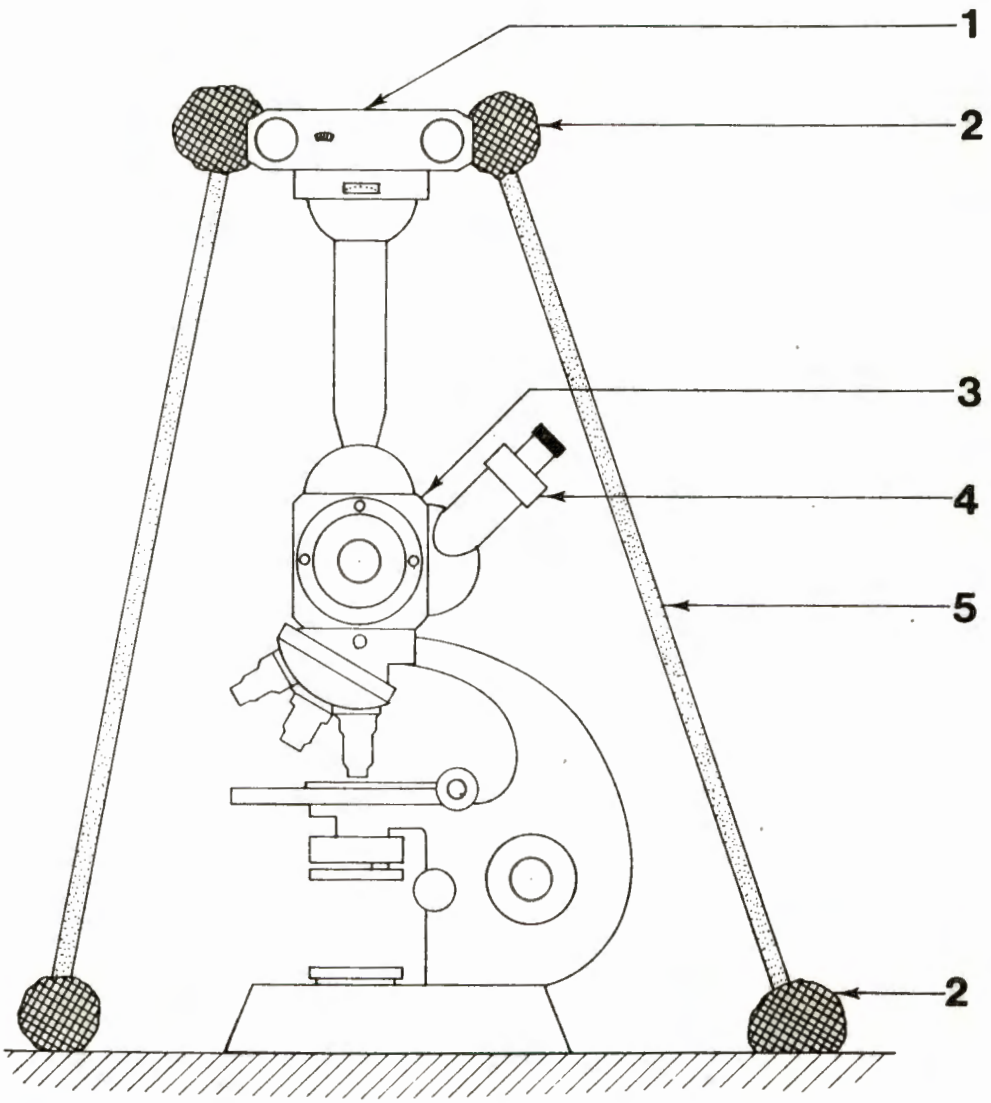


Fig. 5. The vibration-damped arrangement used to photograph chromosome preparations. The components of the system are 1. 35mm camera, 2. balls of adhesive putty, 3. beam splitting prism, 4. binocular head, 5. vibration damper rod attached to microscope and base by balls of adhesive putty.

is released (Newlands, 1979).

The film used was Agfa Gevaert Scientia 50 B 65 AH which is a high resolution, slow film (32 ASA) with a sensitivity peak in the green region of the spectrum. This film was chosen for use with the plan-achromatic objectives as these objectives are designed and corrected for optimal results in the green region of the spectrum. The dark green filter ensured fairly monochromatic light.

Exposure was determined by means of the built-in lightmeter (through the lens light meter) of the Asahi Pentax camera used for most of the photography. When the light levels were too low for the camera's lightmeter, a Gossen Lunasix-3 light meter with microscope adaptor was employed.

2.8.4 Film processing

Agfapan 100 films were developed in Agfa *Rodinal* diluted 1:50 with water at 20°C for 8 minutes (γ=0.7). Agitation was by inversion of the developing tank three times at the end of each minute. The Scientia 50 B 65 AH film was developed in Kodak Developer D-19b for 5 minutes at 20°C (γ=0.9). This developer was very economical and provided good contrast without fogging the film. Development was arrested with a 3% acetic acid stop bath and the films were fixed in Amfix (May Baker) high speed fixer to which the S-type (May-baker) hardener had been added. After fixation, films were washed in running water for 20 minutes and then rinsed in a wetting agent. Films were hung up to dry.

2.9 Species distribution records

Accurate distribution records depend upon precise locality recording for each specimen and this seemingly simple task has been grossly ignored by arachnologists in the past.

Simply providing a place name is not adequate as place names change, are often spelt in numerous ways and many places especially farm names frequently share the same name. There are for example dozens of Rietfonteins, Brakfonteins and Springbokvlaktes in southern Africa.

The species distributional ranges were based upon all the feasible published localities (reviewed by Lamoral and Reynders 1975) and specimens housed in the British Museum (Natural History) in London, Transvaal Museum in Pretoria, South African Museum in Cape Town, State Museum in Windhoek, Natal Museum in Pietermaritzburg and the South African Institute for Medical Research in Johannesburg. All the recorded localities were listed on cards together with the museum accession number. Co-ordinates of latitude and longitude were then obtained for as many of these localities as possible by reference to gazetteers and the official 1:250 000 Topo-cadastral maps drawn on the Gauss conformal projection and published by the Government Printer in Pretoria. The following gazetteers were consulted: Fitzsimons 1962, Surveyor-General 1974, Skead 1973, Nienaber 1963 and the United States of America, Preliminary NIS Gazetteer, 1954.

Although more accurate, localities defined in terms of degrees and minutes latitude and longitude are awkward to plot on outline maps. The quarter degree notation system was found to be sufficiently accurate and very convenient to use for plotting species distributions on outline maps. This system works as follows: Each square degree is divided into 16 smaller squares of 15' by 15' which are designated letters ABC or D according to their position (fig. 6). The four figure number which precedes the letter represents the degrees latitude and longitude (in that order) at the north western corner of the respective square (fig. 6).

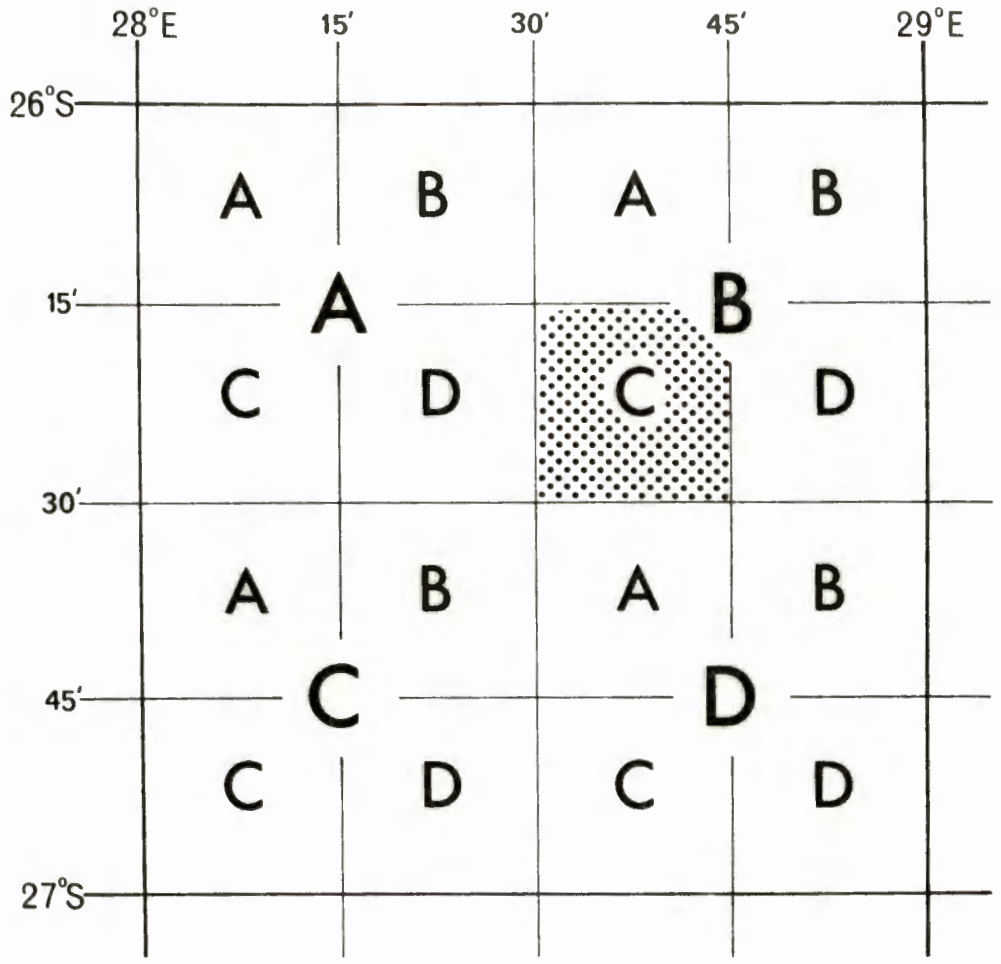


Fig. 6. The system of quarter degree notation used for all specimen localities plotted on outline maps. In the above example, a locality within the hatched block would be given as SE 2628 BC.

Once each specimen locality had been determined in terms of latitude and longitude, the locality was plotted on 1:850 000 outline maps drawn on Alberts equal area projection with standard parallels 20^{o}S and 30^{o}S. With the Albert equal area projection, scale deviation outside the standard parallels is very slight and maps using this projection are suitable in the middle latitudes for indicating distribution without areal distortions in the lower latitudes. These outline maps are available from the Government Printer in Pretoria, and depict southern Africa south of 15^{o}S. Each species was plotted on a separate map.

3.0 NOMENCLATURE, MORPHOLOGY AND ANATOMY

Traditionally, scorpion species are recognizable by virtue of morphological features characteristic of the particular species. The systematic exploitation of species specific characteristics in keys makes the identification of specimens possible. In many cases the morphological differences between the species are very minor and it is thus necessary to be able to define characteristic features precisely. This apparently simple matter is complicated by the lack of an internationally accepted system of notation and nomenclature. Several attempts have been made over the years to achieve this (Abd El-Wahab, 1952; Snodgrass, 1952; Stahnke, 1970 and Vachon 1952, 1973), but as yet no one system has been adopted by practising taxonomists. The matter is further complicated by the fact that the morphology of the species of *Hadogenes* differ in many respects from that of most other scorpions.

For the purpose of this work, the terminology of Snodgrass (1952) shall form the basis, taking into account improvements advocated by Stahnke (1970). Snodgrass did not consider the trichobothria in his account of scorpion morphology and for this study it was decided to follow the methods proposed by Vachon (1973) as these have gained more universal acceptance than the trichobothrial notations of Stahnke (1970) which were poorly defined and incomplete. The only systemic organs used for morphological study by some taxonomists at present is the male paraxial organ. The gonads are of importance in cytogenetical studies.

In this section, the arabic numbers in parenthesis behind an anatomical term correspond with the numbers in figs 7, 10-21 and key to the morphology (3.3) to which the reader should refer.

3.1 External features

3.1.1 Colour

The colour of a given species is fairly constant and the only differences noticed were shade intensities especially of the legs and vesicle. With the exception of *H. tityrus* which are yellowish, all other species were predominantly brownish to blackish. In species where the adult colouration is brownish, the nymphs are blackish through all stages. Recent cytogenetical studies I have conducted on buthid scorpions suggest that colour may be more important than previously suspected. For the present study much of the material examined was spirit preserved museum specimens up to eighty years old and accurate colour determinations were not possible as the subtle colours of the scorpion disappear when preserved in alcohol for long periods. Freshly preserved specimens approximate the colour of the live animal.

3.1.2 Form and size

Species of the genus *Hadogenes* are extremely dorso-ventrally compressed. Relative to other scorpions the body is very broad and flat while in the majority of species the metasoma is laterally compressed, long and slender. The remaining species, viz those of the *H. tityrus* group have very short thin metasomas. All pedipalpal segments are rectangular in cross-section and very flat, and in some cases even concave dorsally. Ecological adaptations to a lithophilous environment have been briefly described by Newlands (1972).

The genus can be divided into two distinct species groups based upon size, viz the *H. troglodytes* group and the *H. tityrus* group. The longest scorpion recorded from any part of the world is a *H. troglodytes* male from the Zoutpansberg and housed

in the Transvaal Museum (TM 1846). This specimen measures 210mm in length. Females of this species attain body masses of up to 23 grams (not gravid). Species of the *H. tityrus* group are amongst the smaller members of the family and attain body lengths of up to 55mm and rarely exceed 2 grams in body mass.

3.1.3 Sexual dimorphism

Considerable sexual dimorphism is evident in adults of all species of *Hadogenes*. Nymphal males resemble females with regard to the secondary sexual characteristics which only appear during the final ecdysis. Adult specimens of all species except females of the *H. tityrus* group are easily recognised by the presence of a large lobe (61) at the base of the pedipalpal tarsus. The characters of primary external sexual dimorphism are the undivided genital operculum (93) of the female which opens as a single flap while in the male the operculum consists of two unconnected sclerites which can open independently and which cover a pair of genital papillae (95).

Secondary characters of sexual dimorphism seen in males are the significantly longer metasoma of all species except those of the *H. tityrus* group and *H. bicolor*, a more slender mesosoma, increased granularity of all sclerites and a higher number of pectinal teeth, slightly more granular sclerites of the male and the higher number of pectinal teeth in the male. The pedipalpal and metasomal segments of females are slightly stouter than those of the male in all species except those of the *H. tityrus* group.

3.1.4 Body segmentation and tagmata

Over the years, various workers have had conflicting views as to the number of body segments present in the scorpion

and Abd El Wahab (1952) has summarised these views. Snodgrass (1952) accepts 19 segments (including the embryonic seventh prosomatic segment discovered by Brauer (1885) which is repressed during development) while Abd El Wahab (1952) accepts 20 body segments as he includes the telson. The telson cannot be regarded as a segment as it has no ganglia and accordingly it seems reasonable to accept that the scorpion has 19 body segments of which 18 are visible in the adult.

All arachnids have two body tagmata, the prosoma (1) and opisthosoma (89). In the scorpion the opisthosoma is further divisible into a broad mesosoma (90) and a slender metasoma (104) which is often erroneously referred to as a tail. Most taxonomists refer to the metasoma as the *cauda*.

3.1.5 The Prosoma

The prosoma (1) is the anterior body region and carries six paired appendages, the chelicerae (25), the pedipalps (30) and four pairs of walking legs (72). A large sclerite, the carapace (2) covers the prosoma dorsally. On the ventral surface the sternum (23) is small and situated between the coxal segments of the leg pairs three and four.

3.1.5.1 The Chelicerae

The most anterior pair of appendages are the chelicerae which are triarticulate and chelate, the three segments being the protomerite (26), deutomerite (27) and tritomerite or moveable finger (29), fig. 7. Vachon (1963) described the cheliceral dentition briefly as a taxonomic aid. The shape and position of the cheliceral teeth have been used by some authors at the specific level (Francke, 1978) but they are more useful at the generic level.

3.1.5.2 The Pedipalps

The six segmented pedipalps are the largest and strongest appendages and are richly endowed with sensory structures such as trichobothria (fig. 8) and what appear to be chemoreceptors. The pedipalpal segments are of considerable taxonomic importance and shall thus be considered in more detail.

3.1.5.2.1 The Coxa

The coxae (31) are the basal segments and lie immediately below the chelicerae. The anterior mesial surface of each coxa has a dense covering of setae and form the lateral walls of the prebuccal cavity. Dorsally, the prebuccal cavity is bounded by the labrum epipharynx and ventrally by the coxal endites of the first two leg pairs. The pedipalpal coxae have no trichobothria.

3.1.5.2.2 The Trochanter

This is a small ring-like segment without trichobothria and is taxonomically unimportant (32).

3.1.5.2.3 The Femur

Some workers call this segment the humerus or forearm but the term femur is preferred as it is analogous with the femur of the legs and most modern workers now use this term. The femur (33) has trichobothria on the anterior (36) dorsal (34) and posterior (37) surfaces. These surfaces are clearly demarcated in *Hadogenes* species by being at a sharp angle to each other and by the presence of a distinct keel at the interfaces. (38, 39, 41 and 42). There are however, keels on some of the surfaces such as the posterior median keel (40) of the femur and the dorsal (51) and posterior median

(53) keels of the patella.

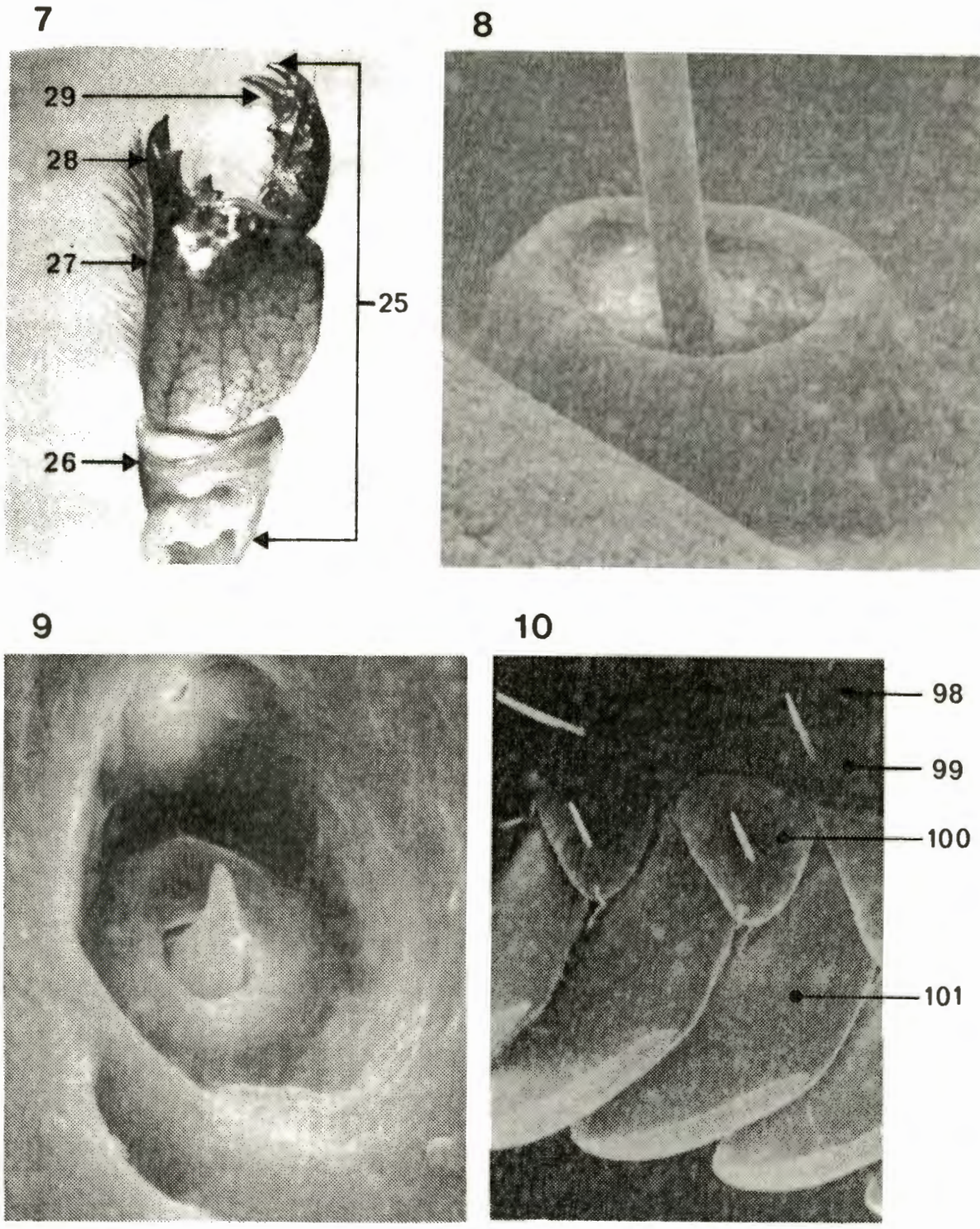
3.1.5.2.4 The Patella

In older works, this segment is termed the *brachium* but many of the modern French workers use the term *tibia* which is very confusing. The homologous segment in the Acari is termed the genu. Snodgrass (1952) points out that as the pedipalps only have six segments the missing segment must be the pretarsus for the moveable finger of each chela only has a closing muscle while the pretarsus has both a closing and opening muscle. The only leg segment with a single muscle is the tarsus and Snodgrass concludes that the moveable finger of the chela must be the tarsus. The "hand" of the chela must therefore be the tibia. It follows then that the preceeding segment is the patella (43).

The patella of *Hadogenes* species differs from that of other scorpions in that there is a very large process (44) on the anterior surface of the segment which appears to shield the intersegmental membrane between the femur and patella. This membrane is otherwise very vulnerable. Like the femur, the patella has four sharply demarcated surfaces separated from each other by very distinct granular keels (49, 50, 52 and 53). The segment is also unusually richly endowed with trichobothria, especially on the ventral (46) and posterior (48) surfaces and is thus of considerable taxonomic interest.

3.1.5.2.5 The Chela

The chela (57) consists of two segments, the tibia (58) and the tarsus (60). The tibia is often called the manus or hand and the tarsus, the moveable finger. The tarsus lacks trichobothria but the tibia has a very high number of these



Figs 7-10. *Hadogenes troglodytes* (Peters). 7. Chelicera enlarged 8X. 8. Pedipalpal trichobothrium (400X with SEM). 9. Receptor near tip of chela (2000X with SEM). 10. Portion of pecten showing teeth and other details (60X with SEM).

special sensory setae in *Hadogenes* species, especially on the ventral (64) and posterior (63) surfaces. The surfaces are clearly discernible and separated from each other by coarsely granular keels (66, 69, 70 and 71). Other smooth and granular keels are present in some species and include the digital (68) and dorso-accessory (67) keels. Near the posterior distal end of the tibial immoveable finger (59), there are a series of very small openings in the cuticle (fig. 9) and these appear to be chemoreceptors.

3.1.5.2.6 Trichobothria

Trichobothria only occur on the three pedipalpal segments the femur, patella and chela. In most scorpions, the number and position of the trichobothria is very constant and ontogenetically stable for a given species. For this reason they have assumed great importance as taxonomic characters in recent years. The trichobothria are specialized sensory setae (fig. 8) which enable scorpions to detect minute eddy currents in the air of their immediate environment.

Morphologically, trichobothria differ from other cuticular outgrowths in that the long setal shaft is very thin, does not taper distally and arise from a deep cup-like areola in the cuticle. The areola has a raised periferal rim which is generally lighter in colour than the surrounding cuticle. The internal texture of the areola is very deeply reticulated and is composed of a chitinous material (fig. 8). An important characteristic is that the diameter of the setal shaft is considerably less than that of the areola. Even in well-fixed museum specimens, trichobothria are easily distinguished from other setae in that they react vigorously to slight air movements. In all other setae, the shaft diameter is only slightly less than the areola diameter and the setal shaft tapers markedly distally. The

areola is shallow and untextured in all other setae.

While the term trichobothrium is now internationally used, Abd El Wahab (1952) applied the name *dermatidia coelothecatae* as advocated by Pavlovsky (1924). Trichobothria were first described by Dahl in 1883 who termed them *Hörhaare* and later, in 1911, he introduced the term *trichobothria*. Vachon pioneered the use of trichobothria in the systematic study of scorpions and devised a system of nomenclature (1952). In 1973 Vachon published an important work in which he described an improved nomenclature and a system of classification which can be applied to the trichobothria of all known scorpion species. In this classification there are three categories, A, B and C, and for each of these, there exists a defined norm which he terms the *orthobothriotaxy* condition. For cases where there are more or less trichobothria than in the orthobothriotaxy condition, the terms *incremental* and *decremental neobothriotaxy* are applied respectively. By applying this system, all species of *Hadogenes* can be classified as neobothriotaxic incremental, Type C. Species of *Hadogenes* have the highest number of trichobothria ever recorded for scorpions. For this reason it is normally impossible to identify individual trichobothria as belonging to the discrete subgroups Vachon defined for most scorpion genera and which Vachon used in his phylogenetic studies (1973).

In using Vachon's trichobothrial notations, it is important to remember that he did not employ the more rational segment notations of Snodgrass (1952) and Stahnke (1970). Accordingly, what Vachon calls the tibia is in fact the patella and not the chela. He also uses vague terms such as exterior for posterior, internal for anterior, terminal for distal and basal for distal when describing pedipalpal segment surfaces and their regions. This usage is unfortunate for it does confuse the issue and appears somewhat irrational

when the individual trichobothrial notation of Vachon is used in conjunction with the more acceptable segment nomenclature. Wherever individual trichobothria of *Hadogenes* species could be identified, Vachon's trichobothrial notation has been applied in this account, as for example in the description of *Hadogenes zumpti* sp. nov. (see 5.2.13).

3.1.5.3 The walking legs

There are four pairs of walking legs (72) which are essentially similar to each other except that they increase in size from the first pair to the last. The legs comprise seven segments each and are as follows (proximally to distally): coxa (73), trochanter (76), femur (77), patella (78), tibia (79), tarsomere I (80) and tarsomere II (81). Tarsomere II bears the pretarsus (86) which consists of two lateral claws or ungues (87) and a median claw or dactyl. The various terms applied to the leg segments have been discussed and equated by Abd El Wahab (1951) and Stahnke (1970).

The only leg segment of *Hadogenes* species which has any taxonomic value as a source of characters is tarsomere II (81) which has two rows of spines on its ventral surface and the relative numbers of these vary in some species.

The coxal endites of the first two leg pairs (74, 75) form the ventral wall of the prebuccal cavity and contain filter beds composed of setae. These filter beds filter off undigested food particles so that only digested food in fluid form reaches the mouth.

3.1.5.4. The Carapace

The carapace (2) is the largest body sclerite and covers the prosoma dorsally. There are three simple lateral ocelli

(5) on each of the antero-lateral regions and a pair of simple median ocelli (6) in the mesial region. Besides these features there are numerous sutures (8-12), invaginations (13-17) and keels (18-22) which are of some taxonomic importance. The invaginations (termed furrows by Stahnke, 1970) are in fact apodemes associated with the prosomal appendages. The carapace of *Hadogenes* species differs from that of other scorpions in that it is extremely flat and has a triangular inset (3) at the anterior margin bounded postero-laterally by a bifurcation of the anterior median suture (3). The origin of this triangular inset is unknown and it cannot therefore be properly named at this stage. In some species it bears a granular keel (19). Traditionally the only taxonomic characters derived from the carapace of *Hadogenes* species has been the degree of granularity, its length relative to the length of the metasoma and the degree of excavation of the anterior margin. Newlands (1970) demonstrated that these latter two characteristics were unreliable in distinguishing between the taxa *H. troglodytes* Peters and *H. gracilis rhodesianus* Hewitt. The sutures, invaginations (apodemes) and keels are depicted in figs. 13, 15, and 14.

3.1.5.5 The Sternum

The sternum (23) is a small pentagonal sclerite situated between the coxae of leg pairs three and four and just anterior to the genital operculum. It is devoid of taxonomically interesting features in *Hadogenes* species.

3.1.6 The Mesosoma

3.1.6.1 The Tergal plates

Each of the seven mesosomal segments is covered dorsally by a tergal plate or tergite (91). The tergites become

progressively longer from the anterior to the posterior and all except the last are roughly rectangular in shape. The last tergite is trapezoid in shape, tapering inwards posteriorly to accomodate the vast difference in width between the mesosoma and metasoma. In some species the width in relation to the length of the last tergite is a useful diagnostic character but otherwise the tergites are of little taxonomic value. A pleural membrane (103) connects the dorsal tergites with the ventral sternites.

3.1.6.2 The Sternal plates

Ventrally, only segments three to seven are completely covered by sternal plates or sternites (96). The second mesosomal segment is covered by a small rectangular sclerite situated between the pectines (97), which Snodgrass (1952), Abd El Wahab (1952) and Stahnke (1970) recognise as the second sternite. Stahnke (1970) has termed this second sternite the *basal piece*, a term which I find unacceptable. However, none of the authors agree as to what constitutes the first sternite. Abd El Wahab (1952) states that in the adult scorpion this sclerite is absent while Snodgrass (1952) claimed that the first sternite of the mesosoma is greatly reduced in size and wedged between the anterior ends of the last coxae. A careful search failed to reveal any such segment on specimens of *Hadogenes*. Stahnke (1970) claimed that the first sternite is represented by two small sclerotized plates, the *genital opercula* (93), and this view appears quite feasible. The genital opercula covers the genital aperture or *gonotreme* (94) as well as two small sclerites the *genital papillae* (95) in the case of males. Sternites of mesosomal segments three to six each bear a pair of respiratory *stigmata* (102) which are slit-like in shape. The stigmata open directly into the atrium of each book-lung.

3.1.6.3 The Pectines

The only appendages of the mesosoma are the *pectines* (97) which are a pair of comb-like tactile organs attached to the second mesosomatic sternite (see fig. 10). The pectines show sexual dimorphism as well as interspecific variation. Each pecten consists of four components viz the *anterior lamellae* (98), the *posterior lamellae* (99), the *fulcra* (100) and the teeth (101). Stahnke (1970) irrationally termed the anterior lamellae as used by Abd El Wahab (1952), the marginal lamellae. Snodgrass (1952) did not name the pectinal components. The number of pectinal teeth is used as a taxonomic characteristic of some species. Each pectinal tooth has a flattish ventral surface which is covered with innervated sensilla which may be chemo-receptive in function.

3.1.7 The Metasoma

Abd El Wahab (1952) regarded the mesosoma and metasoma as consisting of six segments each, while Snodgrass (1952) and Stahnke (1970) accepted a seven segmented mesosoma and five segmented metasoma. The latter decision is more rational based purely on structural differences between the two body regions. The relative proportions of the metasomatic segments, their keels and granularity are an important source of taxonomic characters.

3.1.7.1 Metasomal segments

In each of the metasomal segments (105) which most taxonomists call caudal segments, the tergum and sternum are completely fused. The segments increase in length gradually such that the terminal segment is the longest. In *Hadogenes* species these segments differ from those of other scorpions in the number and position of the longitudinal keels (106-109), the fact that the segments are markedly laterally compressed

and that the males of some species have the longest metasomas relative to the segments diameter of all scorpions. This latter characteristic is true of all species except those of the *H. tityrus* group and *H. bicolor* Purcell.

Of taxonomic importance are the metasomatic keels which are either smooth or granular and variable in number for each segment. Four distinct keels are possible, viz dorso-lateral (109), median lateral (108), ventro-lateral (107) and ventral (106). In some species the dorso-lateral keel terminates with an enlarged spiniform granule. The dorsal surface of all segments is longitudinally grooved in most species. The anterior lateral edges of all metasomatic segments have a heavily sclerotized process which serves as an articulation point against the anterior segment in each case. When metasomatic segments are measured, the length is always taken between articulation points.

In most species of the genus, the postero-ventral region of the last metasomatic segment is flared. This widened region is termed the *anal arch* (110) and it surrounds the peri-anal sclerites (112) and anus (111). The peri-anal sclerites are very small and are sometimes difficult to locate. In some species the anal arch bears transverse granular crests.

3.1.8 The Telson

The telson (113) can be divided into two parts, the vesicle (114) and aculeus or sting (115). The vesicle contains the paired venom glands and venom reservoir. Each gland has an individual duct which opens through a pore on the side of the aculeus near its distal tip. A thick muscular belt covers each gland such that contraction of this muscle squeezes the glands against the vesicular walls and forces the venom content out via the ducts. The relative proportions and granular texture of the telson are used as taxonomic characters.

3.2 Internal anatomy

The only internal organs used directly or indirectly for the taxonomic study of scorpions are the genitalia. These organs are the paraxial organ of the male which is studied morphologically and the gonads which are used in the chromosomal preparations.

3.2.1 The Paraxial organs

Paraxial organs (116) are paired sclerotized structures (fig.20) which form the major portion of the male genitalia. They originate at the gonotreme and extend posteriorly to the fifth or sixth mesosomal segment. Anteriorly each paraxial organ bears an accessory gland (117), a cylindrical gland (118) and is connected to the testicular loop (120) via the vas deferens (119). The proximal (121) and distal (122) lobes are regarded as being of some taxonomic importance in certain scorpion groups but appear to be of little value in *Hadogenes* species. The slender posterior half of the paraxial organ is termed the *flagellum* (123). During mating, the paraxial organs are extruded in unison and unite in the gonotreme (genital opening) to form a single spermatophore (126), (fig. 21). Components of the spermatophore named somewhat unscientifically by Alexander (1957) are the pedal wings (127), the stalk (128), the sacculus (129) and the valve (130), the seminal vesicle (131) and the stem (132). These terms have been accepted with reluctance for the present study and shall need revision for future usage.

3.2.2 The male genitalia

Testicles (120) of scorpions comprise a thin network of thread-like tissue intertwined among the lobes of the digestive gland of the entire mesosoma (fig. 20). The testicular loops are connected to the vas deferens which in

turn leads to the paraxial organ on each side. When the testicular network is dissected and pinned out it is seen to consist of two large loops which are fused anteriorly (124). Each loop has two cross-members (125).

3.2.3 The female genitalia

Relative to the male genitalia, the female organs are very simple structures consisting of a seminal receptacle leading off the gonotreme on each side which connects with the long loop-like oviduct. The oviduct has cross-members similar to those of the testicles. The female organs are used as a source of tissue for chromosome preparations. Embryos develop in bud-like diverticulae which are distributed along the length of the oviduct.

3.3 Key to the morphology of *Hadogenes* species

1. Prosoma
2. Carapace
3. Triangular inset
4. Frontal lobes
5. Lateral ocelli
6. Median ocelli
7. Ocular tubercle

Sutures of the carapace

8. Anterior marginal suture
9. Anterior bifurcated suture
10. Anterior median suture
11. Post-ocular bifurcated suture
12. Posterior marginal suture

Invaginations of the carapace

13. Antero-lateral invagination
14. Antero-median invagination
15. Postero-median invagination
16. Post ocular invagination

17. Posterior marginal invagination

Keels of the carapace

18. Anterior marginal keel
19. Triangular inset median keel
20. Lateral marginal keel
21. Superciliary keel
22. Posterior median keel
23. Sternum
24. Sternal apodeme
25. Chelicerae
26. Cheliceral protomerite
27. Cheliceral deutomerite
28. Cheliceral immoveable finger
29. Cheliceral tritomerite (moveable finger)
30. Pedipalp
31. Pedipalpal coxa
32. Pedipalpal trochanter
33. Pedipalpal femur

Surfaces of pedipalpal femur

34. Dorsal surface
35. Ventral surface
36. Anterior surface (internal surface)
37. Posterior surface (external surface)

Keels of the pedipalpal femur

38. Antero-dorsal keel
39. Postero-dorsal keel
40. Postero-median keel
41. Postero-ventral keel
42. Antero-ventral keel
43. Pedipalpal patella (=tibia of Vachon, 1973)
44. Anterior process of patella

Surfaces of the pedipalpal patella

45. Dorsal surface
46. Ventral surface
47. Anterior surface (internal surface)
48. Posterior surface (external surface)

Keels of the pedipalpal patella

49. Proximal antero-dorsal
50. Distal antero-dorsal
51. Dorsal
52. Postero-dorsal
53. Postero-median
54. Postero-ventral
55. Proximal antero-ventral
56. Distal antero-ventral
57. Chela
58. Pedipalpal tibia
59. Pedipalpal immoveable finger
60. Pedipalpal tarsus (moveable finger)
61. Basal lobe of moveable finger

Surfaces of chela

62. Dorsal surface
63. Posterior surface (exterior surface or handback)
64. Ventral surface
65. Anterior surface (internal surface)

Keels of the chela

66. Antero-dorsal keel
67. Dorso-accessory keel
68. Digital keel
69. Postero-dorsal keel
70. Postero-ventral keel
71. Antero-ventral keel
72. Walking legs (I-IV)
73. Coxa of leg
74. Coxal endite of leg I
75. Coxal endite of leg II
76. Trochanter of leg
77. Femur of leg
78. Patella of leg
79. Tibia of leg
80. Tarsomere I
81. Tarsomere II

82. Pedal spur
83. Interior spines of tarsomere II
84. Median lobe of tarsomere II
85. Lateral lobes of tarsomere II
86. Pretarsus
87. Ungues
88. Unguicular process
89. Opisthosoma
90. Mesosoma
91. Tergites (I-VII)
92. Median keel of tergite
93. Genital operculum
94. Gonotreme (genital aperture)
95. Genital papillae
96. Sternites II-VII
97. Pecten (plural = pectines)
98. Anterior lamellae
99. Posterior lamellae
100. Fulcra
101. Pectinal teeth
102. Stigmata
103. Pleural membrane
104. Metasoma
105. Metasomatic segments (I-V) (caudal segments)

Metasomatic segment keels

106. Ventral keel
107. Ventro-lateral keel
108. Median lateral keel
109. Dorso-lateral keel
110. Anal arch
111. Anus
112. Peri-anal sclerites
113. Telson
114. Vesicle
115. Aculeus (sting)
116. Paraxial organ

117. Accessory gland
118. Cylindrical gland
119. Vas deferens
120. Testicular loop
121. Proximal lobes of paraxial organ
122. Distal lobes of paraxial organ
123. Flagellum
124. Fusion point between right and left testicular loops.
125. Testicular loop cross-members
126. Spermatophore
127. Wings of spermatophore
128. Stalk of spermatophore
129. Sacculus of spermatophore
130. Valve of spermatophore
131. Seminal vesicle of spermatophore
132. Stem of spermatophore

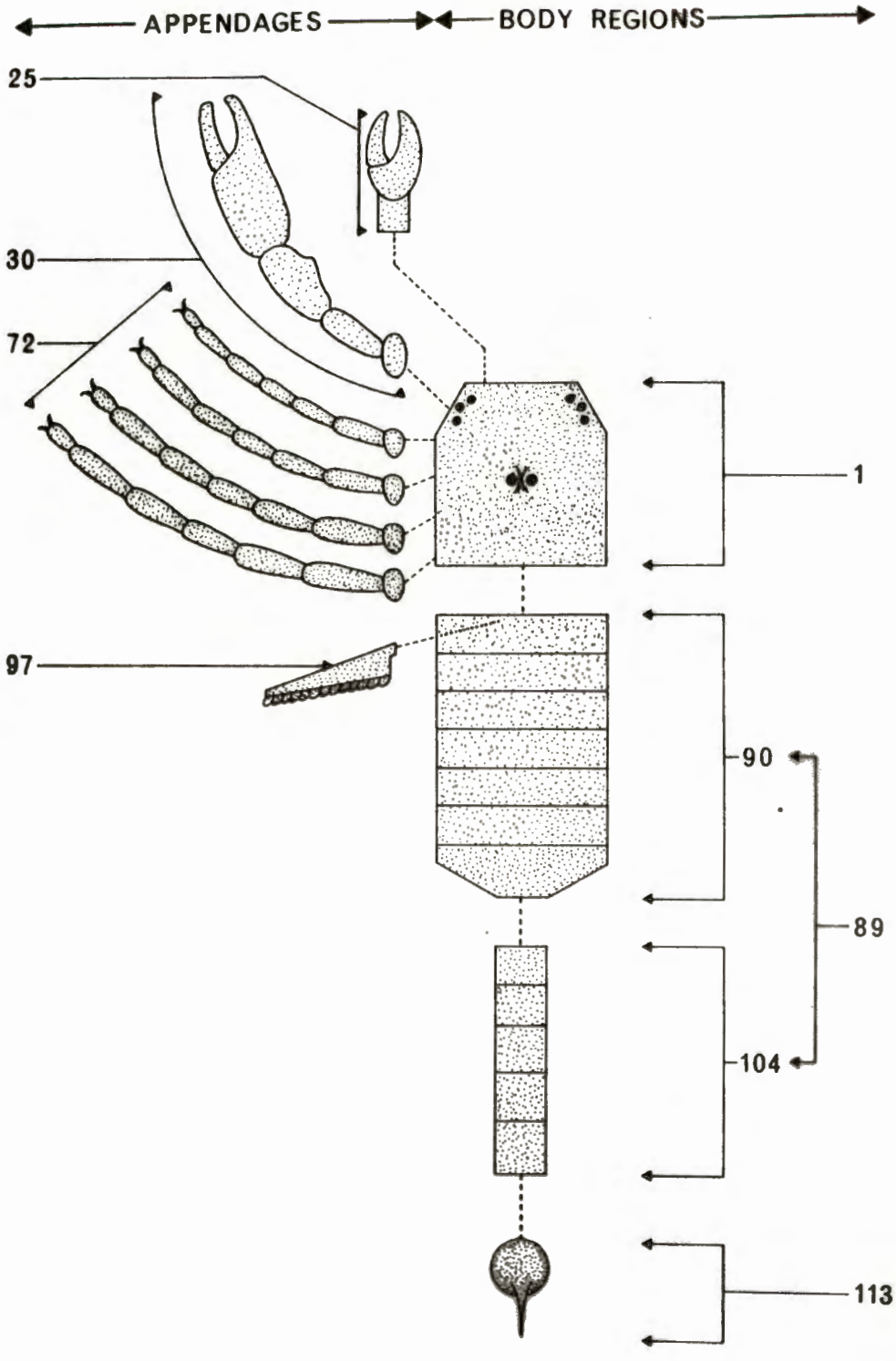
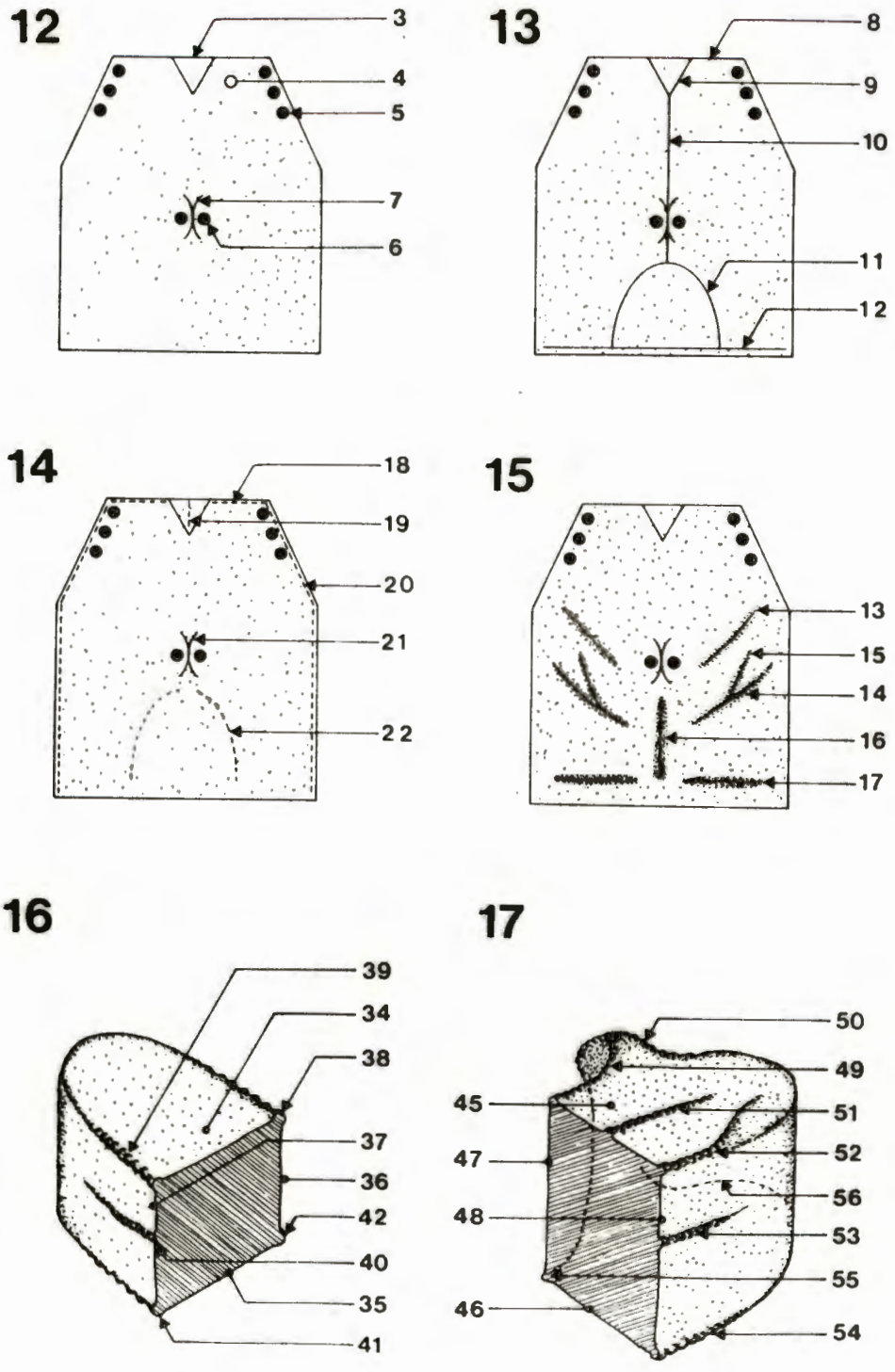


Fig. 11. Exploded diagram of scorpion to show relationship of the tagmata to appendages.



Figs. 12-17. 12. Features of the carapace. 13. Sutures of the carapace. 14. Keels of the carapace. 15. Invaginations of the carapace. 16. Details of the pedipalpal femur. 17. Details of the pedipalpal patella.

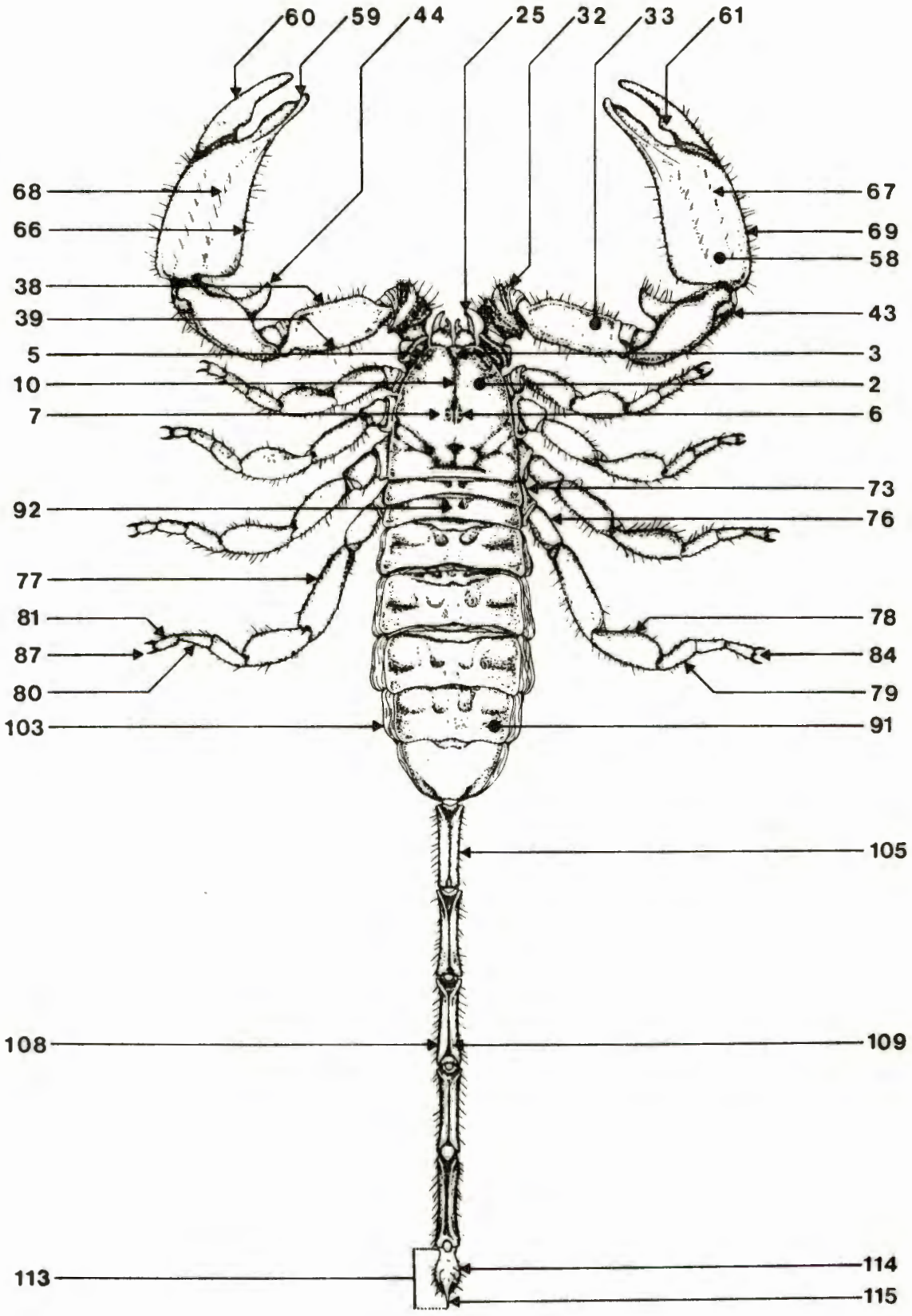


Fig. 18. Dorsal view of *Hadogenes* species showing anatomical details.

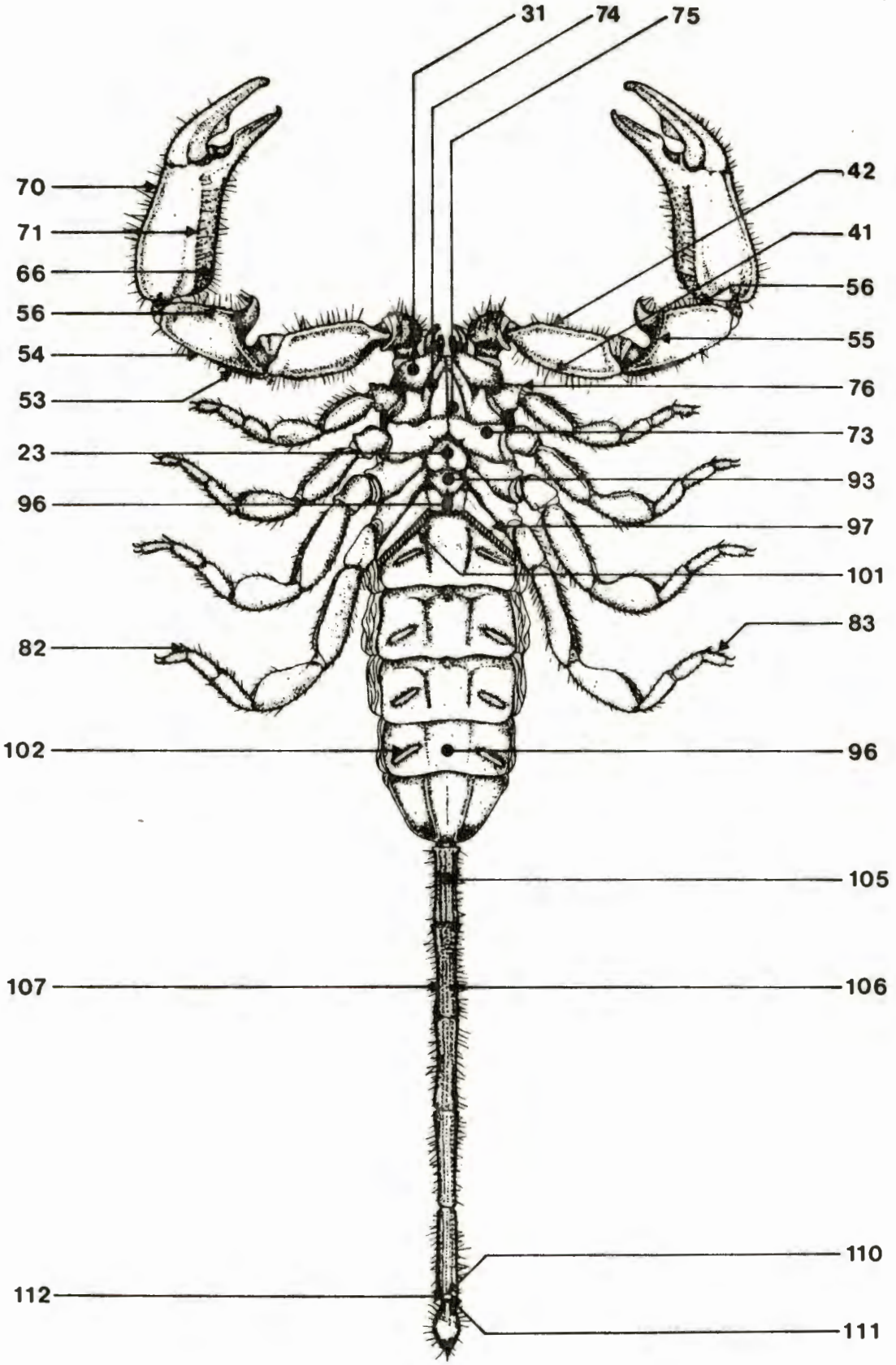


Fig. 19. Ventral view of *Hadogenes* species showing characteristics of the external anatomy.

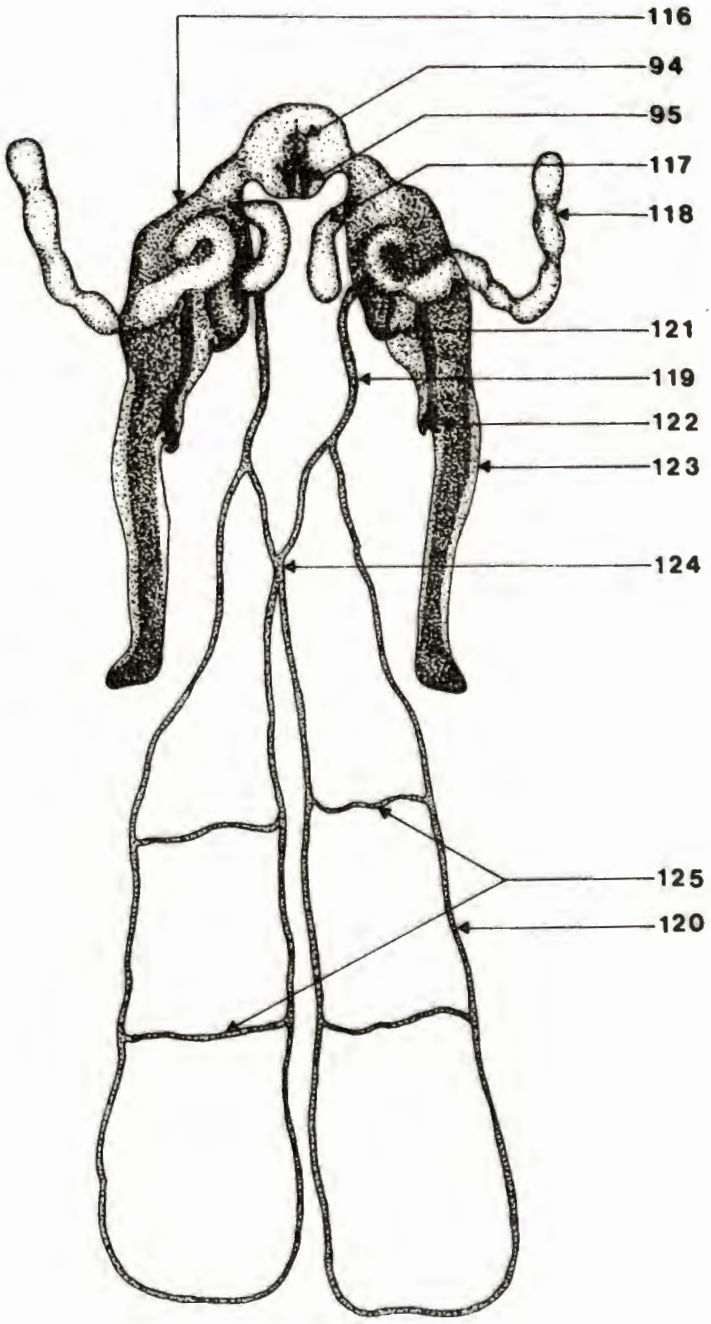


Fig. 20. Internal male genitalia of *Hadogenes* species.

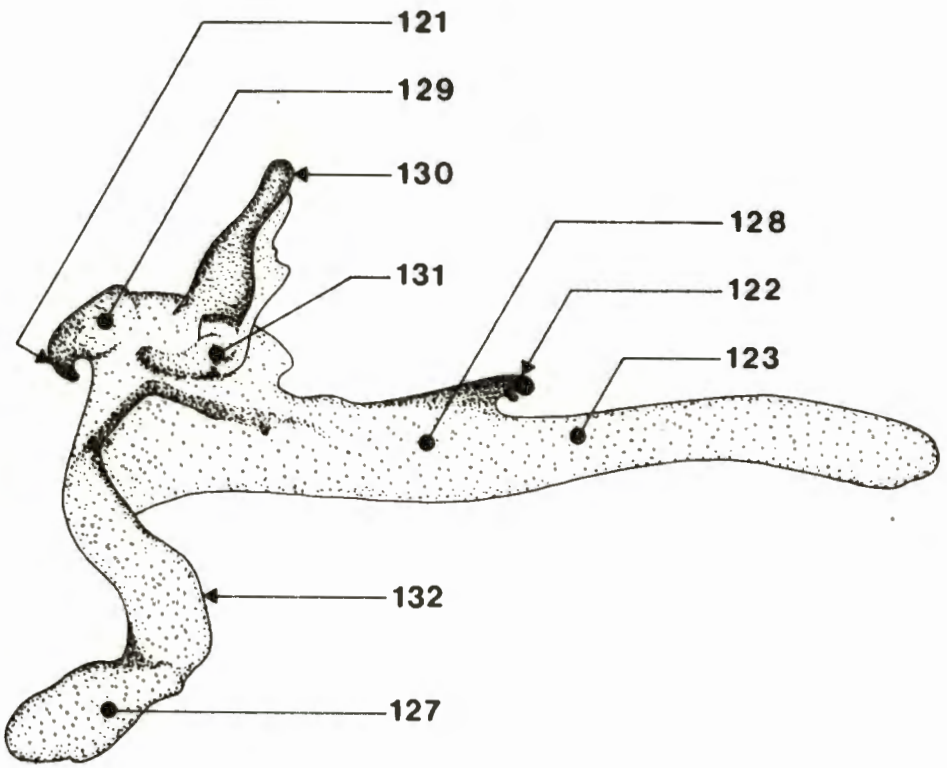


Fig. 21. Morphology of extruded spermatophore of *Hadogenes tityrus* Simon.

4.0 FIELD OBSERVATIONS AND GENERAL ECOLOGICAL BACKGROUND

4.1 Habitat considerations

Suitable habitat formation for lithophilous scorpions is largely dependent upon physical agencies responsible for the systematic disintegration of rock masses. As far as species of *Hadogenes* are concerned the two most important physical agents in the formation of suitable habitats are temperature changes and water. Sudden cooling of rocks by rain or nightfall causes rocks to crack owing to uneven contraction. In areas which are very cold at night, the expansive force of freezing water gradually enlarges the cracks over a period of time. Most rocks conduct heat slowly and large rock masses must therefore expand more in the surface regions than deeper down when exposed to the sun. The resultant differential expansion rates cause the rock to crack a few millimetres below the surface in a plane approximately parallel with the surface. This causes exfoliation which is one of the most important habitat types of *Hadogenes* species.

Habitats suitable for occupation by species of *Hadogenes* are not formed in all rock types exposed to the normal physical agencies of weathering. For example, rocks such as basalt which often appear on the surface as well rounded smooth boulders rarely fracture when exposed to natural temperature extremes and I have never been able to find specimens of the genus in outcrops of this rock type. In basalt the weathering processes act only on the exposed surface as the rock is fine grained and impervious to water and has a high tensile strength. It is probably for this reason that exposed basalt normally has a well rounded and smooth surface. Rocks of the basalt type were located at several collecting sites during field work in the Ermelo to Amsterdam area, near Newcastle and parts of the Drakensberg.

Other rocks with similar properties such as haematite and dolerite were encountered at several localities in the north western Cape and Richtersveld. Specimens of *Hadogenes* species were never found in these rocks but were often found in abundance on nearby granitic or quartzite exposures.

Other rocks found to be free of *Hadogenes* species were coarse grained sandstones and badly weathered, coarse grained granites. These rocks simply crumble when exposed to the action of water at extreme temperature differences. The coarse grained quartzites can be seen in the upper strata of the Magaliesberg while the lower strata of the mountain are mainly fine grained partly metamorphised quartzites which house high population densities of *Hadogenes* species. In general sedimentary rocks such as shale, limestone etc. were found to be unsuitable with regard to habitat potential for *Hadogenes* species and in spite of regular searching, specimens were never found in these rocks.

The most successful collecting was generally accomplished in metamorphic rocks such as fine grained quartzites and igneous rocks such as granite, norite, syenite, diorite and gabbro. These rocks fracture in a manner which forms perfect habitats for *Hadogenes*. Quartzites and igneous rocks of the granite group are extremely common in southern Africa.

When one examines the distribution of species of the genus *Hadogenes* in southern Africa, it is clear that there are vast areas where they do not occur. For example, the Cape flats extending from Kuruman to Klerksdorp and southwards through the Orange Free State into the Karoo are uninhabited by these scorpions. Other uninhabited areas are the Springbuck flats of the Transvaal, the Mozambique plains, the Makatini flats, the entire Kalahari basin, the

sandy areas of the Namib and the Cape Fold Mountains south of the escarpment. In all except the latter, the absence of these scorpions can be ascribed to the fact that no suitable rock formations or outcrops occur in these areas. It is not known why species of the genus is not found in the extreme south western Cape. This area is fairly humid and cold and is inhabited by species of the genus *Opisthacanthus*. The lithophilous species of *Opisthacanthus* have never been found living sympatrically with species of *Hadogenes*. Possibly competition for habitats and prey prevents these closely related, similar sized scorpions from sharing the same area. The distribution of lithophilous species of *Opisthacanthus* is associated with the very humid areas of the country along the southern and eastern coastal zones between the sea and inland plateau. There are several cases where distribution of species of these two genera are sharply demarcated. For example, in the Haenertsburg area, *Opisthacanthus* is found in the higher parts which are very humid while in the lower, drier areas to the east and west, *H. bicolor* Purcell is common. Reference to fig. 22 showing the total distributions of all species (excluding arboreal species) of *Opisthacanthus* and *Hadogenes* will show how they exist allopatrically.

Geomorphological features with which species of *Hadogenes* can be associated are as follows. The intrusion of granite and norite in the Transvaal sediments gave rise to the formation of a gigantic laccolith stretching from Lydenburg in the east to Zeerust in the west and from Pretoria in the south to Potgietersrus in the north. The tremendous mass of intrusive magma caused sediments to subside with the formation of the lopolith. Sediments along the periphery of the lopolith fractured and lifted slightly to form a massive rim around the saucer shaped intrusion which is known as the *Bushveld Igneous Complex* (du Toit, 1966). The uptilted rim is not continuous and each fragment is

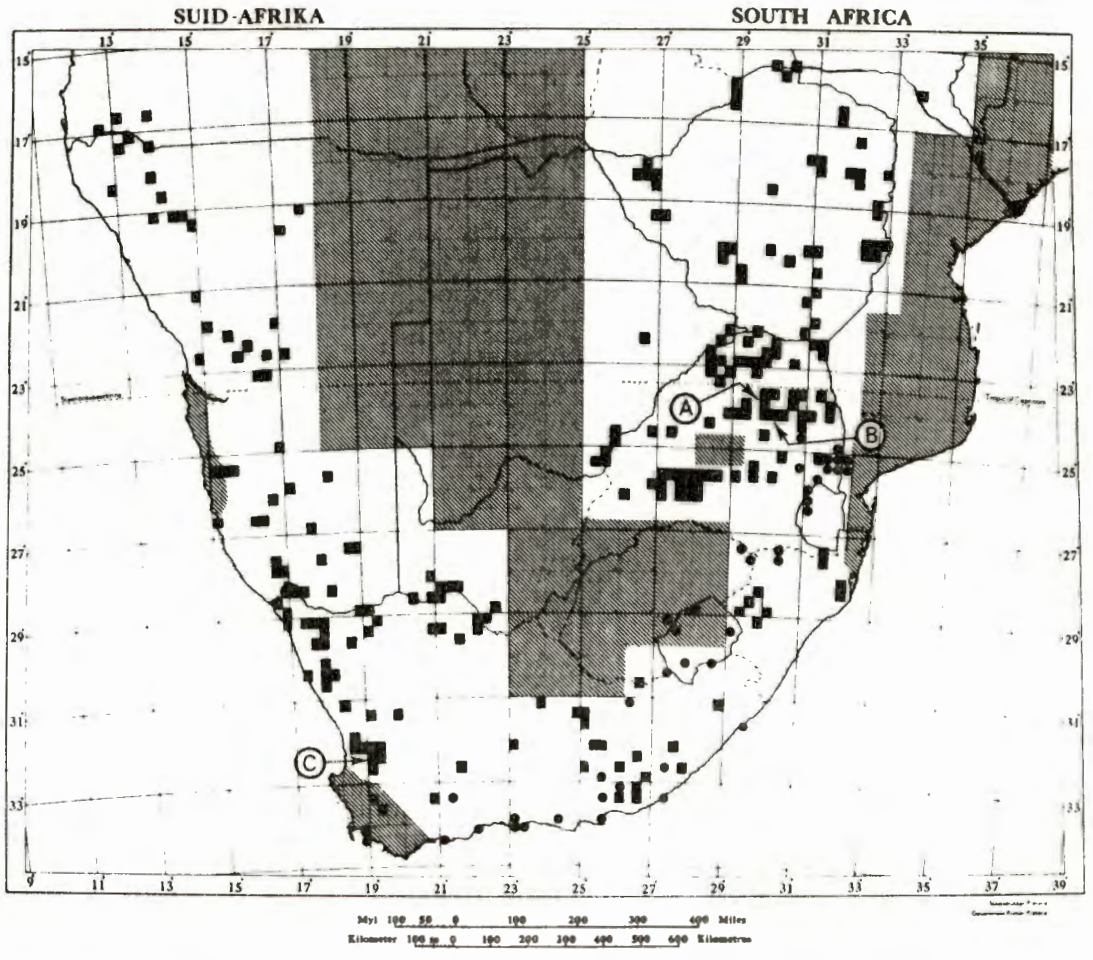


Fig. 22. Map showing the distributions of *Hadogenes* species (squares) and rupicolous of *Opisthacanthus* species (dots). In three cases, species of the two genera occur in the same quarter degree block. In the case of A and B, species of the two genera did not occur sympatrically for species of *Hadogenes* were only found in the lower altitudes and *Opisthacanthus* species at the higher and more humid altitudes of these areas. As I was unable to do field work in the southern Cape, the situation regarding the possible sympatric occurrence of the two genera at C is unknown to me.

inhabited by a given species, for example, the norite outcrops just north of the Magaliesburg are inhabited by *H. gracilis* Hewitt while the main southern rim of the complex, the Magaliesburg is inhabited by *H. gunningi* Purcell. To the western and northern areas the ranges associated with the Waterberg are inhabited by *H. troglodytes* Peters and possibly *H. granulatus* Purcell. The eastern border of the Bushveld Igneous Complex is the Drakensberg which is inhabited by *H. bicolor*.

The Great Escarpment in its broader sense accounts for the distribution of most of the remaining species. Along the arid western coast the start of the inland plateau is associated with *H. taeniurus* Thorell in the north and *H. phyllodes* Thorell and the *H. tityrus* Simon complex in the central parts. Further south *H. minor* Purcell can be associated with the escarpment. Along the southern Cape, the escarpment occurs north of the Cape Fold mountains and then gradually turns northwards up the humid eastern coast. The southern and eastern regions of the escarpment as far as Zululand are inhabited by species of the *H. trichiurus* (Gervais) group. Further north *H. bicolor* and *H. troglodytes* occur in some of the escarpment rocky exposures.

Species such as *H. tityrus*, *H. phyllodes* and *H. zumpti* sp. nov. occur in the mountain ranges between the Richtersveld and Kuruman. An isolated species *H. paucidens* Pocock occurs somewhere along the rim of the Congo basin in the north western area and the furthest north a species of the genus has been recorded in the east is in the Zambezi trough at Tete which is the type locality of *H. troglodytes*.

4.2 Ecological adaptations

In general, *Hadogenes* species choose rock cracks into which

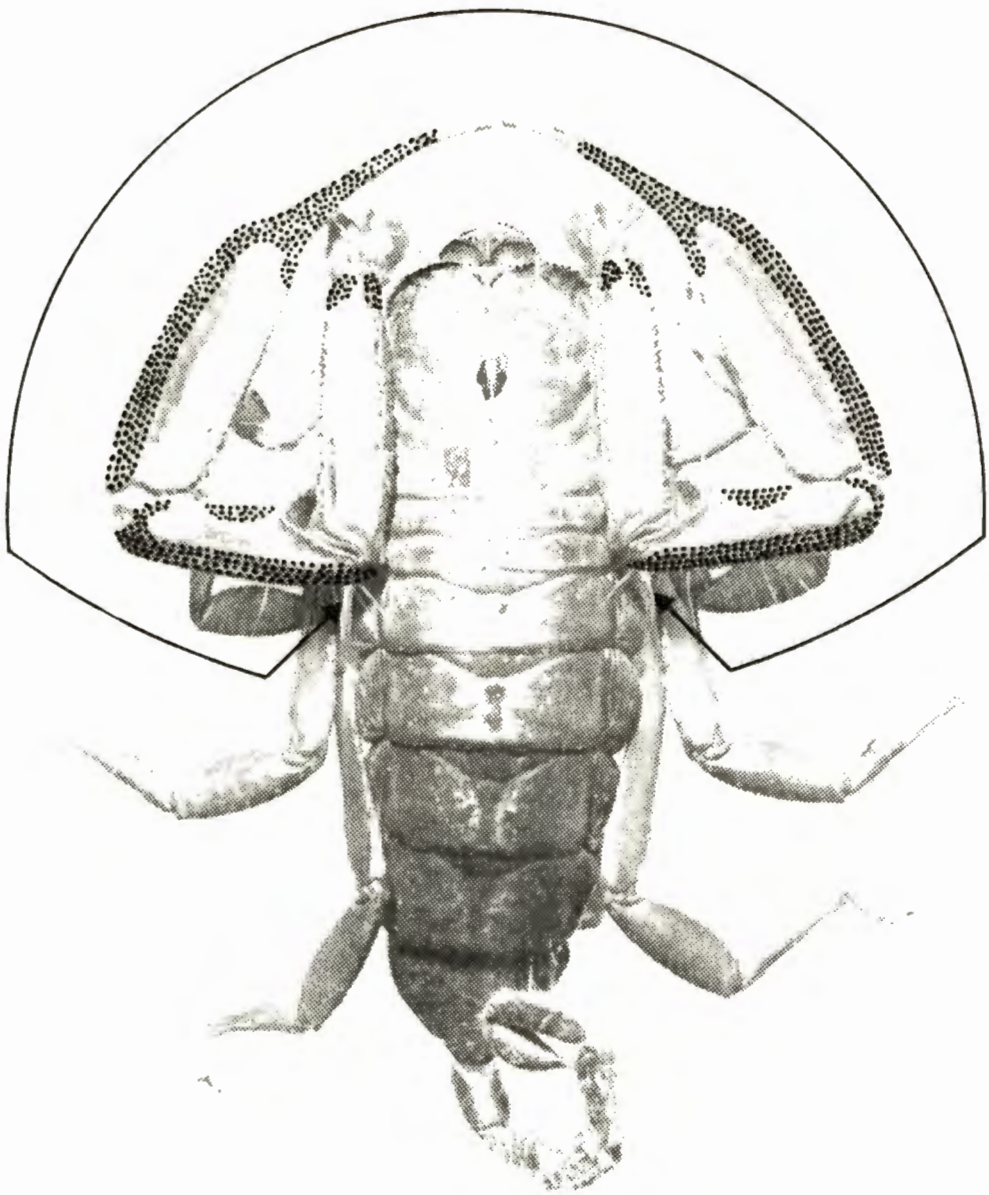


Fig. 23. Photograph of a live specimen of *Hadogenes lawrencei* Newlands in its normal resting posture showing how the pedipalps shield the anterior half of the scorpion. The shaded areas of the pedipalps represent the regions which are densely covered in trichobothria. The line represents the area protected.

they fit snugly and because they are so dorso-ventrally compressed, a large specimen can fit into surprisingly narrow cracks. In the crack the scorpion normally positions itself such that the folded pedipalps face the crack opening. The pedipalpal segments of *Hadogenes* species are extremely robust and reinforced with numerous heavily sclerotized thick granular keels. Because the pedipalps are so large and thick, they effectively seal off the crack to the front of the scorpion. In the normal resting position, the folded pedipalps provide a semi-circular barrier about the prosoma (fig. 23). The regions of the pedipalpal segments which are exposed to possible attack or to prey items entering the crack are densely covered with trichobothria (fig. 23). It is assumed that the trichobothria, which are mechanoreceptors, serve to warn the scorpion of approaching predators or prey.

4.3 Population densities

No attempt was made to assess population density at collecting sites but an idea of relative abundance can be assessed from the time taken to collect each specimen at any given locality. In general, specimens were found to be evenly distributed throughout the entire rocky outcrop or mountain when suitable habitats were available. An exception to this was at the Hauchab mountains in the Namib where specimens were only found in rock masses facing the southern parts and never along the northern slopes. The reason for this can possibly be accounted for in terms of the fog which blows in from the coast and condenses on the southern parts of the mountain. The vegetation on the southern side is slightly more lush than along the northern region. Specimens were always found in well drained areas.

The best collecting was in the semi-arid to sub-humid regions of southern Africa which receive between 100 and

600mm mean annual precipitation. In these areas catches of one to two specimens per hour of unaided intensive collecting was average. In the arid areas of the Namib and Richtersveld which receive 0 to 100mm average annual precipitation the average catch was less than one specimen per five hour period of intensive unaided collecting.

4.4 Prey and Predators

Based upon observations during collecting in the field, the following prey items were observed being eaten or as remains in the habitats associated with the scorpion. Millipedes (Diplopoda) formed the most common remains associated with *H. troglodytes*, *H. gracilis*, *H. gunningi* and *H. bicolor* which is interesting as very few animals feed on these arthropods owing to the pungent secretions they exude when molested. Another unusual prey item which was seen being eaten by *H. troglodytes* in the Pietersburg district was a terrestrial mollusc. Not many insect remains were found associated with *Hadogenes* species but those found belonged to the order Orthoptera and Hymenoptera.

5.0 SYSTEMATICS OF THE GENUS *HADOGENES*

5.1 Generic classification and characteristics.

Family: Scorpionidae

Subfamily: Ischnurinae

Genus: *Hadogenes* Kraepelin 1894

Type of the genus: *Scorpio trichiurus* Gervais 1843

Definition: Small to very large scorpions which may be recognised by having all the following characteristics: Tibia of all legs without distal spine, tarsomere I equipped with single distal spine, lateral lobes of tarsomere II truncated, median lobe of tarsomere II longer that lateral lobes. Pedipalpal patella and tibia with 1-3 rows of trichobothria near ventral margins. Greatly enlarged anterior process on pedipalpal patella, chela rectangular in cross-section and with flat inter-keel surfaces. Adults with large well-defined proximal lobe on pedipalpal tarsus. Vachon's (1973) trichobothrial category: neobothriotaxic major, type C. Prosoma and mesosoma strongly compressed dorso-ventrally, metasoma laterally compressed, lateral surfaces of metasoma without granular keels, metasoma of male greatly elongated in adult males of most species. Sternum large and distinctly pentagonal.

Distribution: South Africa, northwards through South West Africa into Angola and Congo, Zimbabwe-Rhodesia and Mozambique.

5.2 Checklist, distribution and descriptions of the species.

5.2.1 *Hadogenes tityrus* (Simon), figs 24-28.

Ischnurus tityrus Simon, 1887 p. 383-384

Hadogenes tityrus (Simon) Kraepelin, 1894 p. 118

Hadogenes bifossulatus Roewer, 1943 p. 232-234. syn. nov.

Type specimen: A badly preserved specimen ♀ (RS 0378) from South West Africa (exact locality unknown) housed in the Museum National d'Histoire Naturelle, Paris. Simon's male type was not seen.

Distribution: See fig. 24.

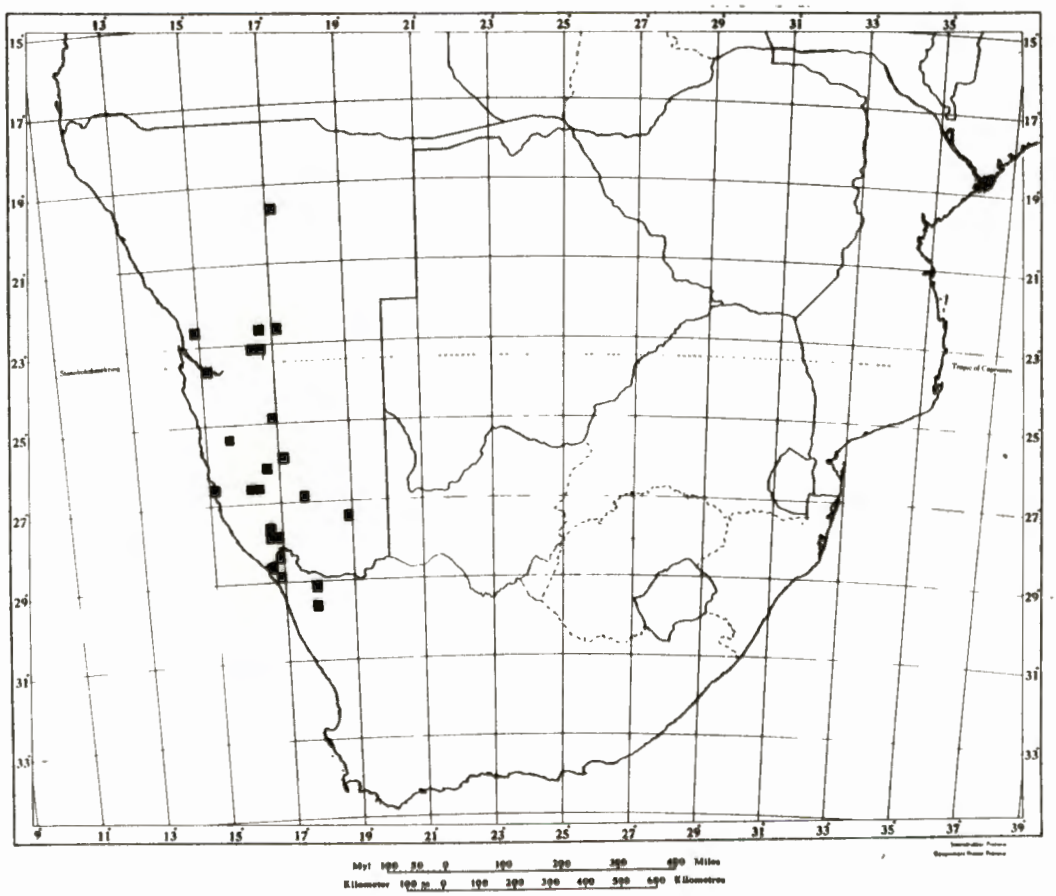


Fig. 24. Map showing the distributional range of *H. tityrus* Simon.

Material Examined: SAIMR 808 N. Steinkopf (2917 BB), SAIMR 1153, 1172, 1203, 1220, 1260, 1261, 1264, 1304, 1305, 1308, 1313, 1314 Helskloof (2816 BD), SAIMR 1352 Montane (1917 CA), SAIMR 1233, 1249, 1254 Avis Dam (2217 CA), SAIMR 1247, 1262, Kelpie (2216 DA), SAIMR 1188 Lekkersing (2917 AA), SAIMR 1217, 1218, 1248, 1318, 1319, 1344, 1362 Tierhoek (2817 CA), TM 9384, 9386 Valencia (2316 AB), TM 9302, 9406, 9407 Tiras (2616 BA), TM 9302, 9306 Palmenhorst (2214 DB), TM 1062 Narudas (2718 BD), TM 9591, 9592 Macmillans Pass (2716 DD), TM 9686, 9687 Okiep (2917 DB), TM 9385 Hope Mine (2315 CA), TM 9691, 9692 N.E. Rosh Pinah (2716 DC), TM 9301 Lekkersing (2517 CC), SAM C59 Namuskluft (2716 DD), SAM N. Rosh Pinah (2716 DA), SAM Annisfontein (2816 BD), SAM C61 Grootderm (2816 DA), AM Lekkersing (2517 CC), SMN Möltkablick (2217 CA), SMN Hoogland (2416 CD).

Colour: Spirit preserved specimen TM 9306 from Tiras: Pedipalp chela yellow (5Y7/6), carapace olive yellow (5Y6/4), tergites olive yellow (7,5Y5/3) and sternites olive gray (10Y4/2).

Size: A small scorpion measuring less than 60mm in total length.

Sexual dimorphism: Only males have a basal lobe on the pedipalpal tarsus, males with lower number of pectinal teeth, divided genital operculum and genital papillae.

Description:

Carapace: Without granulation in specimens from Richtersveld and Namaqualand but slightly granular along the lateral border of the type specimen. Anterior margin distinctly concave, lateral ocelli same size as median ocelli, triangular inset smooth.

Pedipalps: Dorsal surface of chela weakly reticulated, all other pedipalpal surfaces very finely granular. No trace of dorsal keel on patella, anterior process of patella relatively small. Keels of pedipalps less prominent than in other species of the genus. Movable finger of chela shorter than length of the chela along the posterior ventral keel.

Trichobothria: Neobothriotaxic major, type C. Counts were as follows: femur 3, patella 50-85 (average 62), chela 56-94 (average 77) with a total number per pedipalp of between 110 and 168 (average 142). Note that the trichobothrial count on the left and right pedipalp often varied considerably. The anterior surface of the patella often had two trichobothria which is rather unique, (e.g. SAM C53). The usual number of trichobothria on the anterior surface of the patella is one in *Hadogenes* species.

Legs: Tarsomere II of all legs with 3:3 ventral spines, two ventral keels of femur very prominent, ventral keel of patella poorly developed.

Mesosoma: Tergites and sternites smooth and polished in both sexes, tergite VII and sternite VII distinctly wider than long in both sexes.

Pectines: Female with 9-10 teeth, male 16.

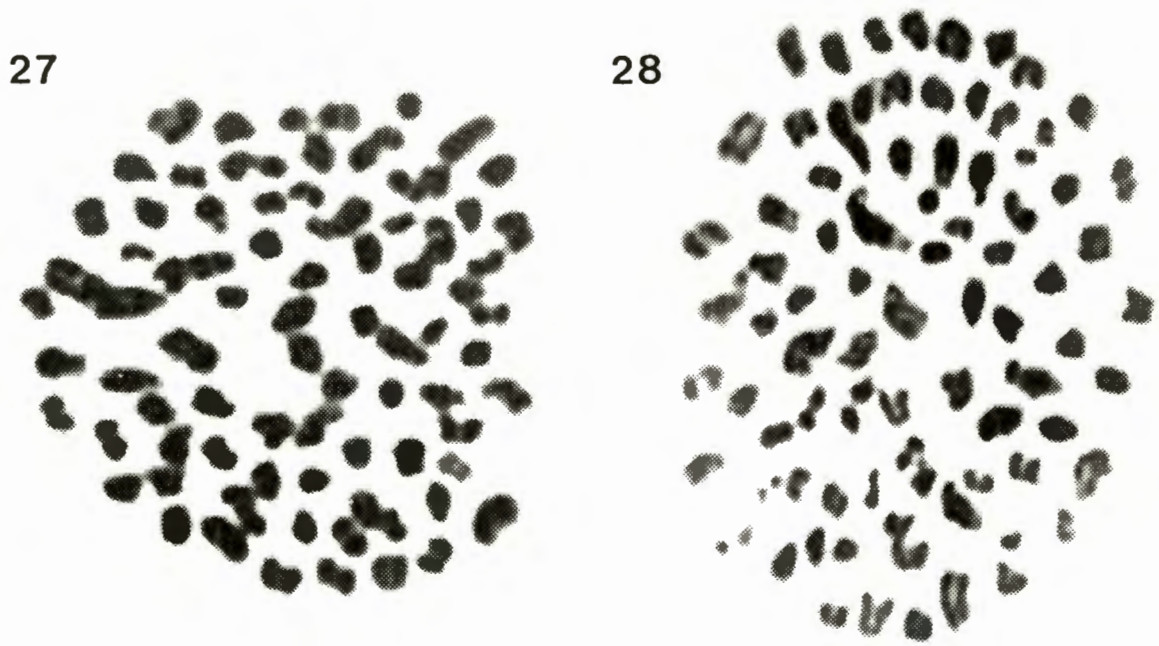
Metasoma: The metasoma of *H. tityrus* is considerably shorter than the pedipalp and is smooth and shiny except on the ventral interkeel surfaces of segments II-V. Segment I much wider than deep and almost twice as wide as segment II. Ventral and ventro-lateral keels of segment II composed of a few anteriorly directed pointed granules; segment III smooth ventrally, segment IV weakly granular with well rounded granules ventrally and segment V with enlarged posteriorly directed spiniform granules.

Figs 25-26. *Hadogenes tityrus* (Simon, 1887). 25. Dorsal view of a male from Helskloof, Richtersveld. 26. Ventral view of the same specimen.

Telson: Smooth and shiny over whole surface.

Measurements: (Determined on type ♀ RS 0378). Carapace anterior width 7,3mm, posterior width 13,8mm, length 13,9mm and median ocelli 6,6mm from anterior margin. Length of chela along postero-ventral keel 13,3mm, movable finger length 9,4mm. Metasoma segment I, 5,7mm long, 4,0mm wide and 3,0mm high; segment II, 7,5mm long, 3,0mm wide and 4,0mm high; segment III, 6,5mm long, 2,8mm wide and 4,5mm high; segment IV, 8,4mm long, 2,8mm wide and 3,8mm high, segment V, 9,0mm long, 2,6mm high and 3,5mm wide. Telson 10,5mm long, 3,1mm wide and 3,8mm high.

Chromosome number: Based on specimens from Helskloof, Richtersveld. 2n=168, figs 27-28. This is the highest number of chromosomes ever recorded for a scorpion.



Figs 27-28. Photomicrographs of the testicular chromosomes of *H. tityrus* from Helskloof, Richtersveld.

Notes: Clearly *H. tityrus* as described above encompasses a species complex comprising at least three sibling species. This is evident from the electrophoretic differences seen between the dark coloured forms and the light coloured form

seen from Namaqualand to Windhoek. The dark form represented here by specimens from Lekkersing (TM 9301, SAIMR 1188), Valencia (TM 9384, 9386), Avis Dam (SAIMR 1233, 1249, 1254), Kelpie (SAIMR 1247, 1262) and Tierhoek (SAIMR 1217, 1218, 1248, 1318, 1319, 1344 and 1362) differ in electrophoretic pattern of venom bands and being slightly larger. The male spermatophores of the darker form are considerably larger than those of the lighter form. However, the species complex needs to be studied in considerable detail before it will be possible to allocate species names. On purely morphological grounds, *H. bifossulatus* Roewer is here synonymised with the yellow form (typical form) of *H. tityrus*. Roewer's type was compared with the type of *H. tityrus* and differed only in that the chela was slightly more rounded and had the following trichobothrial numbers: femur 3, patella 68, chela 75 (total = 146). This synonymy is a tentative one based solely on morphological grounds. When this species complex is studied cytogenetically it may be possible to resurrect Roewers species.

An examination of the electrophoretic gels (samples 1-7) (fig. 105) clearly shows that the Richtersveld yellow *H. tityrus* differs considerably from the Awasib specimens and the dark form from the Richtersveld. While there are distinct differences between the *H. tityrus* specimens and *H. lawrencei*, it is nevertheless clear that these species are closely related. Females of *H. minor* are very similar in appearance to *H. tityrus* but the males differ considerably.

5.2.2 *Hadogenes lawrencei* Newlands, figs 27-29.
H. lawrencei Newlands, 1972 p. 133-134.

Types: The type series consists of a holotype ♀, (TM 9362) and two subadult paratypes ♂ and ♀ (TM 9395, TM 9364). The holotype and one paratype (TM 9364) are presently housed in the State Museum, Windhoek.

Type locality: The type locality was given as Harus water-hole, Uri-Hauchab mountains, Namibia ($25^{o}24'S:15^{o}10'E$). The type site was revisited with W.D. Haacke in March 1979 and it was discovered that it was not near Harus water-hole nor on the Uri-Hauchab mountain but on the Hauchab mountain. The co-ordinates were approximately correct however.

Material examined: SAIMR 1219, 1310, 1317, 1361 Hauchab mountain (2515 AD), TM 9362 = (SMN 387), 9364, 9395 Hauchab mountain (2515 AC).

Distribution: See fig. 27.

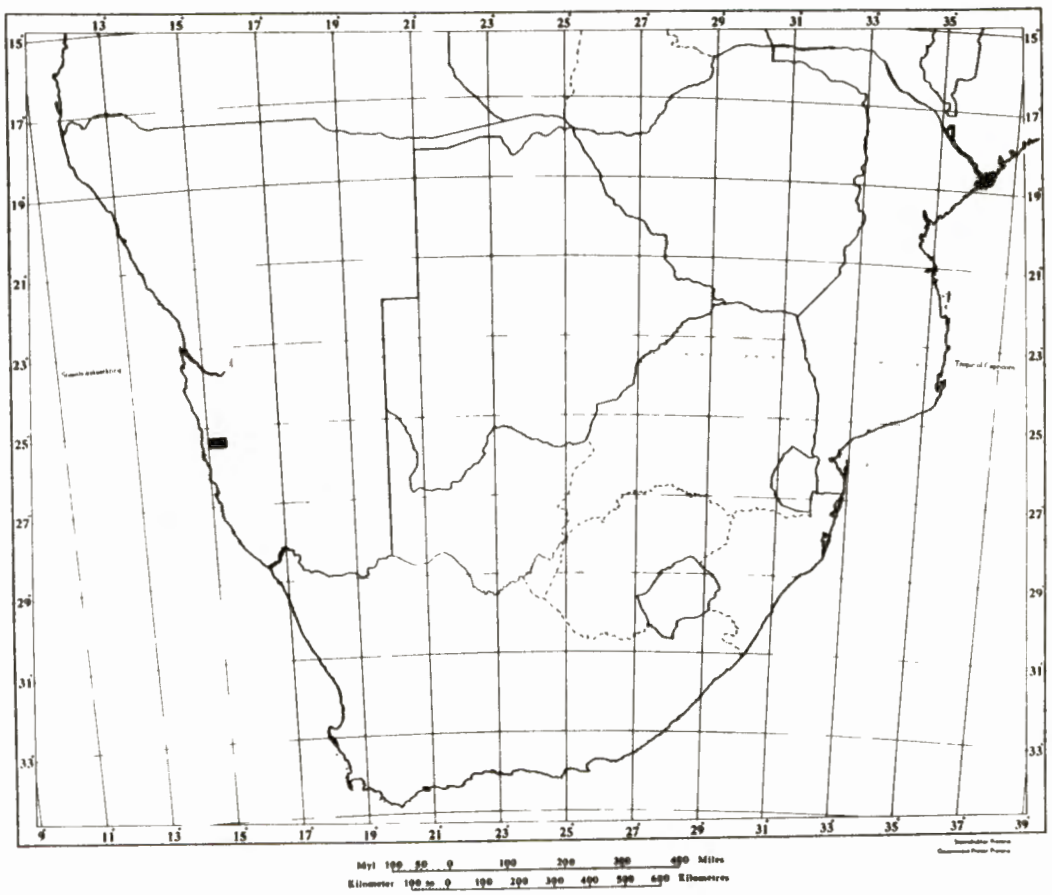


Fig. 27. Map showing the limited distribution range of *Hadogenes lawrencei* Newlands.

Colour: (Fresh spirit preserved TM 9362). Chela brownish

black (7,5 YR2/2), carapace very dark reddish brown (5YR2/3) tergites brownish black (10YR3/2), sternites dull reddish brown (5YR4/3).

Size: A small, very slender species less than 50mm in total length.

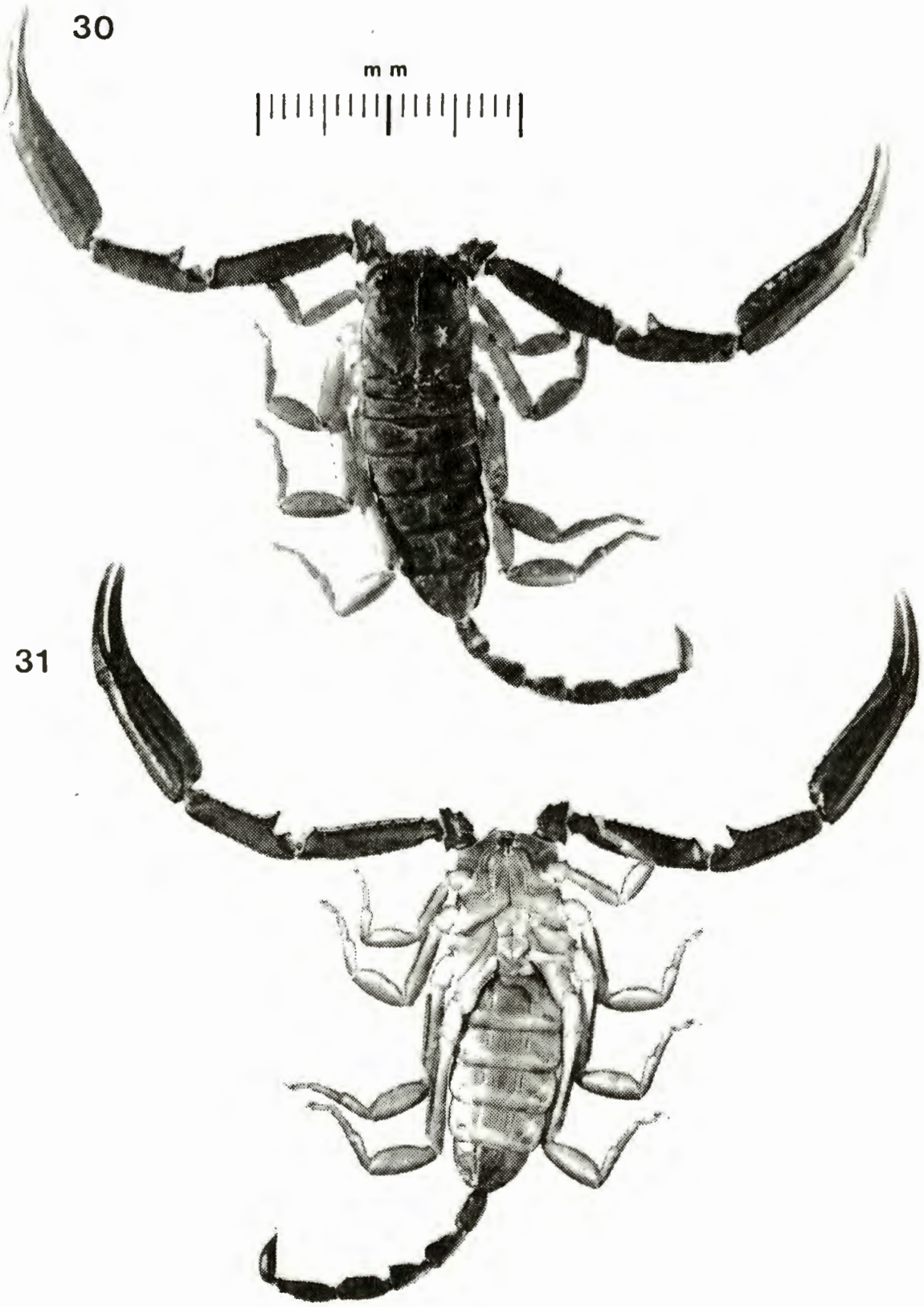
Sexual dimorphism: The adult male of this species is unknown and the secondary sexual characteristics cannot be assessed accurately from the nymphal male. The nymphal male had a divided operculum and higher number of pectinal teeth, (♂ 11, ♀ 6). All females seen had 6 pectinal teeth.

Description: Carapace: Anterior margin of carapace slightly convex, triangular inset without granulation or keels but bearing a pair of small setae near the anterior margin. The triangular inset of the male paratype is weakly granular. Post-ocular bifurcated suture reaches posterior carapace margin. Anterior marginal suture missing, only lateral marginal keel and superciliary keels present. Lateral ocelli 1,4 times diameter of median ocelli.

Pedipalps: Extremely long and slender, the width across the pedipalps being 1,6-1,8 times the total length of the scorpion. Interkeel surfaces of pedipalpal segments very flat and finely granular. Dorsal keel of patella absent and anterior process greatly reduced in size. Movable finger of chela considerably shorter than length of chela along postero-ventral keel.

Trichobothria: Neobothriotaxic major type C. Femur with 3 trichobothria, patella with 62 and chela with 68-69. The total number per pedipalp is thus 133-134 which is a very low count relative to other species of the genus.

Legs: Femur and patella of all legs with very prominent



Figs 30-31. *Hadogenes lawrencei* Newlands, 1972. 30. Dorsal view of the female holotype from the Hauchab mountains in the southern Namib. 31. Ventral view of the holotype.

granular ventral keels, tarsomere II of leg I with 3:2 ventral spines and 3:3 ventral spines on legs II-IV.

Mesosoma: Pectines ♂:11, ♀:6. Genital operculum of female oval in shape while that of male is pentangular. Tergites and sternites smooth in female, tergite and sternite VII distinctly wider than long.

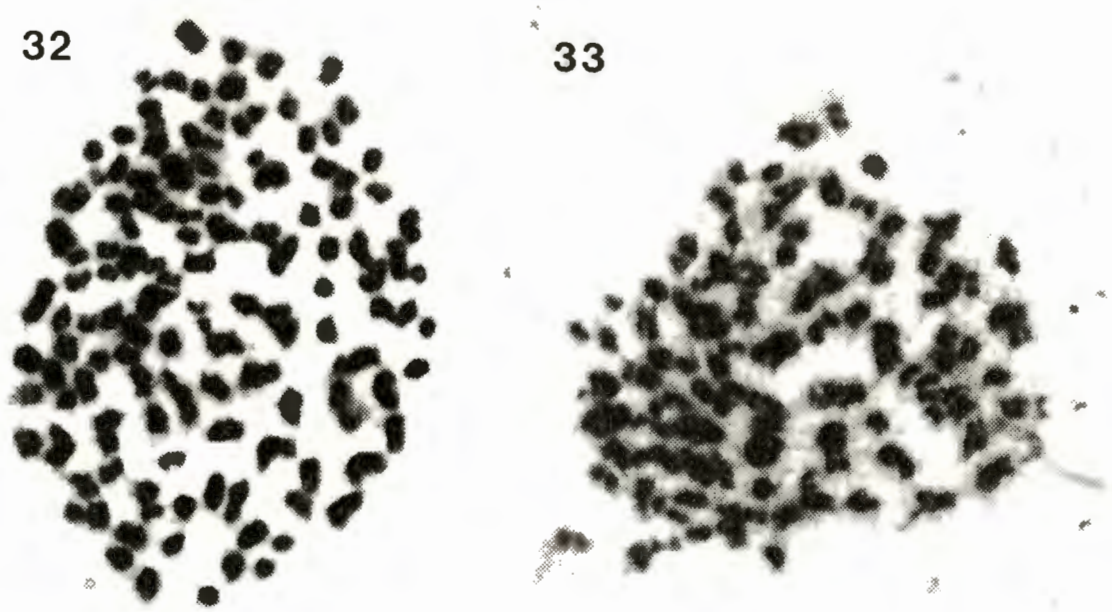
Metasoma: Metasomal segments very short, segment I much wider than deep posteriorly and twice as wide as segment V. Ventral and ventro-lateral keels of metasomal segment II represented by a few spiniform granules directed anteriorly. Ventral keels of segment III smooth, ventral keels of segment IV granular. Ventral keels of segment V composed of posteriorly directed subspiniform granules.

Telson: Elongated in shape and smooth.

Measurements: (Holotype) Carapace anterior width 4,5mm, posterior width 8,4mm length 8,9mm, length of chela along postero-ventral keel 12,0mm, movable finger length 7,9mm. Metasomal segment I, 2,1mm wide, 1,5mm high and 3,0mm long, metasomal segment V, 1,1mm wide, 5,0mm long and 1,6mm high. Telson 4,6mm long and 1,3mm high. Prosoma plus mesosoma 27,8mm long and metasoma 23,5mm long.

Chromosomes: 2n=132. (Based on embryonic tissue, no adult males were collected). (See figs 32-33).

Notes: This distinct species belongs to the *H. tityrus* species complex but differs from other members of the complex in chromosome number, morphology and in the electrophoretic banding patterns of the venom. The species is restricted to the Hauchab Mountains of the southern Namib and is positively isolated from the rest of the species complex by a 27km belt of soft dune sand. The Hauchab Mountains are



Figs 32-33. Chromosome spreads obtained from developing embryos of *Hadogenes lawrencei*.

completely surrounded by sand dunes. These scorpions walk with difficulty in sand, their tarsi being adapted to locomotion on rock substrates. As there are no rocks in the area between the Hauchab Mountains and the inland plateau, there is no shelter and it is thus totally impossible for gene flow to take place between the populations. Scorpions are very sensitive to heat with the lethal temperature being slightly over 40^{o}C and as the surface temperatures of the Namib sand reach 70^{o}C in summer it is clear that a rock scorpion would not survive in the sand between the Hauchab Mountains and the inland plateau. How long the Hauchab Mountains have been isolated from the inland plateau is uncertain, but King (1951) is of the opinion that the Namib sands blew in from the coast during the Pliocene. This means that the scorpion populations on the Hauchab Mountains have been isolated from the inland populations for at least one million years.

Until very recently, this species was only known from the

types but four days of collecting at the Hauchab Mountains yielded a further 9 females, most of which are still alive for ongoing biochemical and genetical studies.

5.2.3 *Hadogenes minor* Purcell, figs 34-39.
H. minor Purcell, 1899, p. 436-437.

Type specimens: One adult ♀ and five nymphs (SAM 1207) all housed in the South African Museum and collected at Onder Bokkeveld, Bokkeveld Mountains, Calvinia district.

Distribution: See fig. 34

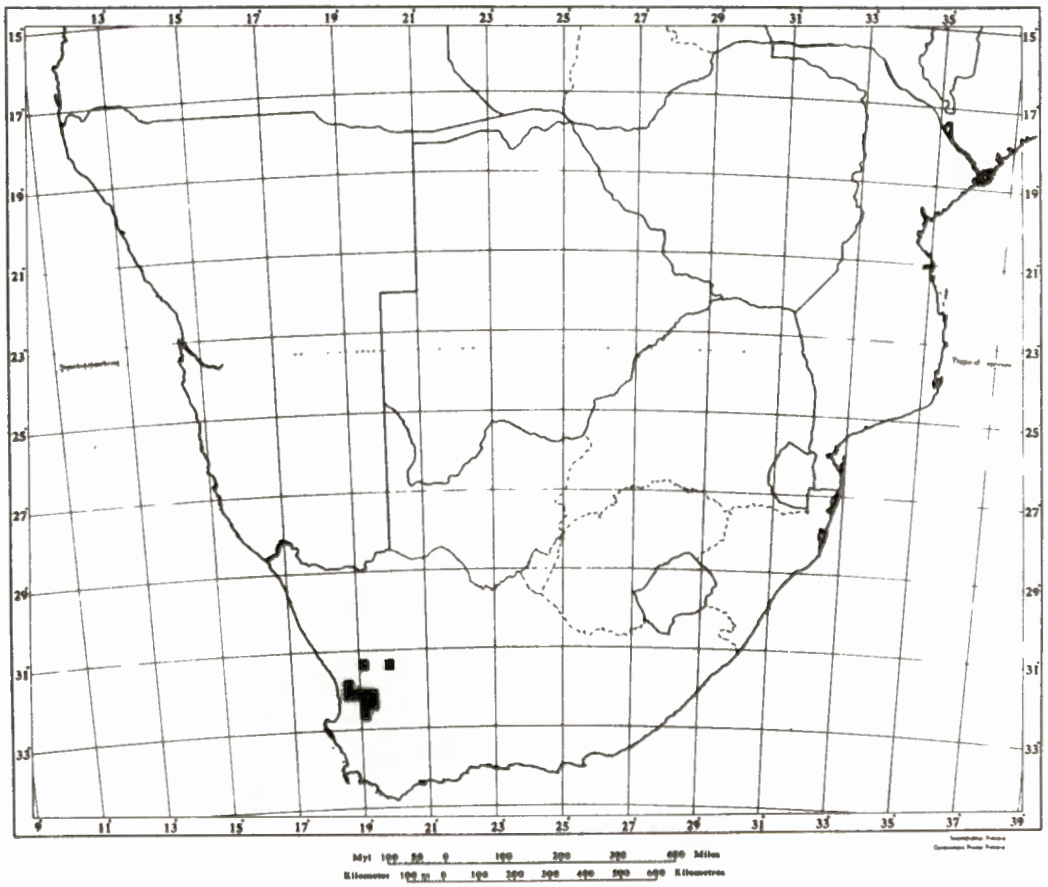


Fig. 34. Map showing the restricted distribution of *Hadogenes minor* in the Clanwilliam district.

Material examined: SAIMR 1199, 1200, 1339 Windhoek (3118 DC), SAIMR 1227, 1328 Seekoevlei (3218 BA), SAIMR 1250,1329, 1348, 1349, 1350 Elandskraal (3219 CA), SAIMR 1302, 1338, 1326, 1327 Nieuwoutville (3119 AC). TM 9500, 9501, 9502, 9503, Pakhuis Pass (3219 AA), SAM 1207 Bokkeveld Mountain (3119 AC), SAM Krakadouw Pass (3219 AA), SAM Keurboschkraal River (3219 AD), SAM Langkuil (3219 AB), SAM Sneeukop (3219 AC).

Colour: (Live specimen from Nieuwoutville). Pedipalps reddish black (2,5YR1,7/1), carapace very dark reddish brown (2,5YR2/2), tergites very dark reddish brown (2,5YR2/3), sternites yellowish brown (2,5Y5/3) and legs grayish olive (5Y4/2). Colour of old spirit preserved specimen TM 8330: pedipalps dark red (7,5R3/4), carapace and tergites dark reddish brown (2,5R3/3), sternites dull reddish brown (5YR4/4) and legs reddish brown (5YR4/8).

Size: A medium sized scorpion, adults measuring 90-130mm in length.

Sexual dimorphism: Male with greatly elongated, laterally compressed metasoma, segments IV and V of which are dorsally and ventrally embellished with large posteriorly directed subspiniform granules. Male with greater number of pectinal teeth, genital papillae and divided genital operculum.

Description: Carapace: Anterior margin of carapace deeply concave, whole surface of male evenly and finely granular, lateral ocelli marginally smaller than median ocelli.

Pedipalps: Evenly and finely granular over all surfaces, dorsal keel of patella absent, anterior process of patella with single dorsal keel proximally, chela rather bulbous proximally (see fig. 35) and similarly shaped in both sexes. Chela without finger and accessory keels, male upper chela surfaces slightly reticulate in texture.

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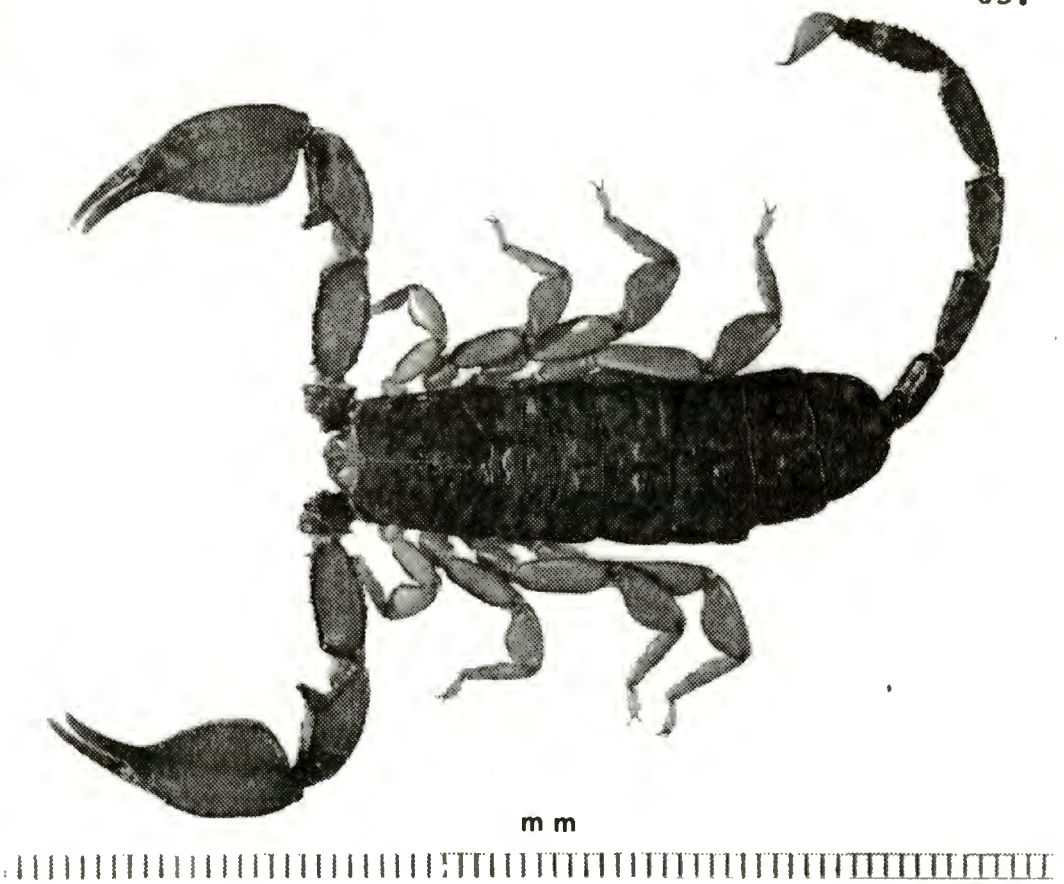

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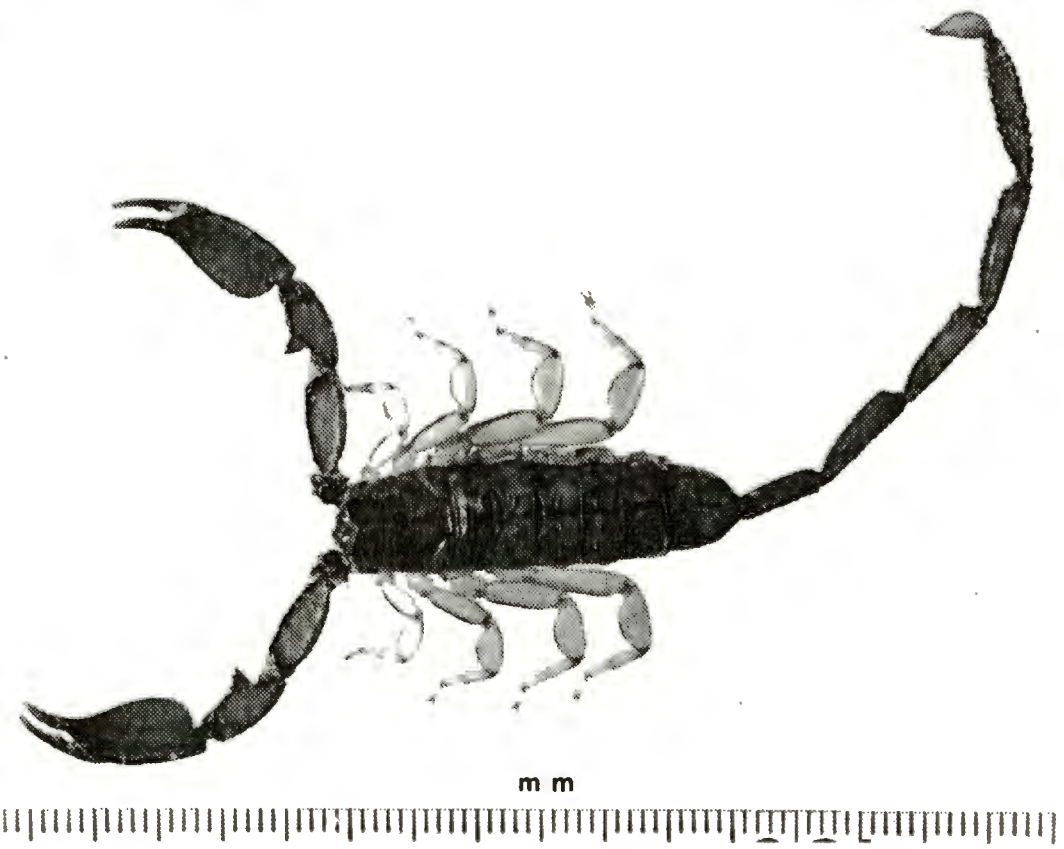


Figs 35-36. *Hadogenes minor* Purcell, 1899. 35. Dorsal view of a female from Clanwilliam. 36. Dorsal view of a male from Clanwilliam.

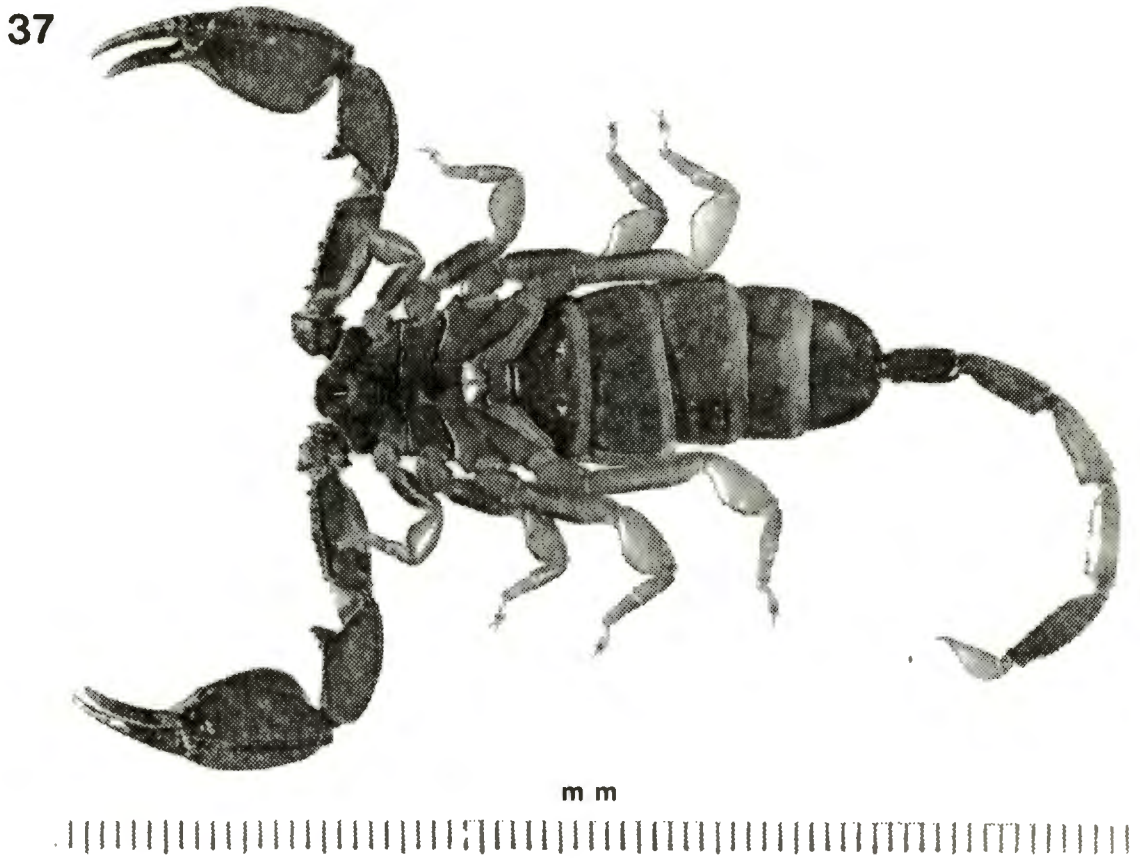


Fig. 37. *Hadogenes minor* Purcell, 1899. Ventral view of a female from Clanwilliam.

Trichobothria: Neobothriotaxic major, type C. Counts for the type series were as follows: femur 3, patella 54-66 (average 58) and chela 125-134 (average 127). The average total number of trichobothria per pedipalp: 188.

Legs: Tarsomere II of legs I-II with 3:2 ventral spines, legs III-IV with 3:3 ventral spines. Legs very finely and evenly granular all over in male.

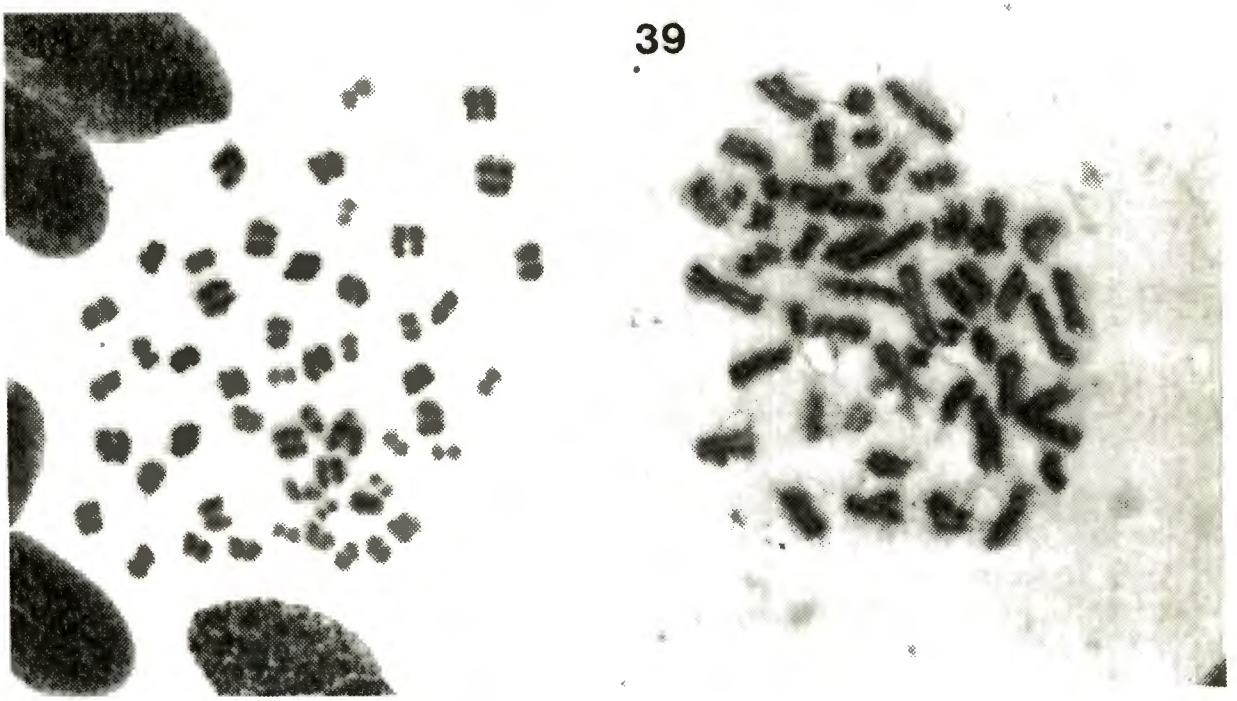
Mesosoma: Pectines: of ♂:13-15, ♀:10-13.

Tergites: Very finely and evenly granular imparting a dull matt appearance in the male while smooth and shiny in females.

Sternites: Sternites slightly matt in appearance but of smooth surface texture.

Metasoma: Long and elongated, dorsal keels granular on segments I-III, ventral keels weakly granular, dorsal and ventral keels of metasomal segments IV-V densely covered in posteriorly directed large subspiniform granules. Vesicle distinctly granular with dorsal and ventral granular keels. In a smaller specimen from Clanwilliam (TM 9500) the vesicle is much less granular but is still more granular than most other species of the genus. Another similar small sized male (TM 9503) has a very granular vesicle with distinct keels. A characteristic feature of the last metasomal segment of the male is that it is very deep mesially, and tapers gently both proximally and distally.

Chromosome number: 2n=106 (based on embryonic and testicular tissue).



Figs 38-39. Chromosome spreads obtained from the testicular tissue of *Hadogenes minor*.

Measurements: Measurements of the two largest specimens are as follows: ♀ TM 8322: Carapace anterior width 5,6mm, posterior width 11,8mm, length 12,1mm. Length of chela along postero-ventral keel 12,2mm, movable finger length 13,1mm, width of the chela 6,9mm. Metasomal segment I, 3,0mm wide, 2,2mm high and 5,8mm long. Metasomal segment V, 1,8mm wide 2,8mm high and 10,2mm long. Telson 8,1mm long, 2,0mm wide and 2,7mm high. ♂ TM 8330: Carapace anterior width 5,3mm, posterior width 11,9mm and length 12,2mm. Length of chela along postero-ventral keel 12,0mm, movable finger length 13,1mm and width 6,5mm. Metasomal segment I, 3,4mm wide, 2,6mm high and 10,0mm long. Metasomal segment V, 1,6mm wide, 3,4mm high and 16,5mm long. Telson 8,7mm long, 1,9mm wide and 3,0mm high.

Notes: This variable species has a restricted distribution and is very similar in appearance to *H. trichiurus* (Gervais). It may yet prove to be conspecific with *H. trichiurus* but very little is known about both these species.

5.2.4 *Hadogenes trichiurus* (Gervais), figs 40-43.
Scorpio trichiurus Gervais, 1843
Ischnurus melampus Koch, 1843 p. 1. Kraepelin, 1894.
Ischnurus pectinator Thorell, 1877 p. 258. Kraepelin, 1894
H. trichiurus caffer Hewitt, 1918 p. 166. syn. nov.
H. trichiurus graciloides Hewitt, 1918 p. 165. syn. nov.
H. trichiurus pallidus Pocock, 1898 p. 198. syn. nov.
H. trichiurus parvus Hewitt, 1925 p. 292-294. syn. nov.
H. trichiurus whitei Purcell, 1899 p. 436. syn. nov.

Type specimens: The whereabouts of Gervais' type is unknown and the type locality was simply given as "La Cafrerie (Delalande)".

Distribution: See fig. 40.

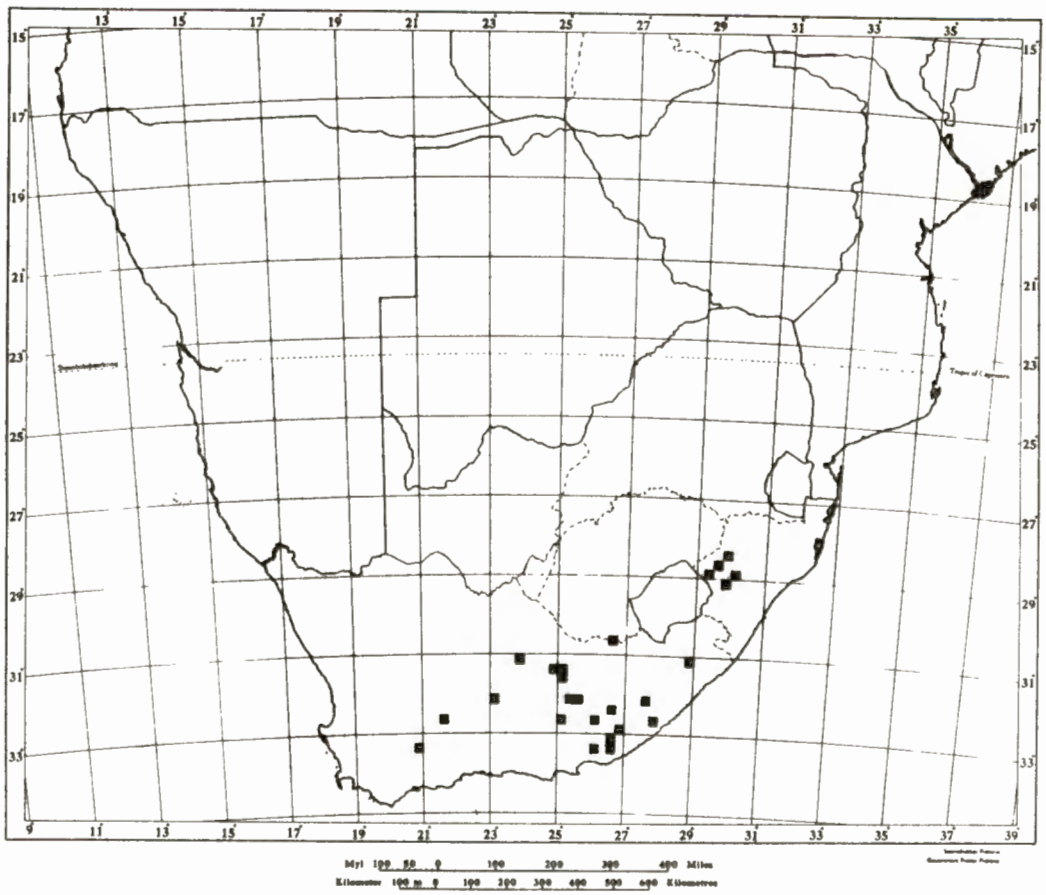


Fig. 40. Map showing the wide distributional range of *Hadogenes trichiurus*.

Material examined: SAIMR 319-322 Middelburg (3124 BD), SAIMR 1191, 1192 Boesmanskloof (3225 AB). TM 9662 Kei River (3227 DB), TM 10906 Merweville (3221 DA), TM 10689, 10690 Achleean (2830 CC), TM 10820 Ladysmith (2829 DA). SAM Bedford (3226 CA), SAM Grahamstown (3326 BC), SAM 12025 Pearston, (3225 CA), SAM 12730 Aliwal North (3026DA), SAM 14369 Nelspoort (3223 AA), SAM Rooinek Pass (3320 BD).

Colour: SAIMR 1191 (male), SAIMR 1192 (female) from Boesmanskloof, spirit preserved. Pedipalps reddish brown (2,5YR4/8), carapace very dark reddish brown (2,5YR2/4), tergites dull reddish brown (2,5YR4/4), sternites and legs bright brown (7,5YR5/6).

Size: A medium sized species measuring between 90-135mm.

Sexual dimorphism: Male with slender chela, weakly developed basal lobe pedipalpal movable finger, higher number of pectinal teeth, divided genital operculum, genital papillae and a greatly elongated metasoma. In addition, terminal granules of metasomal dorsal keels of segments II and III are very large and spiniform.

Description: Carapace: Finely granular in mesial and periferal regions of males and females, frontal lobes smooth and shiny. Triangular inset very far back causing the anterior carapace margin to be very deeply concave. Lateral ocelli much larger than median ocelli. Anterior marginal suture absent.

Pedipalps: Dorsal surface of patella and chela weakly reticulated, all other surfaces of pedipalpal segments granular. Dorsal keel of patella obsolete, anterior process of patella relatively poorly developed. All pedipalpal keels present are distinct and composed of sclerotized granules. An unusual feature is that the basal lobe of the pedipalpal movable finger is less prominent in males than in females.

Trichobothria: (specimens from Middelburg and Graaff-Reinet) Neobothriotaxic major, type C. Femur 3, patella 66-93 (average 76), chela 55-95 (average 70) and an average total number of 149 trichobothria per pedipalp (129-191).

Legs: Femur and patella with two distinct granular keels on ventral surface. Tarsomere II of all legs with 3:3 spines ventrally. These ventral spines differ from other scorpions seen in that the two distal spines on each side are considerably longer and stouter than the more normal proximal spine. Ungues also very long and ungual process does not

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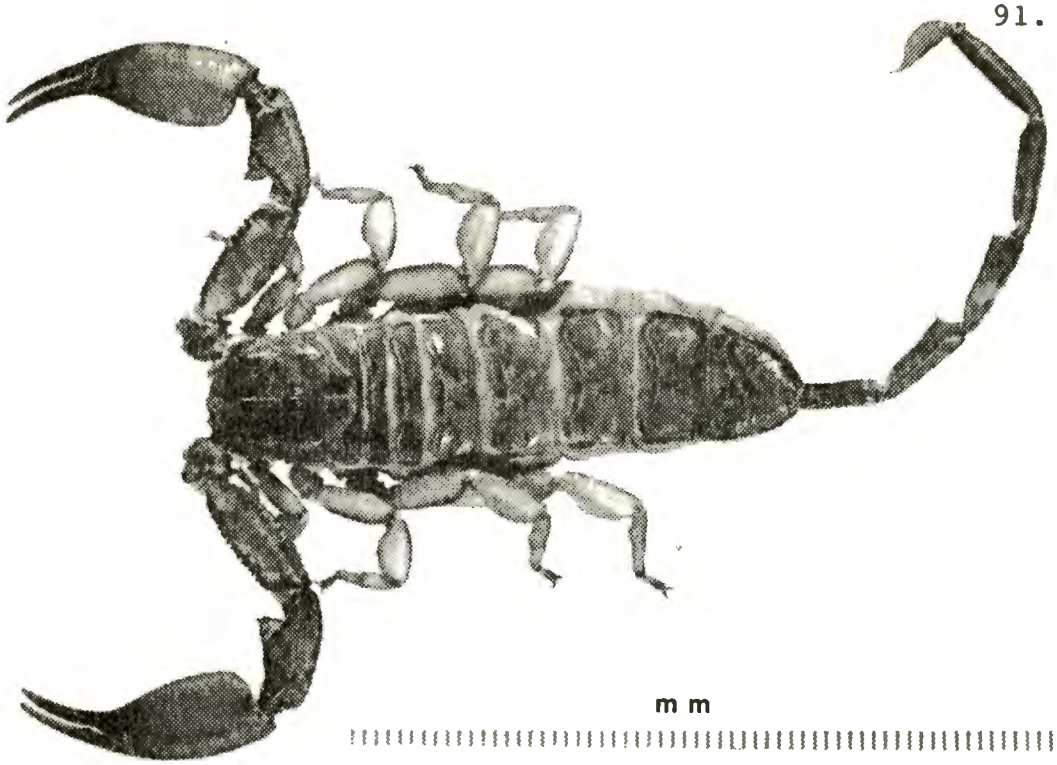

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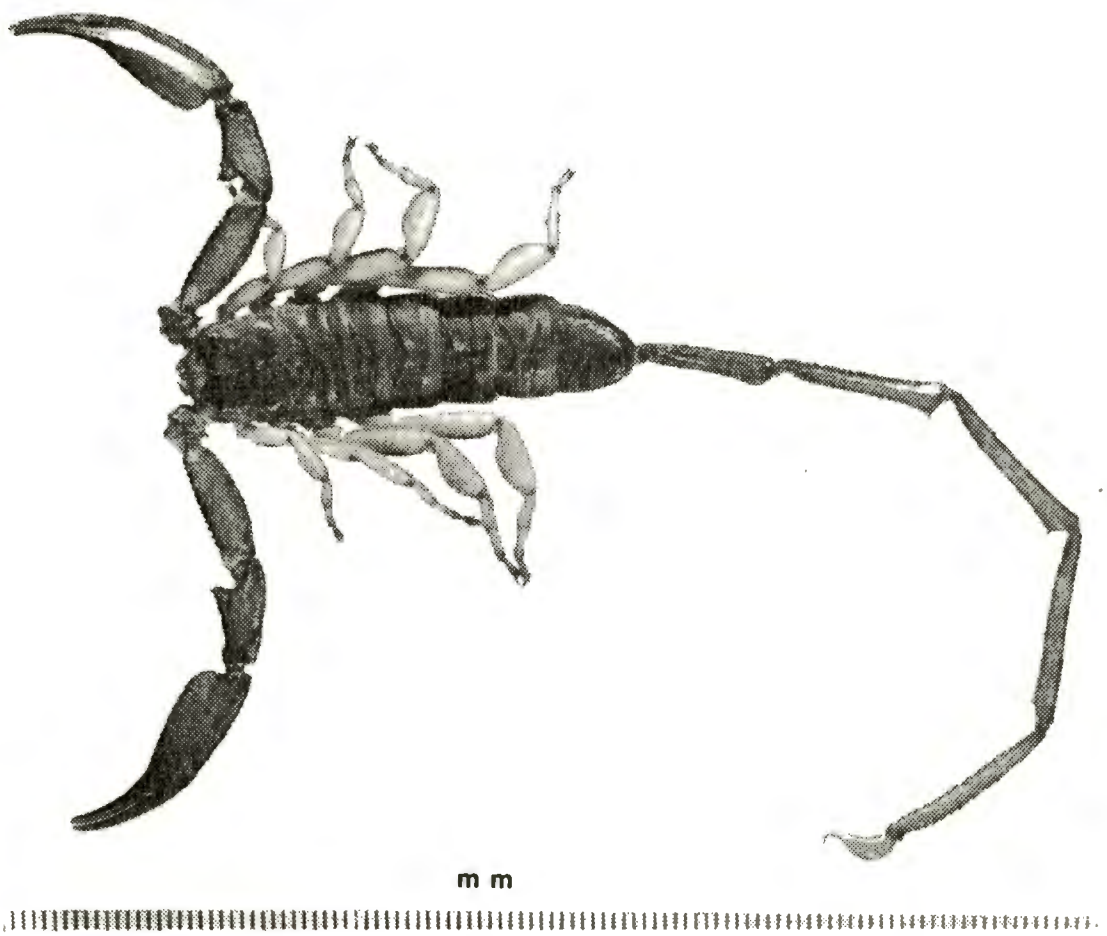

Figs 41-42. *Hadogenes trichiurus* (Gervais, 1843). 41. Dorsal view of a female from Boesmanskloof, eastern Cape Province. 42. Dorsal view of a male from Boesmanskloof.

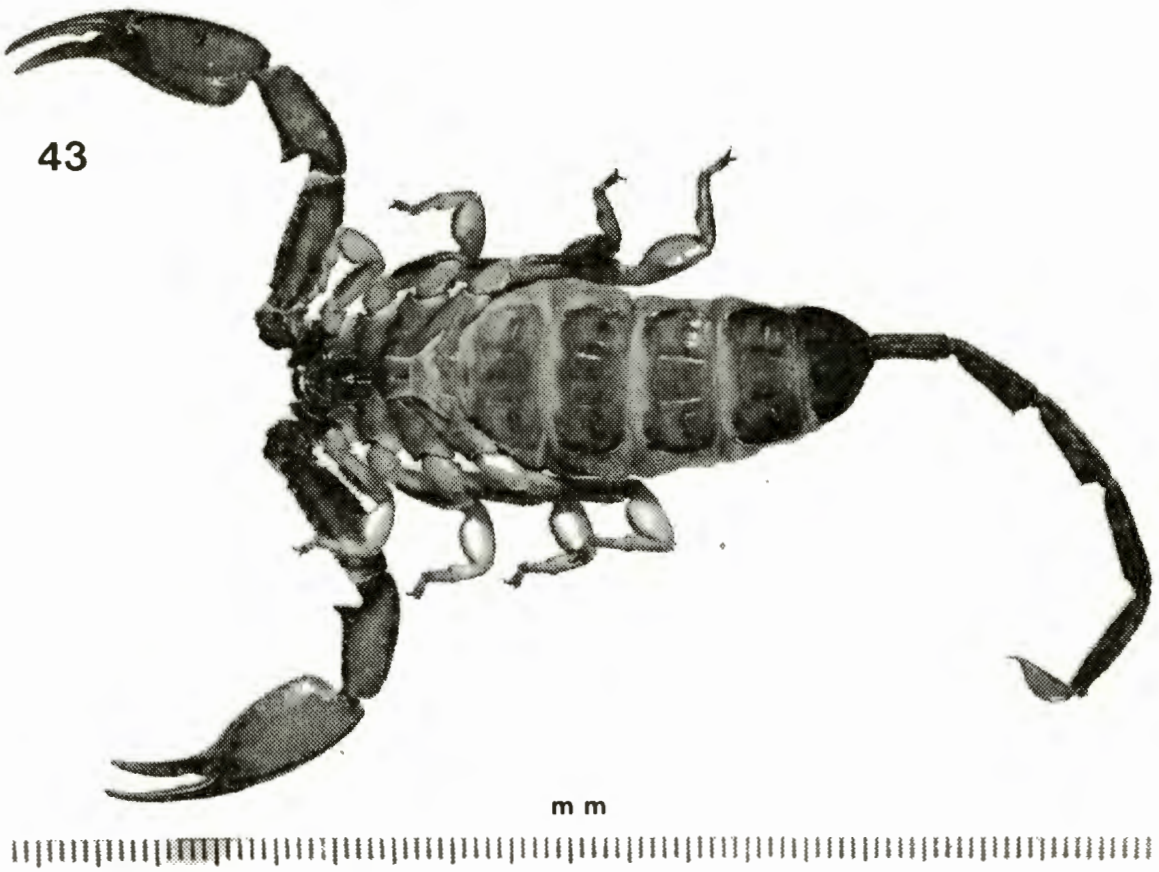

Fig. 43. *Hadogenes trichiurus* (Gervais, 1843). Ventral view of a female from Boesmanskloof.

protrude beyond the ventral spines of tarsomere II.

Mesosoma: Tergites and sternites without special features, smooth and polished in female but tergites of male slightly matt in appearance. Tergite VII and sternite VII of male longer than wide and wider than long in female.

Pectines: 13-15 in females, males 17 teeth.

Metasoma: Metasomal segment higher than wide, and in male, dorso-lateral keels of segments II and III terminate distally with greatly enlarged spiniform granules while in the female, these granules are very weakly developed. Keels of the ventral and dorsal surfaces evenly granular. Profile of male vesicle distinctly concave dorsally but in female, the dorsal surface is straight.

Measurements: Female, carapace anterior width 5,3mm, posterior width 11,5mm, length 11,5mm. Length of chela along postero-ventral keel 11,1mm, movable finger length 12,6mm, width 6,1mm. Metasomal segment I, 2,2mm wide, 2,7mm high, 6,6mm long. Metasomal segment V, 1,6mm wide, 2,2mm high and 10,2mm long. Telson 7,0mm long, 1,7mm wide and 2,2mm high. Male, anterior carapace width 5,3mm, posterior width 10,8mm and length 11,1mm. Length of chela along postero-ventral keel 11,8mm, movable finger length 12,1mm, width 5,8mm. Metasomal segment I, 2,2mm wide, 3,0mm high and 13,2mm long. Metasomal segment V, 1,3mm wide, 2,2mm high and 18,4mm long. Telson 7,1mm long, 1,9mm wide and 2,4mm high. Total length of male metasoma 94mm.

Notes: This species represents a taxonomic problem and the solutions attempted by Hewitt (1918, 1925) and Lawrence (1937, 1955) are as interesting as they are annoying. As the whereabouts of Gervais' type is not known and the original species description is of no diagnostic value, Hewitt (1918, 1925) and Lawrence (1937, 1955) simply ignored the typical form and described numerous subspecies (termed "varieties" by Hewitt). These authors regard a subspecies simply as a specimen that differed very slightly from the "typical form". Two described species *H. pallidus* Pocock and *H. whitei* Purcell considered to be conspecific with *H. trichiurus* were reduced to subspecific status rather than being sunk. The nett result is that until now, six subspecies (including *H. trichiurus zuluanus*, see 5.2.5) were accepted while the typical form remained unknown. To complicate the matter further, it is thought that Hewitt's type specimens were destroyed during one of the two fires which broke out in the Albany Museum during the early years. The types could thus not be consulted. In attempting to plot the distributional ranges of each subspecies described and identified by Hewitt (1918, 1925) and Lawrence (1955) it was soon clear that the subspecies ranges overlapped frequently and at random. In view of this I have decided to

abolish the subspecies of the Cape and to raise the Natal species *H. trichiurus zuluanus* to full specific status. This latter "subspecies" differs considerably from the Cape specimens and is probably a valid species. It must be stressed that the provisional sinking of these subspecies is tentative and is based upon the fact that insufficient evidence was had by the original authors, the clinal variation expected in a species with a wide distribution and the fact that in most cases, the subspecies distributional ranges overlapped considerably. However, the possibility that at least some of the subspecies may prove to be sibling species must not be ignored although such a study was beyond the scope of the present account.

Only one specimen was obtained alive (SAM Rooinek Pass) and this was compared electrophoretically with *H. trichiurus zuluanus* (samples 6-9, fig. 107) and can also be compared with *H. minor* as represented on electrophoretogram samples 8-9 fig. 105. It will immediately be apparent that these scorpions differ quite markedly electrophoretically, but a larger sample would be needed to see how much individual variation is possible in terms of a cline.

5.2.5 *Hadogenes zuluanus* Lawrence, figs 44-47
Hadogenes trichiurus zuluanus Lawrence, 1937, p. 259-261.

Type specimens: This species was based upon a male and five females from the Hluhluwe Game Reserve. The types are in the Natal Museum, Pietermaritzburg.

Distribution: See fig. 44.

Material examined: SAIMR 1029-1031, 1050, 1101, 1102, 1105, 1108, 1166, 1167, Magut (2731 DA).

Colour: (SAIMR 1050, freshly preserved). Pedipalps dark

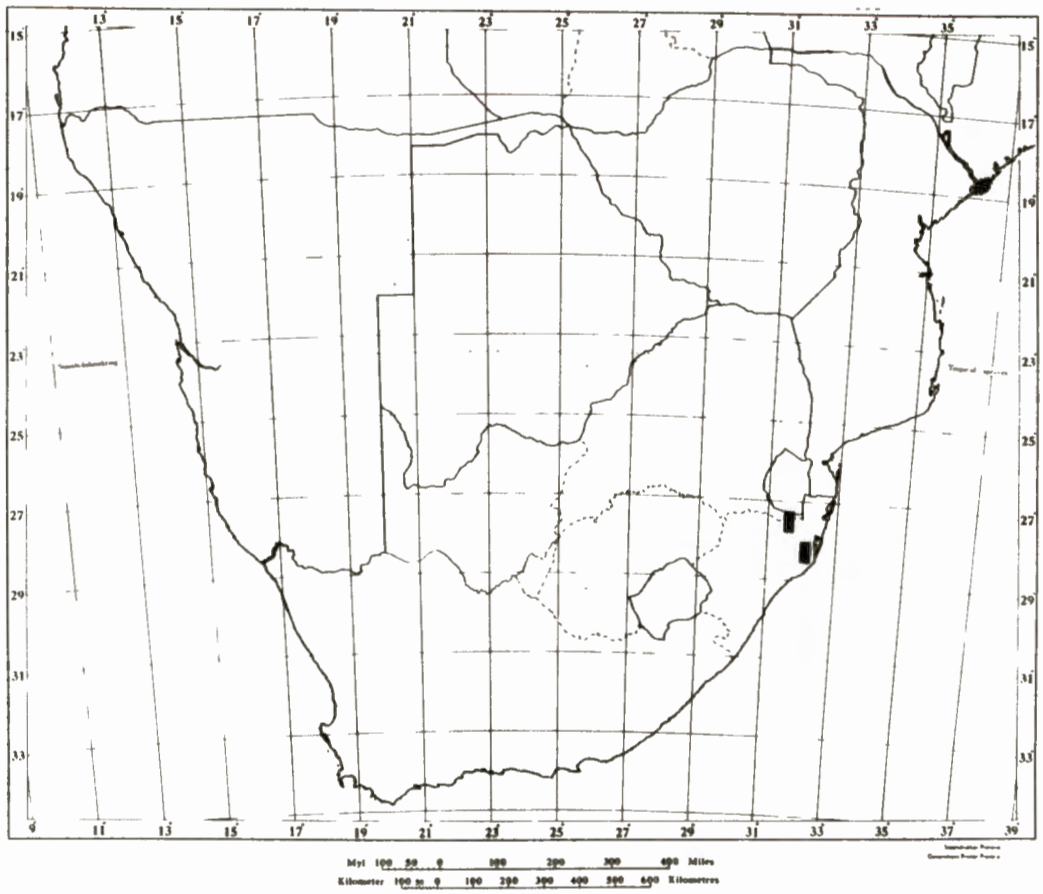

Fig. 44. Distribution of *Hadogenes zuluanus* in southern Africa.

red (7,5R3/6), carapace very dark reddish brown (7,5R2/3), tergites dark red (7,5R3/4), sternites dark reddish brown (2,5YR3/3) and legs reddish brown (5YR4/6).

Size: A medium sized scorpion measuring 120-157mm.

Sexual dimorphism: Male pedipalp, prosoma and mesosoma indistinguishable from that of female with regard to proportions. Male with elongated metasoma bearing distinctly spiniform terminal granules to metasomal dorso-lateral keels on segments II and III, with divided operculum, genital papillae and higher number of pectinal teeth.

Description: (SAIMR 1050 ♀, 1105 ♂).

Carapace: Frontal lobes widely separated with triangular inset very far back imparting a very deeply excavated anterior margin. Triangular inset longer than wide and smooth. Carapace weakly and finely granular over whole surface. Median ocelli very slightly larger than lateral ocelli.

Pedipalps: Finely granular over whole surface except dorsum of chela which is reticulated. Dorsal keel of patella obsolete, digital and accessory keels of chela barely discernable.

Trichobothria: Neobothriotaxic major, type C. The following counts were obtained: femur 3, patella 68-87 (average 80), chela 70-103 (average 84) and with an average total number of 167 per pedipalp. In addition to usual *it* and *ib* (Vachon's "internal" chela surface, see fig. 100) trichobothria, there are 1-3 accessory trichobothria between the *it* and *ib* trichobothria in this species.

Legs: Femur of legs I-III with two granular ventral keels, femur of legs IV with two weakly developed granular keels in the distal half only.

Mesosoma: Tergites of female very smooth, tergites of males very finely and evenly granular and of matt appearance. Sternites of both sexes smooth and shiny. Tergite VII and sternite VII much wider than long.

Pectinal teeth: ♂ :20-22, ♀:15-16.

Metasoma: Ventral and ventro-lateral keels of segment V in female distinctly granular, all other metasomal keels smooth or very weakly granular. Dorso-lateral keels of segments II and III terminate distally with a weak tooth-like granule in female. In male ventral, ventro-lateral

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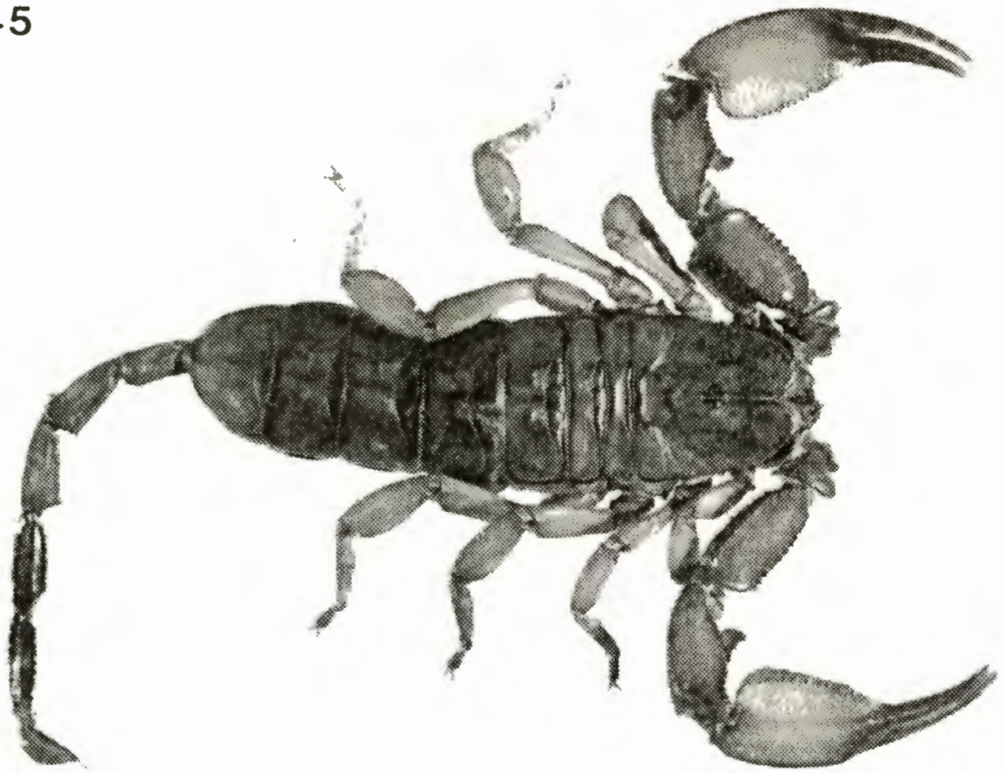

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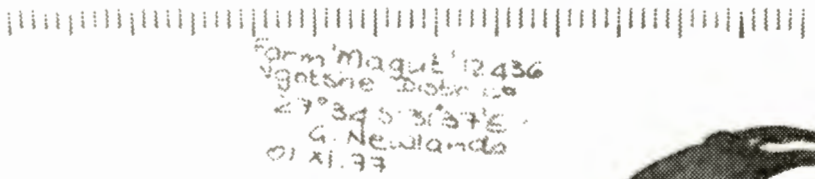

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Figs 45-46. *Hadogenes zuluanus* Lawrence 1937. 45. Dorsal view of female from Magudu. 46. Dorsal view of a male from Magudu.

Fig. 47. Ventral view of *Hadogenes zuluanus* Lawrence 1937 from Magudu.

and dorso-lateral keels of segments II-V granular with the dorso-lateral keels of segments II, III and IV terminating distally with greatly enlarged spiniform granules.

Telson: Smooth and with very slightly concave dorsal profile.

Measurements: (SAIMR 1050 ♀): carapace anterior width, 7,5mm, posterior width, 14,9mm, and length 15,3mm. Chela movable finger length 17,8mm, chelal postero-ventral keel length 14,9mm, width, 10,0mm. Metasomal segment I, 3,1mm wide, 3,4mm high and 6,7mm long. Metasomal segment V,1,7mm wide, 2,8mm high and 10,9mm long. Telson damaged. (SAIMR 1105 ♂): Anterior carapace width 7,8mm, posterior width 15,4mm and length 15,2mm. Chela movable finger 16,3mm long, chelal postero-ventral keel 15,3mm and width 9,9mm. Metasomal

segment I, 4,0mm wide, 3,9mm high and 10,0mm long.

Notes: This species was originally described as a subspecies of *H. trichiurus* (Gervais) but it differs considerably from examples of this latter species studied (see 5.2.4) in the following details: No pedipalpal or mesosomal sexual dimorphism in regard to proportions of these segments, 1-3 accessory trichobothria between the chelal *it* and *ib* trichobothria, presence of dorsal terminal spiniform granule on metasomal segment IV, *H. zuluanus* much larger than *H. trichiurus* and electrophoretic banding pattern different. In view of these considerations and the specimens seen from the Cape, I am convinced that *H. zuluanus* deserves specific status. Besides these morphological differences it appears that *H. trichiurus* is a species associated with the southern and eastern ridges of the great escarpment while *H. zuluanus* is probably restricted to the Lebombo and closely associated mountains of northern Natal. Extensive collecting in the field during October 1977, failed to yield any specimens west of Magudu. The geomorphology of the hills differs in the area between Magudu and Vryheid in that the boulders are composed of basaltic rock which is well rounded and without cracks and crevices. There are thus no suitable habitats for species of *Hadogenes* in this area.

5.2.6 *Hadogenes bicolor* Purcell, figs 48-51
H. bicolor Purcell, 1899, p. 437-438.

Type specimens: Female holotype and several nymphs housed in the Transvaal Museum (TM 4062) from 32km east of Pietersburg, N. Transvaal (2329 DD).

Material examined: SAIMR 268 Noupoort (2529 DA), SAIMR 552, 769, 770 Boyne (2329 DD), SAIMR 1102, 1144, 1157 Zusterstroom (2529 CA), SAIMR 999-1000, 1044-1049, 1107 Haffenden Heights

(2430 AA), SAIMR 1122, 1300 Leopards Crag (2430 AA), SAIMR 1258 Farm Lillie (2430 BB), SAIMR 1335-1336 Makapansgat (2429 AA). TM 4062 Pietersburg (2329 DD), TM 112-128 Mooketsi (2330 CA), TM 1055 Woodbush (2329 DD), TM 1057 Clearwaters (2429 BB), TM 1058 Munniksfarm (2329 DB), TM 2184 Potgietersrus (2429 AA), TM 6273 Zeekoegat (2431 AA), TM 2231 Shaholle (2330 DC), TM 10781 Makapansgat (2429 AA). TM 6086 Perkoe (2430 BD), TM 6108 Maribashoek (2429 AA).

Distribution: See fig. 48.

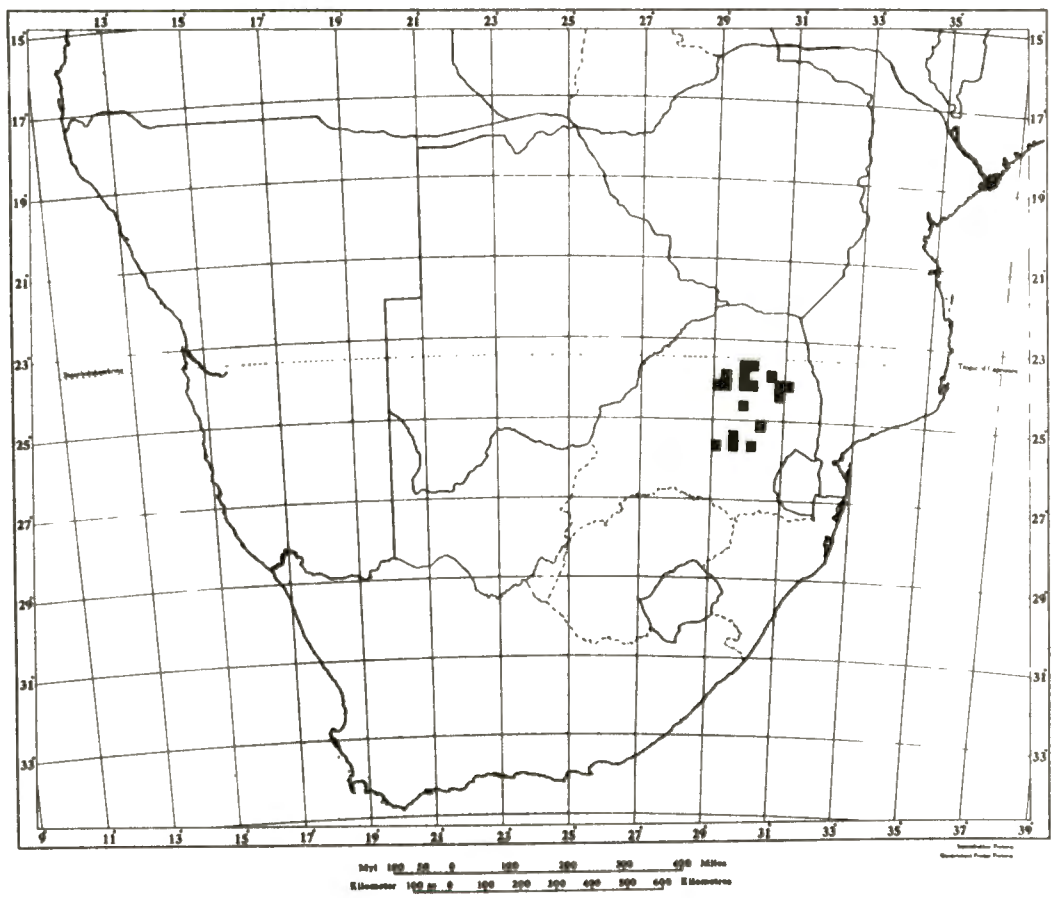


Fig. 48. Map showing the distribution of *Hadogenes bicolor* Purcell in the eastern Transvaal.

Colour: (Fresh spirit preserved specimen SAIMR 1107). Chela dark red (7,5R3/6), carapace and tergites very dark reddish brown (7,5R2/3) and sternites dull yellowish brown (10YR5/3).

Size: Large species 110-135mm in length.

Sexual dimorphism: Male chela more slender, pedipalpal femur and patella longer, finely granular tergites of matt appearance (female tergites smooth and shiny), with genital papillae and divided genital operculum.

Description: Carapace: Anterior margin of carapace deeply concave with triangular inset set far back. Triangular inset without granulation or keel. Anterior marginal suture absent. Lateral ocelli same size as median ocelli. Carapace finely granular all over except for a small area on each frontal lobe which is smooth and the central area of the carapace which is more coarsely granular.

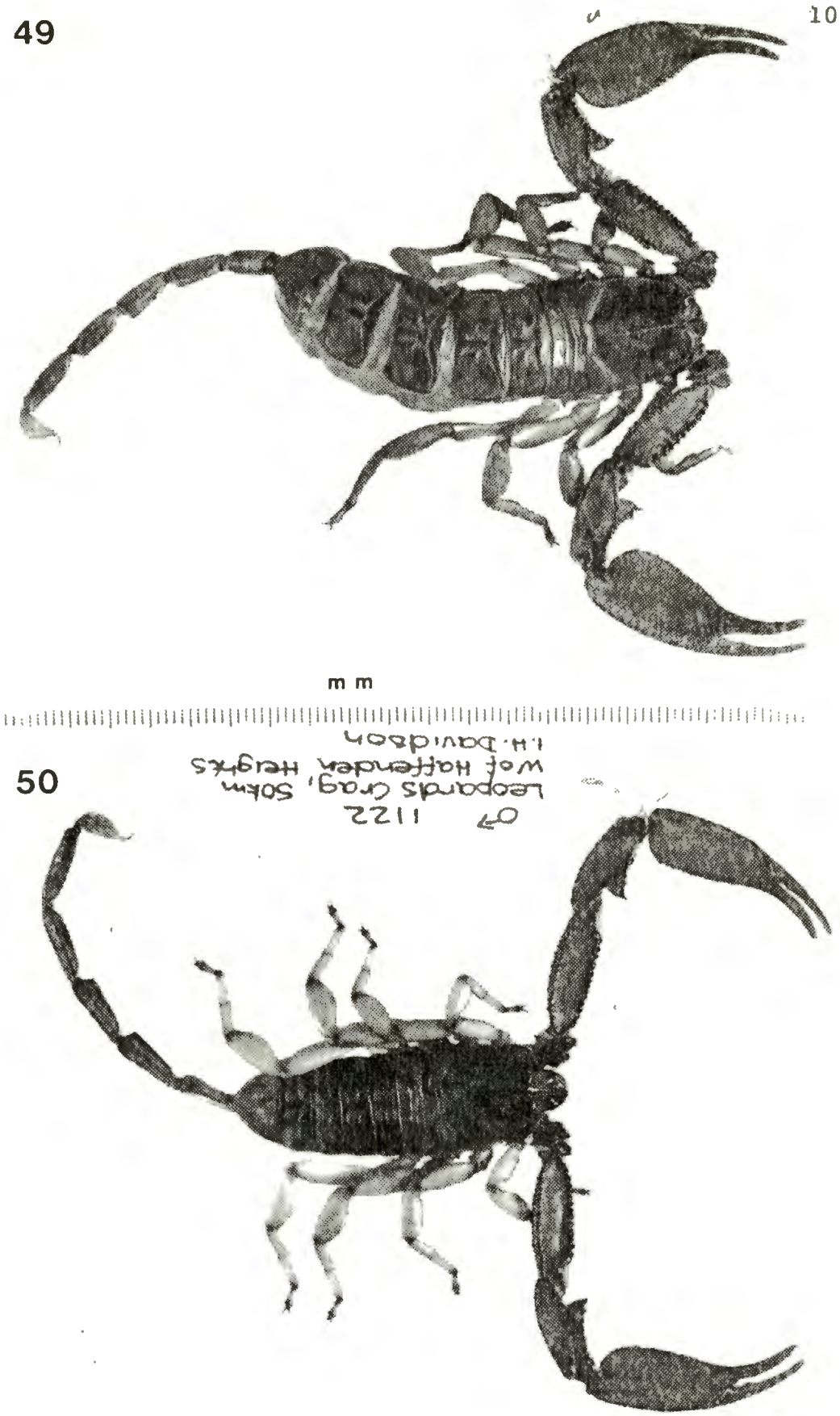
Pedipalps: Dorsal surfaces of femur and patella deeply concave. Dorsal keel of patella distinct and granular, antero-dorsal keel of femur composed of very large heavily sclerotized granules. Inter-keel surfaces of pedipalpal segments finely granular. Movable finger of chela shorter than length of chela along the postero-ventral keel. Basal lobe of pedipalpal tarsus very large, especially in males.

Trichobothria: Neobothriotaxic major type C. Counts were as follows: femur 3, patella 79-91, chela 89-98 with an average total number of 182 per pedipalp.

Legs: Femur with two well-developed granular keels ventrally. Tarsomere II of legs I-IV with 3:3 ventral spines.

Mesosoma: Genital operculum of female with distinct distal lobes and only connected by a membrane in the anterior 2/3rds of the sclerites.

Pectinal teeth: ♂:20-21, ♀:13-16.



Figs 49-50. *Hadogenes bicolor* Purcell, 1899. 49. Dorsal view of a female from Haffenden Heights. 50. Dorsal view of a male from Haffenden Heights.

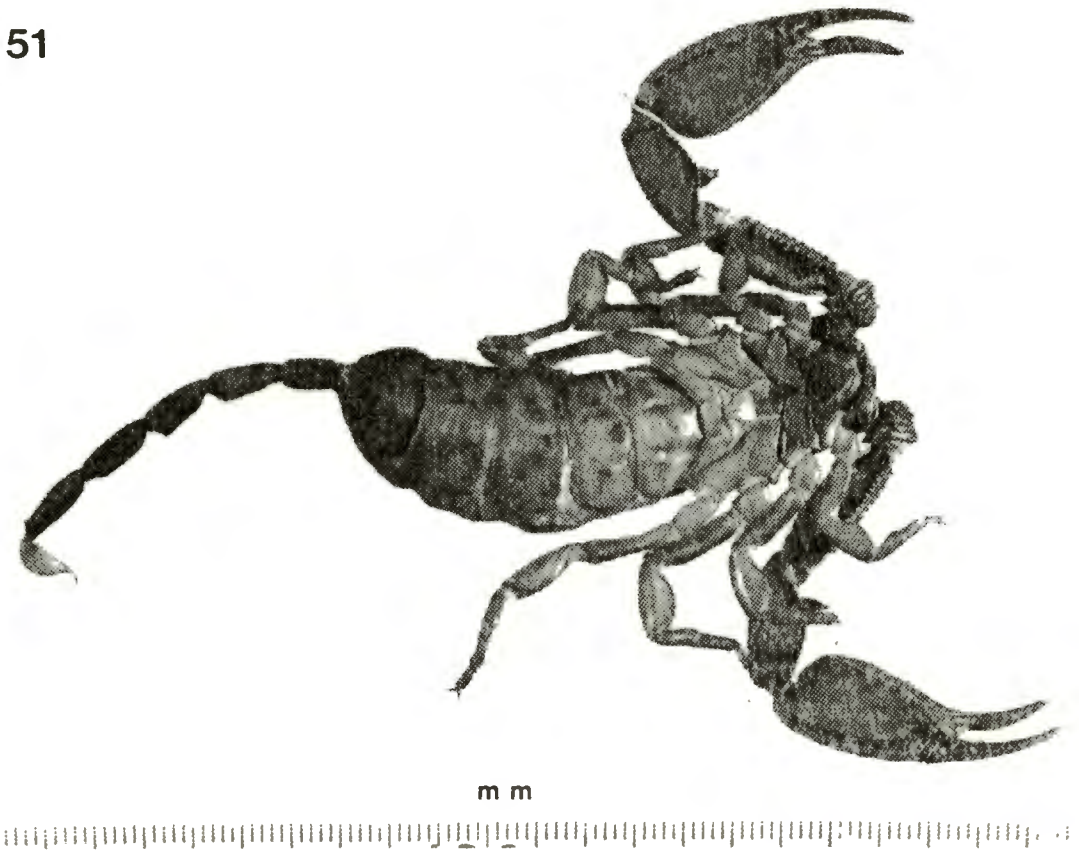


Fig. 51. Ventral view of a *Hadogenes bicolor* Purcell, 1899, female from Haffenden Heights.

Tergites: Tergites of male evenly and finely granular all over such that they have a matt appearance. Tergites of female smooth and shiny. Tergite VII wider than long in both sexes.

Sternites: Smooth and shiny.

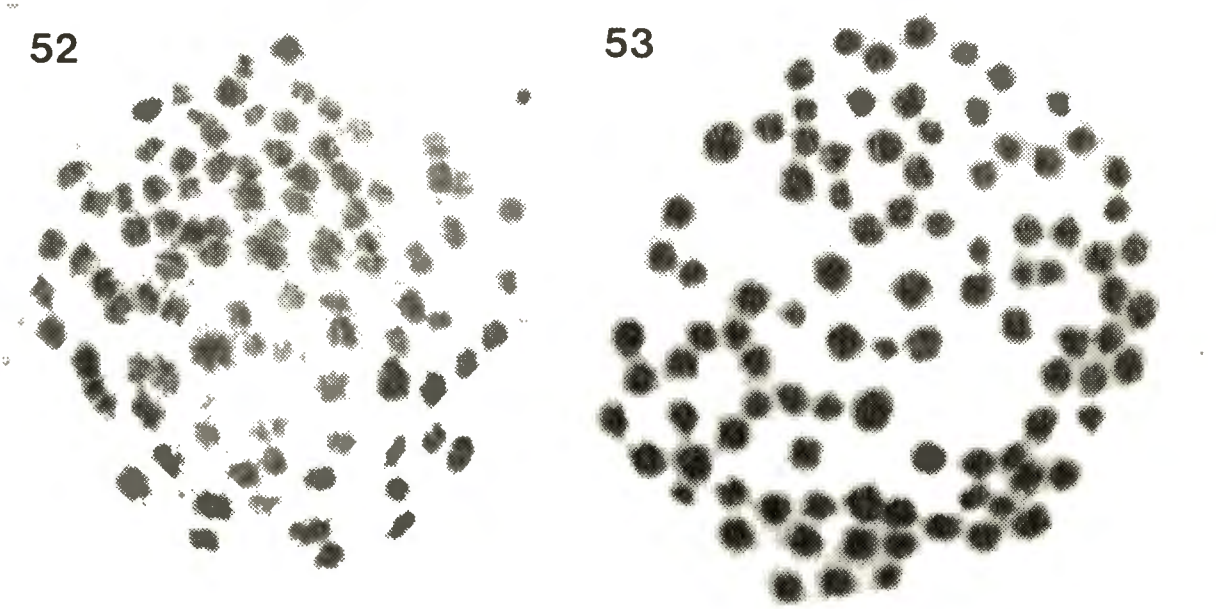
Metasoma: Segments II and III terminate distally with a prominent tooth-like granule on each side dorsally. Segment I wider than high posteriorly.

Telson: Smooth and shiny in both sexes.

Measurements: Specimen (♀ SAIMR 1107) (Haffenden Heights) Carapace anterior margin 6,6mm, posterior carapace width 14,1mm, length 14,1mm. Chela movable finger length 14,7mm,

chela length along postero-ventral keel 15,8mm and width 9,7mm. Metasomal segment I, 3,3mm wide, 2,8mm high and 6,9mm long, segment V, 1,8mm wide, 2,75mm high and 9,1mm long. Telson 7,6mm long, 2,1mm wide and 2,9mm high. Metasoma length 46mm. Male specimen (SAIMR 1122) (Leopards Crag) Carapace, anterior width 4,9mm, posterior width 13,8mm, length 13,1mm. Chela movable finger 13,6mm long, chela length along postero-ventral keel 15,0mm, chela width 7,6mm. Metasomal segment I, 2,6mm wide, 2,6mm high and 7,2mm long. Metasomal segment V 1,1mm wide, 2,75mm high and 11mm long. Telson 7,2mm long, 2,9mm high. Metasoma 55mm long.

Chromosome number: 2n=96 as based on testicular and ovarian tissue. The quadruploid number (192) was seen very frequently.



Figs 52-53. Chromosomes of *Hadogenes bicolor* Purcell. 52.Spread seen in a testicular preparation. 53. Typical spread seen in an ovarian preparation.

Notes: This species differs from most other species of the genus in that the male metasoma is not obviously longer

than that of the female. Morphologically this species is most closely related to *H. gunningi*, *H. paucidens* and *H. trichiurus*. Its distribution is associated with the mountains forming the eastern rim of the Bushveld Igneous Complex in the Transvaal.

5.2.7 *Hadogenes gunningi* Purcell, figs 54-59.
H. gunningi Purcell, 1899, p. 435.

Type: This species was based on a single Transvaal Museum specimen (♀) from Pretoria (TM 4041).

Material examined: SAIMR 39 Hennops River (2527 DD), SAIMR 55, 135, 192-204, 205-206, 207, 208-209, 774 Pretoria (2528 CA), SAIMR 134 Meyers Park (2528 CB), SAIMR 139 Tierpoort (2528 DA), SAIMR 190-191 Pelindaba (2527 DD), SAIMR 875 Rustenburg (2527 CA), SAIMR 921-924, 1124 Melville (2628 AA), SAIMR 925-928 Magaliesburg (2627 BA), SAIMR 930 Hekpoort (2527 DC), SAIMR 1189 Bartletts farm (2627 DC), SAIMR 1194-1195 Krom River (2527 CD), HPC Lanseria Airport (2528 CC), TM 713, 739, 740, 746, 752, 753, 756, 761, 1837, 1841-1843, 1844, 9436, 10540, 10676 Pretoria (2528 CA), TM 747-751 Roodeplaat (2528 CB), TM 1840 Garsfontein (2528 CB), TM 11229 Boekenhoutskloof (2528 DA), NM 9939-9940 Roodeplaat (2528 CB).

Distribution: See fig. 54.

Colour: (Fresh spirit preserved, SAIMR 928) Chela dark red (7,5R3/6), carapace very dark reddish brown (7,5R2/2), tergites very dark reddish brown (10R2/3), sternites dark brown (10YR3/4).

Size: A moderately large species; ♀ up to 105mm, ♂ to 132mm.

Sexual dimorphism: Chela and mesosoma of male more slender

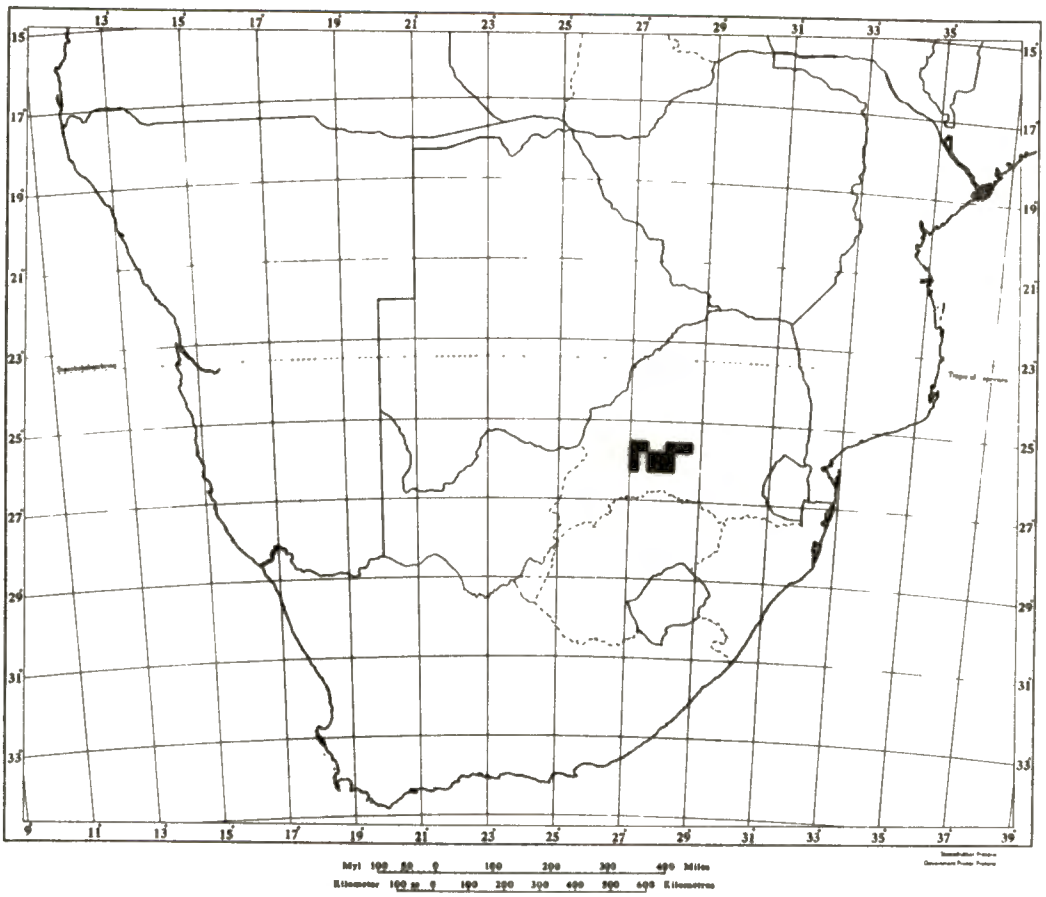


Fig. 54. Map showing the distribution of *Hadogenes gunningi* which is restricted to the Pretoria-Johannesburg environs.

than those of females, metasoma of male approximately 30% longer than that of female, tergites of male very finely granular, tergites of female smooth and shiny, male with higher number of pectinal teeth, with divided operculum and genital papillae.

Description: Carapace: Anterior margin slightly concave, anterior marginal suture absent, triangular inset keelless but granular, carapace granular all over except for a small area of the frontal lobes. Median ocelli only slightly larger than lateral ocelli.

Pedipalps: Dorsal keel of patella absent. Anterior process of patella very large, movable finger of chela slightly

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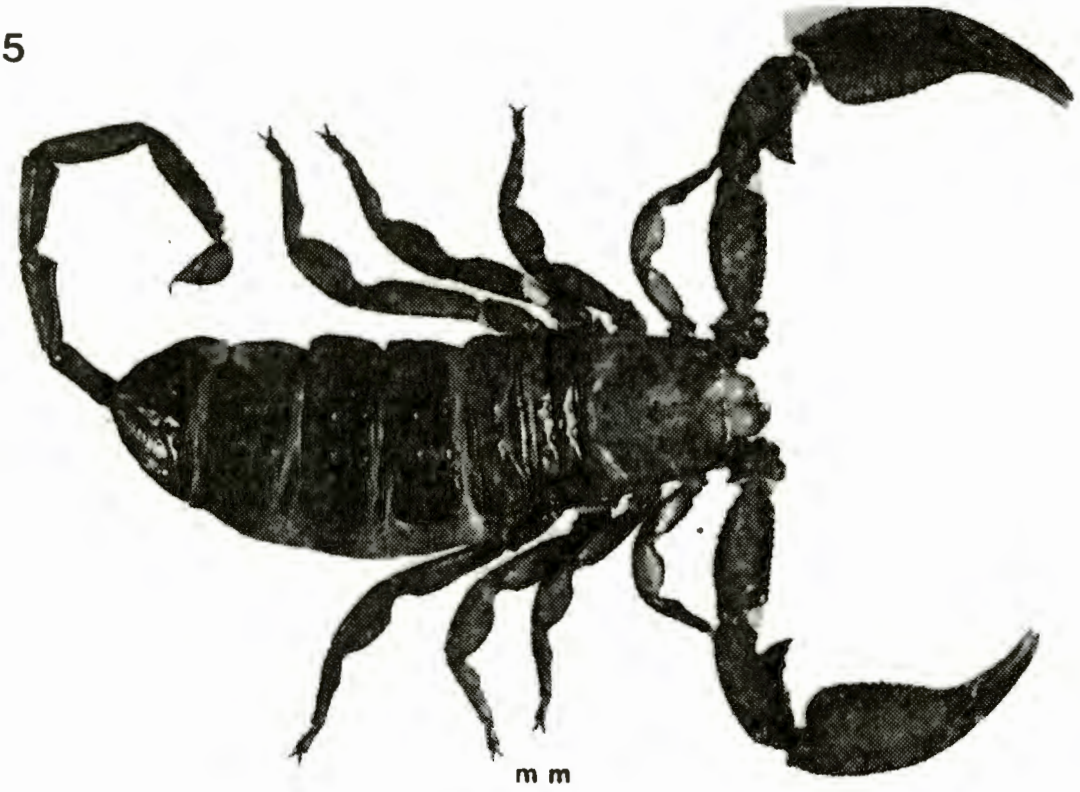

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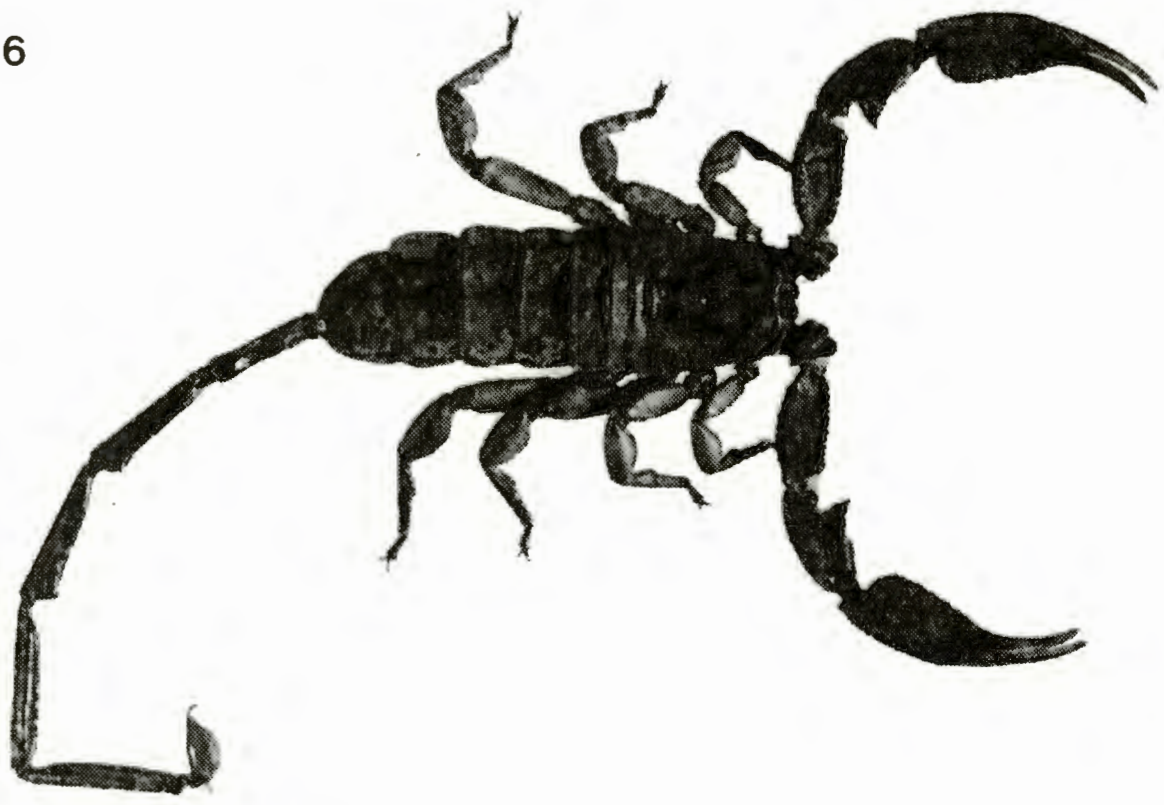


Figs 55-56. *Hadogenes gunningi* Purcell, 1899. 55. Dorsal view of female. 56. Dorsal view of male.

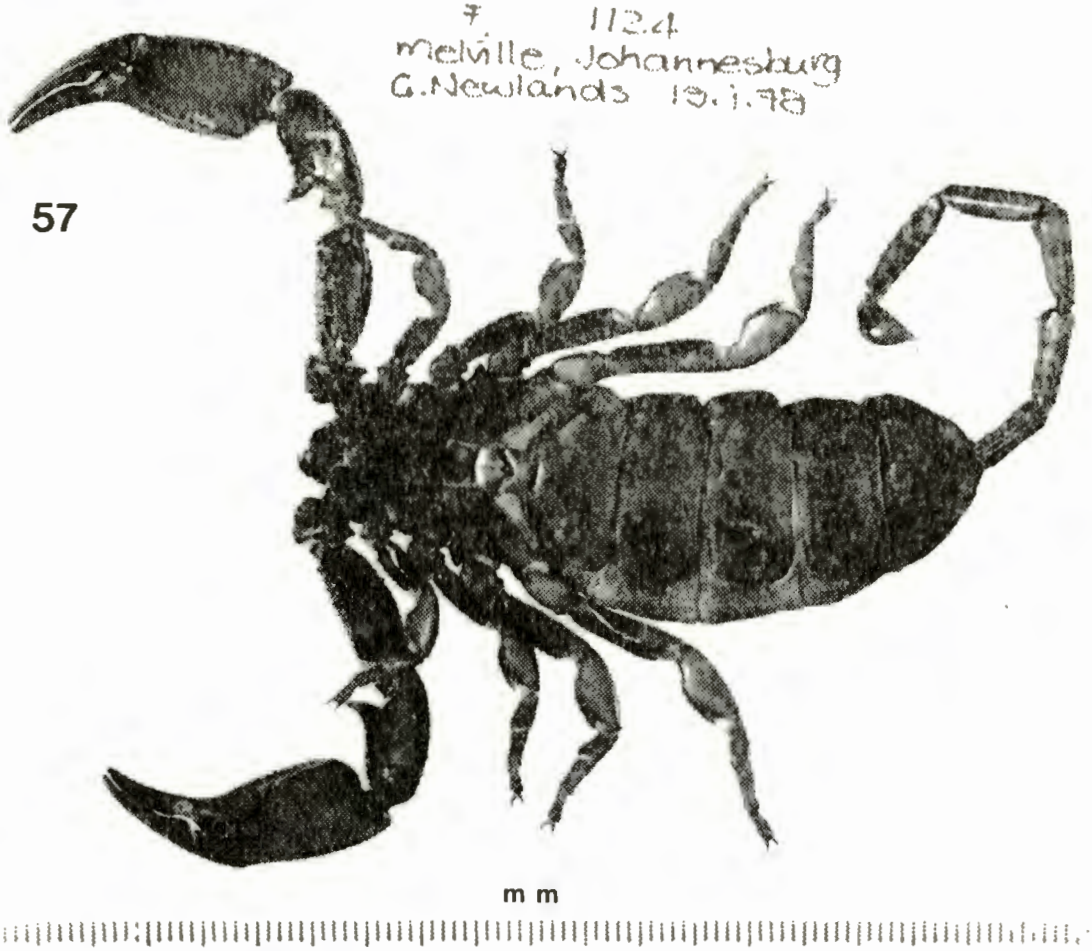


Fig. 57. Ventral view of a female *Hadogenes gunningi* Purcell, 1899.

shorter than length of chela along the postero-ventral keel.

Trichobothria: Neobothriotaxic major, type C. Femur 3, patella 74-86 with average of 81, chela 66-83 with average of 74. Average total number of trichobothria per pedipalp 159, (maximum 168). A specimen from Krom River (SAIMR 1194) had 3:111:95 (femur:patella:chela) with a total of 209 trichobothria per pedipalp.

Legs: With distinct granular keels on the venter of the femur and patella of all legs, tarsomere II with 3:3 spines ventrally.

Mesosoma: Tergites of male densely and very finely granular which imparts a matt appearance in these sclerites.

Tergites of female shiny and without granulation. Tergite VII of male and female wider than long. Sternites of male and female smooth and shiny.

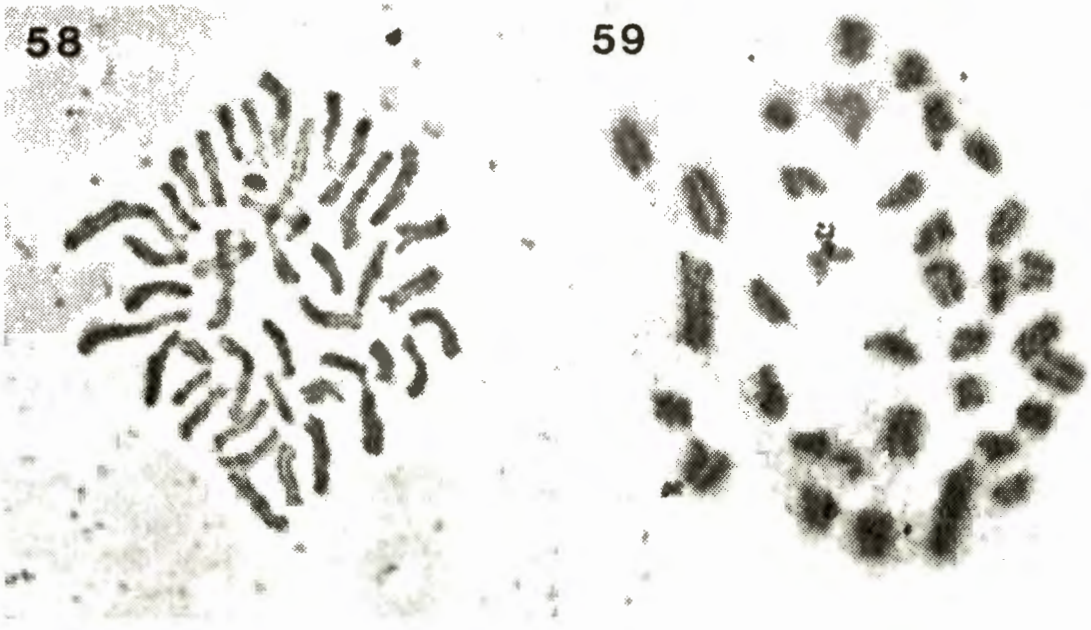
Pectinal teeth: ♂:16-20, ♀:14-17.

Metasoma: Dorso-lateral keels of segments II and III terminate with a slightly spiniform granule. First segment narrower than high posteriorly. Vesicle smooth and shiny in both sexes.

Measurements: Female (SAIMR 192): Carapace anterior width 6,7mm, posterior width 13,3mm and length 13,4mm. Movable finger of chela 13,7mm long, chelal length along postero-ventral keel 14,3mm, and chela width 8,8mm. Metasomal segment I, 3,1mm high, 2,8mm wide and 6,3mm long. Metasomal segment V, 2,9mm high, 2,3mm wide and 9,8mm long. Telson 7,4mm long, 3,1mm high and 2,5mm wide. Male (SAIMR 139): Carapace anterior width 6,2mm, posterior width 12,6mm and length 12,4mm. Movable finger of chela 12,2mm long, chelal length along postero-ventral keel 13,0mm and width 6,7mm. Metasomal segment I, 3,5mm high 2,7mm wide and 8,8mm long. Metasomal segment V, 2,8mm high, 1,8mm wide and 14,0mm long. Telson 7,0mm long, 2,9mm high and 2,3mm wide.

Chromosomes: 2n=88 based on the testicular tissue of a male from Melville, Johannesburg. See figs 58-59.

Notes: Hewitt (1918) was of the opinion that this species was "connected with *H. troglodytes* through *H. troglodytes matoppoanus*." In my opinion this species bears very little relation to *H. troglodytes* but is very similar to *H. bicolor*, especially in the case of the females. In fact, morphologically, females of these species are difficult to separate. The males are more easily distinguished as *H. bicolor* does not exhibit the same degree of sexual dimorphism as does *H. gunningi*,



Figs 58-59. Chromosome spreads seen in testicular tissue preparations of a *Hadogenes gunningi* Purcell from Johannesburg

the most striking feature being the greatly elongated metasoma of the latter species. Electrophoretically, the venom proteins of *H. gunningi*, *H. bicolor* and *H. troglodytes* are very different (see figs 107-108). This species has a very limited distribution and is restricted to the Magaliesberg and smaller ranges to the south associated with the Witwatersrand.

5.2.8 *Hadogenes paucidens* Pocock, figs 61-62.
H. paucidens Pocock, 1896:316-317.

Type specimen: 1 ♀ from West Africa housed in the British Museum (1890.7.1.209). The specimen was originally a dry specimen but was rehydrated in 1975 and transferred to 70% ethanol by the keeper of zoology at the British Museum. Before this specimen was deposited in the British Museum, it had belonged to the Keyserling collection and was originally labelled *Ischnurus melampus* C.K.

Distribution: Uncertain, the type was simply labelled "West Africa". Kraepelin (1899) records it as having come from the Congo. Lamoral and Reynders (1975) quote Pocock (1896) as listing the localities Tete, Mozambique and the Umfuli River in Zimbabwe-Rhodesia for this species but these authors clearly misunderstood Pocock's statement as he was recording these localities for *H. troglodytes* Peters.

Colour: Holotype: Pedipalps very dark reddish brown (10R2/3), carapace very dark reddish brown (10R2/2), tergites very dark reddish brown (10R2/3), sternites dark red (10R3/6).

Size: A large species measuring 115mm in total length.

Sexual dimorphism: Species only known from female holotype.

Description: Carapace: Anterior margin slightly concave, without anterior marginal suture or granulation on triangular inset. Carapace finely granular in the mesial and periferal regions, the frontal lobes being quite smooth and shiny. Median ocelli larger than lateral ocelli. Triangular inset almost twice as long as wide.

Pedipalps: Finely granular interkeel surfaces of all segments except the dorsal surface of the chela behind the anterior keel and in front of the posterior keel where the granulation merges into a coarser reticulated condition. Anterior process of patella very large and prominent, dorsal keel of patella obsolete. All pedipalpal keels present are distinct and composed of heavily sclerotized granules. Movable finger of chela shorter than length of chela along the postero-ventral keel.

Trichobothria: Neobothriotaxic major, type C, femur 3, patella 111, chela 139. Total number of trichobothria per pedipalp: 253.

Figs 61-62. *Hadogenes paucidens* Pocock, 1896. 61. Dorsal view of the female holotype. 62. Ventral view of the holotype.

Legs: Femur of all legs with granular dorsal keel and two granular ventral keels. Tarsomere II with 3:3 ventral spines on all legs.

Mesosoma: Tergites I-VII smooth and polished but sparsely punctate, tergite VII and sternite VII wider than long. Sternites smooth, sternite VII with a postero-lateral deep oval depression on each side.

Pectinal teeth: 15-14 (left to right).

Metasoma: Metasomal segment III, shorter than segments II or IV, metasomal segment I wider than high posteriorly, metasomal segment II with sharply pointed anteriorly directed granules on ventral surface, metasomal segment V with sharply pointed posteriorly directed granules on ventral surface, all other segment without granular ventral surfaces or only weakly granular.

Vesicle: Smooth and without keels.

Measurements: Anterior carapace width 7,3mm, posterior carapace width 16,8mm, carapace length 15,7mm, median ocelli 8,0mm from carapace anterior margin, width of chela 9,5mm, posterior length of chela 16,3mm, length of chela movable finger 14,9mm, metasomal segment I, 3,4mm wide, 6,6mm long and 2,9mm high, metasomal segment II, 2,4mm wide, 9,2mm long and 3,7mm high, metasomal segment III, 2,36mm wide, 7,7mm long and 3,6mm high, metasomal segment IV 2,28mm wide, 10,5mm long and 2,9mm high, metasomal segment V, 2,5mm wide, 10,2mm long and 2,8mm high, telson 8,2mm long, 2,4mm wide and 3,0mm high, length of prosoma plus mesosoma 59mm and length of metasoma 56mm.

Notes: Although this species is only known from the type specimen housed in the British Museum, it appears to be a

very distinct species, the nearest relative of which is probably *H. bicolor*.

5.2.9 *Hadogenes taeniurus* (Thorell), figs 62-64.
Ischnurus taeniurus Thorell, 1877 p. 254.

Type specimen: A single female specimen from "Africa meridionalis" housed in the Goteborg Museum, Sweden. The type could not be obtained from the Goteborg Museum for study. Mr B. Lamoral who had been able to examine the type has created a homotype which is now housed in the Natal Museum (NM 10670). The homotype came from Okamiparara in the Otjiwarongo district (20°35'S:17°28'E) and the description below is based largely upon this specimen and larger Transvaal Museum specimens from Angola. A homotype is a specimen which has been compared with the holotype and found to be similar but it has no taxonomic status.

Material examined: SAIMR 258 Uis Tin Mines (2114 BB). TM 9416 Uis (2114 BB), TM 9786 Uithoek 770 (1917 BA), TM 9789-9794 Swartboois Drift (1713 BD), TM 9798, 9799 Epupa Falls (1713 AB), TM9811 Sanitatas (1812 BD), TM 10373-10374 Cainbanbo-Cubal (1513 CA), TM 10422, 10423 Saiona River (1513 CA), TM 10424 Iona (1612 DC), TM 10425 W. Otchinjau (1613 DB), TM 10442 Zebra Mountain (1713 AC), AM Okahandja (2116 DD), NM 10670 Okamiparara (2017 AD).

Distribution: See fig. 62.

Colour: Based upon fairly recently preserved specimen TM 10425; pedipalps reddish brown (2,5YR4/8), carapace dark reddish brown (2,5YR3/6), tergites bright brown (7,5YR5/6), legs bright brown (7,5YR5/8), sternites bright yellowish brown (10YR6/6).

Size: A very large species with females measuring 108-140mm. The only adult male seen measured 160mm.

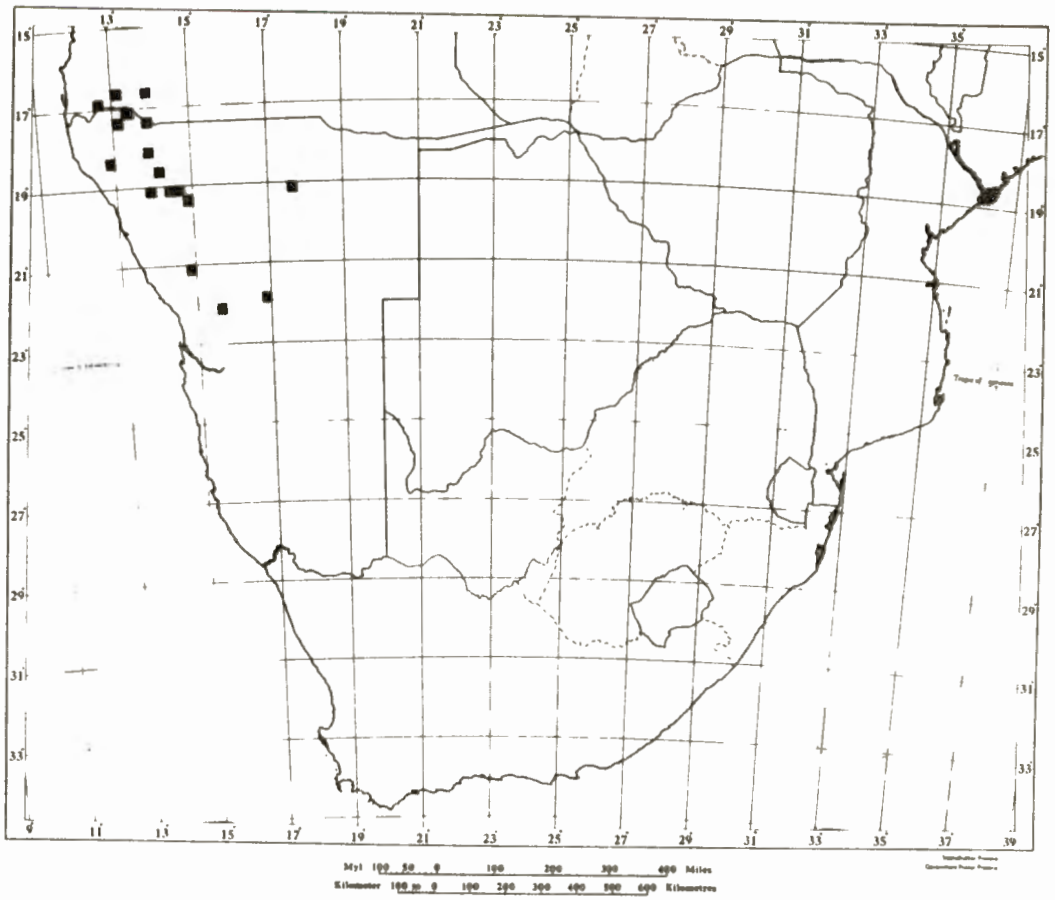
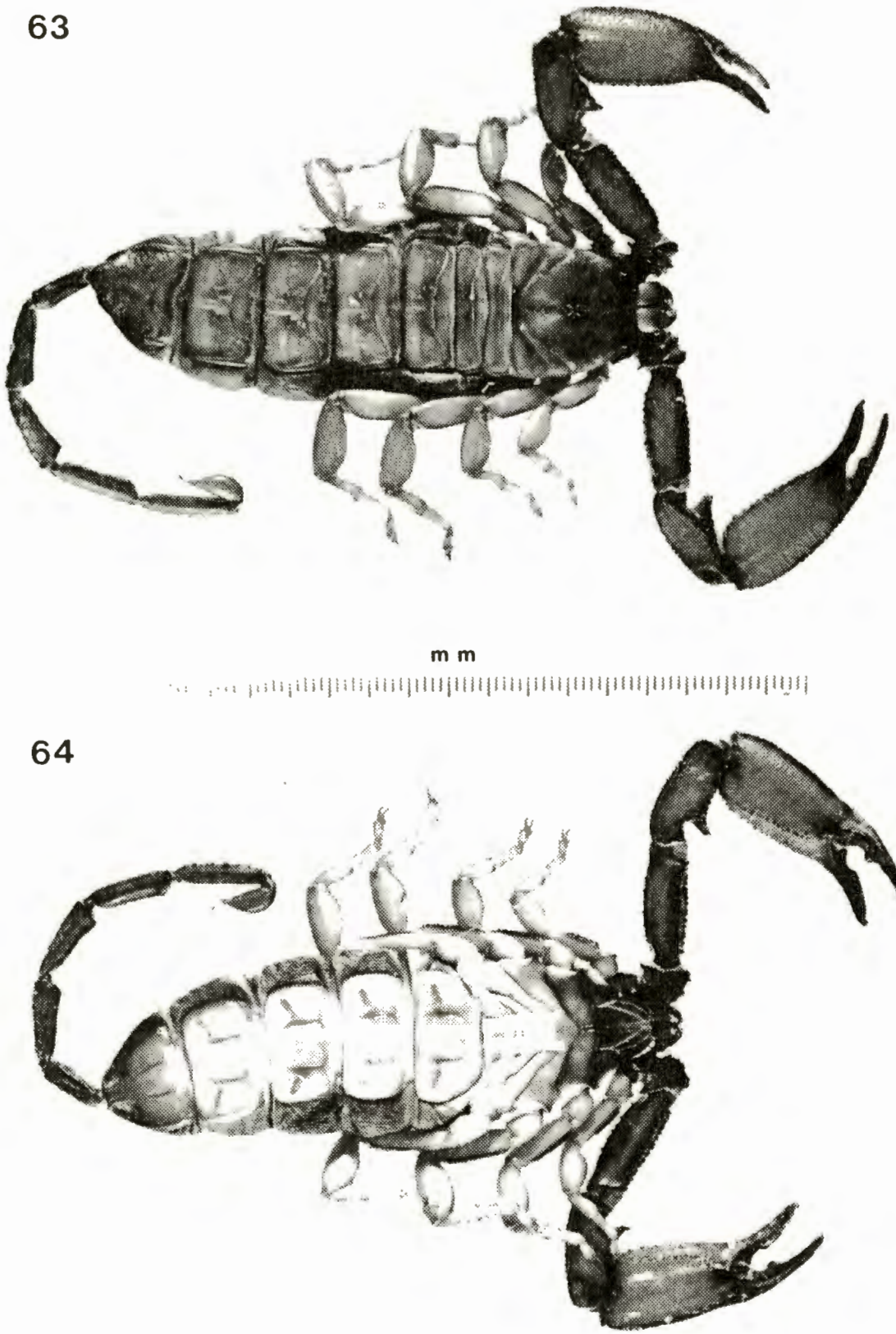


Fig. 62. Map showing the wide distribution of *Hadogenes taeniurus*.

Sexual dimorphism: Male with divided genital operculum, genital papillae, very finely and evenly granular tergites (female's tergites smooth and polished), higher number of pectinal teeth and with more slender mesosoma and pedipalpal chela.

Description: Carapace: Only keels present are the smooth supercillary and granular marginal keel. Triangular inset finely granular. No coarse granulation anywhere on carapace but virtually the whole surface is covered with a fairly fine granulation in both sexes. Lateral ocelli much smaller than median ocelli.

Pedipalps: All pedipalpal segments covered with very fine granules on inter-keel surfaces except the dorso-anterior



Figs 63-64. *Hadogenes taeniurus* (Thorell, 1877). 63. Dorsal view of a female from the Kaokoveld. 64. Ventral view of same specimen.

surface of the chela which is weakly reticulated. Vestigial trace of patella dorsal keel in males and females. Anterior process of patella very large.

Trichobothria: Neobothriotaxic major, type C. Homotype with following counts: femur 3, patella 101, chela 94 and a total of 198 trichobothria per pedipalp. The other specimens examined had the following trichobothrial counts: femur 3, patella 93-103 (average 99), chela 92-106 (average 100) and a total number of 184-221 (average 201) per pedipalp.

Legs: Tarsomere II of leg I with 3:2 spines and legs II-IV with 3:3 spines. Prominent, heavily sclerotized ventral surface and keels on femur of all legs.

Mesosoma: Tergites: Of matt appearance in male owing to very fine even granular covering, smooth and polished in female, tergite VII as wide as long in female but longer than wide in male.

Sternites: Smooth and shiny. Sternite VII with very deep large oval depression on each side distally.

Pectinal teeth: Females 15-18, male 19.

Metasoma: Lateral surfaces smooth and shiny, no spiniform terminal granules of dorsal keels. Except for segment V in female and IV and V in male, all keels weakly granular.

Telson: Smooth in female but with very sparse granulation in male.

Measurements: Homotype (NM 10670), carapace anterior width 7,22mm, posterior width 16,5mm, length 14,8mm. Length of prosoma plus mesosoma 52mm, of metasoma 56mm. Chelal

postero-ventral keel length 17,2mm and length of chela movable finger 14,0mm. Metasomal segment I, 3,4mm wide, 7,7mm long and 2,8mm high; metasomal segment II, 2,4mm wide, 9,9mm long and 3,45mm high. Metasomal segment V, 2,2mm wide, 12,0mm long and 2,7mm high. Telson 8,2mm long, 2,7mm high and 2,4mm wide.

Notes: Records of this species from Namaqualand, viz Steinkopf and Kamaggas, (Kraepelin 1908) are clearly based upon misidentified specimens unless Kraepelin regarded this species as conspecific with *H. phyllodes* which was originally described as a subspecies of *H. taeniurus*. Likewise a specimen in the Albany Museum (not seen) from Kub (2417 BC) has probably been misidentified. The most southern specimens I saw were from the Uis tin mine (2114 BB), which were morphologically identical with the Angola specimens but differed in being very slightly darker in colour.

Newlands (1972) was of the opinion that *H. bifossulatus* Roewer was a synonym of *H. taeniurus* but now that Roewers type has been examined it is clear that *H. bifossulatus* and *H. tityrus* are conspecific.

5.2.10 *Hadogenes granulatus* Purcell, figs 65-70.
H. granulatus Purcell, 1901 p. 204-206.

Type specimen: A single ♂ (SAM 401) allegedly from the Rustenburg district which is kept in the South African Museum, Cape Town. The type is a dried specimen.

Material examined: SAIMR 628-630, 723, 724 Macheke (1831 BB), SAIMR 632 near Macheke (1831 BB), SAIMR 709-713, 720-722, 744-745 Lake McIlwaine (1730 DD), SAIMR 714 Birchenough Bridge (1932 CD), SAIMR 917 Kariba (1628 BD), SAIMR 1190, 1257 Chiredzi (2131 AA), SAIMR 1222, 1252, 1309, 1330 Shamva (1731 BC), TM 10342 Chewore River (1530 CC), TM 10371,

10372 Chewore Mouth (1529 DB), TM 696-697 Wankie (1826 AD), TM 10342 near Chewore River (1530 CC), TM 10344-10352 Chirundu (1628 BB), TM 10371-10372 Chewore River Mouth (1529 DB), TM 5682 near Mica Hills (1826 BC), TM 5683-5685 Titumi (2027 CA), TM 8074 Tanganda River (2032 BD), TM 10695-10696 Kariba (1628 BD), TM 8118, 8121, 8191 Birchenough Bridge (1932 CD), NM 8312, 8314, 8315 Kapami (1826BD) NM 8313 Matetsi confluence (1826 BA), NM 8343 Inyanga (1832 BB), NM 8348 Baddeley (1832 AC), UM/S Wankie (1826 AD), UM/S Kamatini (1826 DB), UM/S Kariba (1628 BD), UM/S Kapami (1826 BD), UM/S Chikawarawara (2029 CC).

Distribution: See fig. 65.

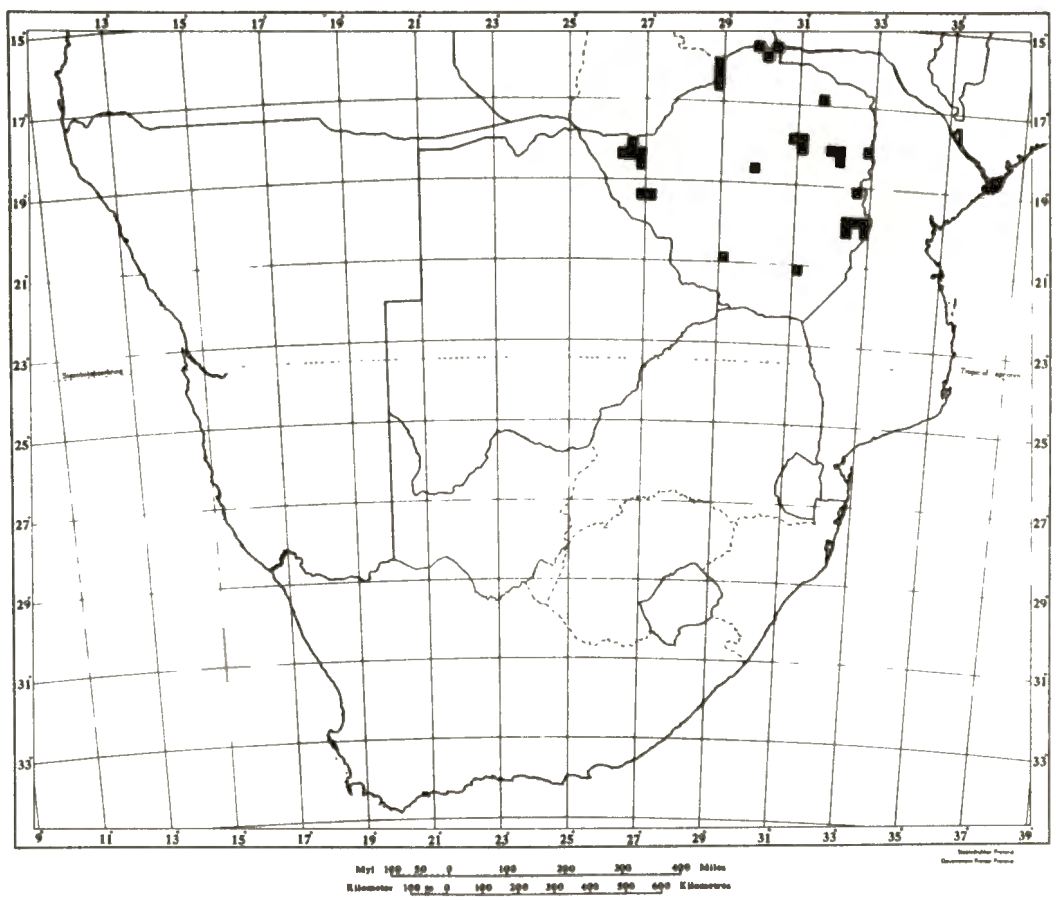


Fig. 65. The distribution of *Hadogenes granulatus* Purcell in southern Africa.

Colour: (Live female specimen from Shamva). Chela very dark reddish brown (7,5R2/3), carapace very dark reddish brown (7,5R2/2), tergites very dark reddish brown (10R2/3), sternites dull yellowish brown (10YR4/3). Alcohol preserved male (SAIMR 1222), chela very dark reddish brown (2,5YR2/4), carapace brownish black (5YR2/2), tergites very dark reddish brown 5YR2/4), sternites brown (10YR4/4).

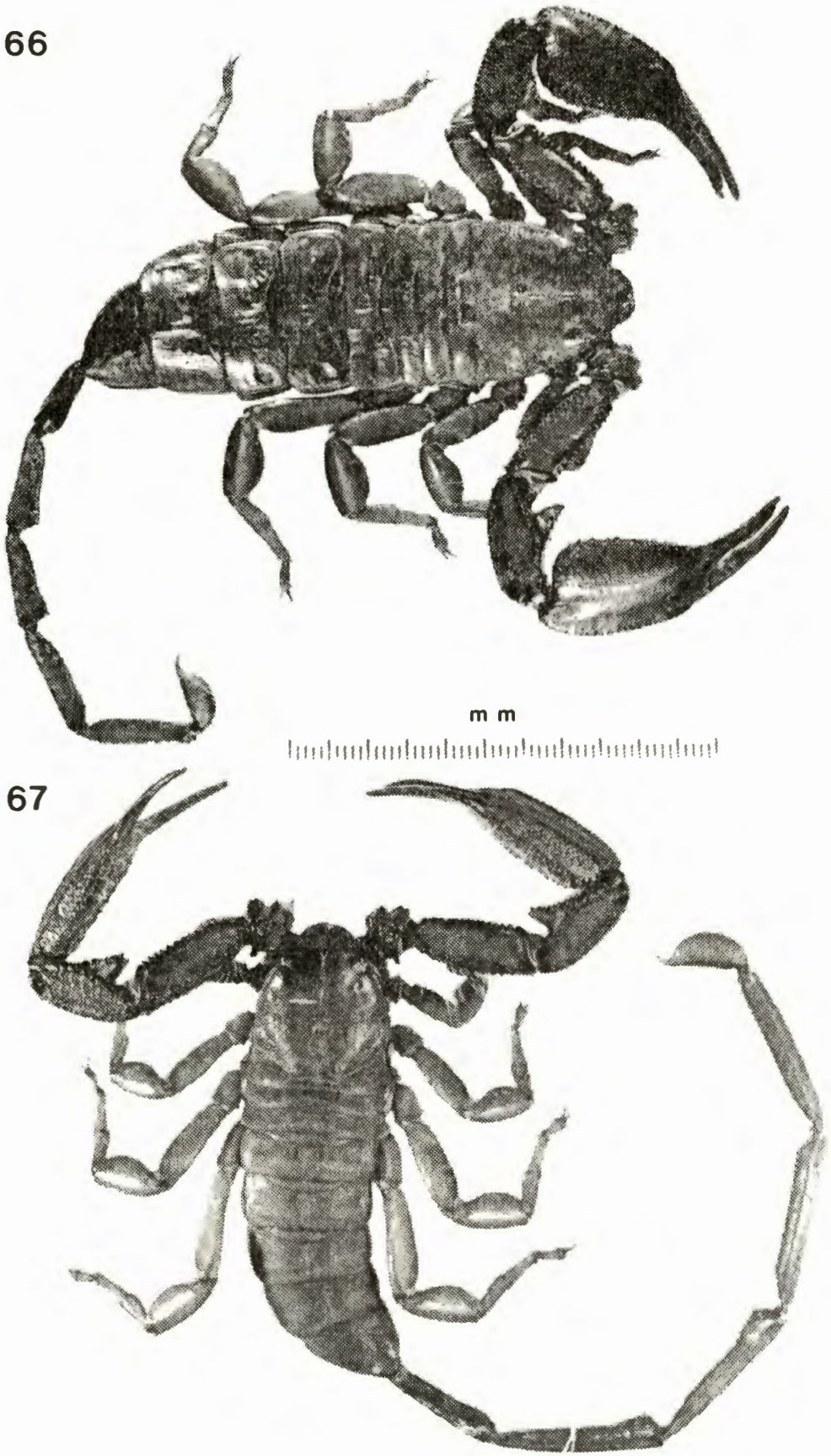
Size: A very large species measuring up to 180mm (♂) and 150mm (♀).

Sexual dimorphism: Male slightly darker, with narrower chela, interface keels of pedipalpal femur and patella less prominent, with divided operculum, higher number of pectinal teeth and with genital papillae. Mesosoma much more slender in male, tergites slightly granular while smooth and shiny in female. Tergite VII of female wider than long but as long as wide in male. Male vesicle large, bulbous and very granular. Metasoma much longer in male.

Description: Carapace: With anterior marginal suture, outline of anterior margin slightly concave, triangular inset keelless, carapace granular all over but coarsely granular mesially. Median ocelli much larger than lateral ocelli.

Pedipalps: Patella with prominent anterior process, dorsal keel of patella absent, movable finger of chela shorter than length of chela along postero-ventral keel.

Trichobothria: Neobothriotaxic major, type C. Total number of trichobothria between 164 and 197 on each palp with an average number of 182. Counts for the three segments are femur 3, patella 81-92 (average 86) and chela 77-107 (average 93).



Figs 66-67. *Hadogenes granulatus* Purcell 1901. 66. Dorsal view of a female from Salisbury. 67. Dorsal view of a male from the upper reaches of the Zambesi River.

Fig. 68. Ventral view of a female *Hadogenes granulatus* Purcell 1901 from Salisbury.

Legs: Femur and patella of all legs with two ventral granular keels and 3:3 spines ventrally on tarsomere II.

Mesosoma: Tergites very finely granular all over in male while shiny in female, last sternite of mesosoma with a prominent distal depression on each side.

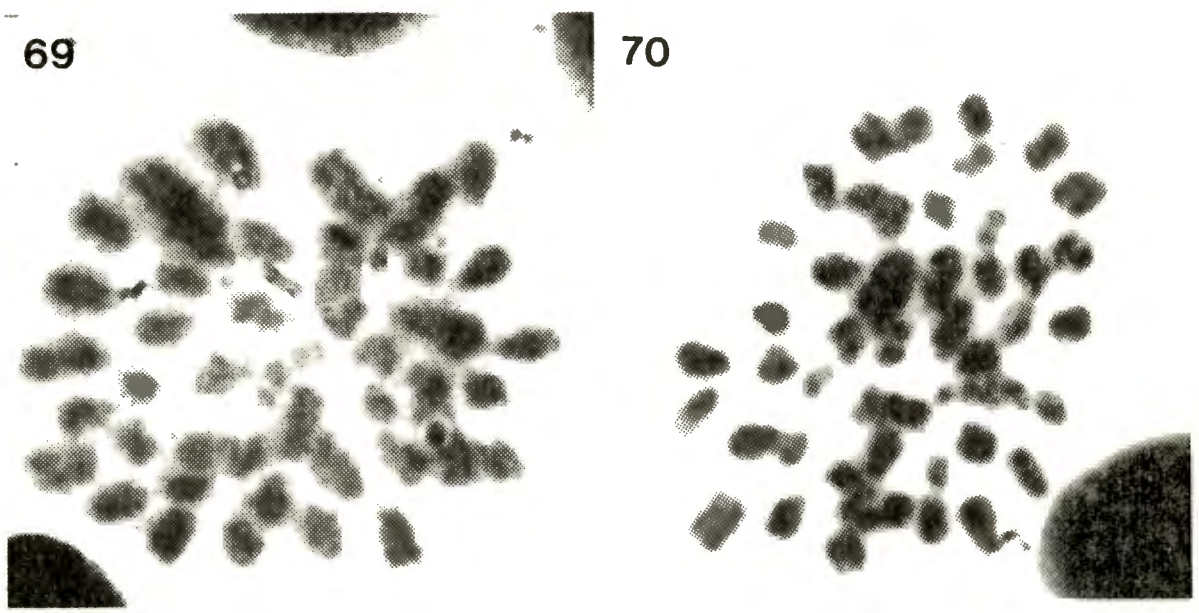
Pectinal teeth: ♂:19-24, ♀:15-19.

Metasoma: Full complement of keels on all segments but dorso-lateral keels of segments II and III without a greatly enlarged terminal granule. Segment I wider than deep posteriorly.

Telson: Male vesicle very long, bulbous and granular.

Measurements: Male, UM/S 193 (Kariba). Carapace anterior width 7,4mm, posterior width 15,8mm, length 15,4mm; chelal postero-ventral keel length 16,7mm, movable finger length 14,8mm. Metasomal segment I, width 3,9mm, length 12,4mm and height 3,1mm, metasomal segment V, 2,6mm wide, 18,8mm long and 3,0mm high. Telson 3,8mm wide, 10,9mm long and 4,0mm high. Total of metasoma, 98mm, and prosoma plus mesosoma 53mm. Female UM/S (Kamatini, Dett). Carapace anterior width 9,5mm, posterior width 20,8mm, length 19,7mm. Chelal postero-ventral keel length 20,5mm and movable finger 18,6mm long. Metasomal segment I, 4,22mm wide, 9,75mm long and 3,50mm high. Segment V, 3,4mm wide, 16,3mm long and 3,4mm high. Telson 3,5mm wide, 10,7mm long and 4,5mm high.

Chromosome number: 2n=96 as determined from preparation of testicular tissue. This count is tentative as insufficient material was seen to enable the bimodal number to be determined with certainty.



Figs 69-70. Chromosome spreads seen in testicular tissue preparation of specimens of *Hadogenes granulatus* from Shamva, Zimbabwe-Rhodesia.

Notes: A specimen from Chikawarawara (UM/S) was difficult to identify as the first metasomal segment resembled that of *H. troglodytes* in that it was narrower than high posteriorly. However, the vesicle shape was distinctly that of *H. granulatus*. In all other specimens from Zimbabwe-Rhodesia, metasomal segment I was wider than high posteriorly in *H. granulatus* and higher than wide in *H. troglodytes*. This species is very distinct and easily recognizable. Its closest relative is *H. taeniurus* Thorell which occurs in southern Angola and Namibia. These species are widely separated by the sandy flats of the Kalahari basin. There are no records of *Hadogenes* species from northern Zambia and it seems unlikely that *H. granulatus* and *H. taeniurus* are geographical variants of a single species connected via Zaïre. Several overseas museums housing big arachnid collections dating back to colonial times were approached for specimens from Zambia and Zaïre but no *Hadogenes* species could be located. Based on the morphological distinctness and the vast geographic isolation, I have decided to accept both species. Live *H. taeniurus* could not be obtained for electrophoretic and chromosomal comparison with *H. granulatus*.

5.2.11 *Hadogenes troglodytes* (Peters), figs 71-76

Ischnurus troglodytes Peters, 1861, p. 513.

Hadogenes betschuanicus Penther 1900, p. 162; see Newlands 1970.

Hadogenes gracilis rhodesianus Hewitt 1935, p. 475; see Newlands 1970.

Hadogenes troglodytes crassicaudatus Hewitt, 1918, p. 157. syn. nov.

Hadogenes troglodytes dentatus Hewitt, 1918, p. 157. syn. nov.

Hadogenes troglodytes letabensis Werner 1933, p. 324. syn. nov.

Hadogenes troglodytes matoppoanus Hewitt, 1918, p. 159. syn. nov.

Type specimens: Peters' types came from Tete, Mozambique and their whereabouts is unknown. Penthers' type of *H. betschuanicus* was a nymph from Botswana and is housed in the Naturhistorisches Museum in Vienna. The type of *H. gracilis rhodesianus* Hewitt came from a locality given as 32km north of the Limpopo River between Messina and Fort Victoria, while *H. troglodytes crassicaudatus* Hewitt was from Serowe and is deposited in the Albany Museum. Hewitt's type specimen, *H. troglodytes dentatus* housed in the Transvaal Museum, was collected at Vliegenpoort in the Thabazimbi district and not from Vliesenpoort in the Magaliesburg district as erroneously stated in the description and subsequent literature. The type of *H. troglodytes letabensis* Werner came from the Letaba Camp, Kruger National Park and is in the collection of the Naturhistorische Museum, Senckenberg. The Umtali Museum, Zimbabwe-Rhodesia houses the types of Hewitt's *H. troglodytes matoppoanus*. The only types not seen were *H. troglodytes crassicaudatus* and *H. troglodytes mattopoanus* but specimens from the type locality areas were examined.

Material examined: SAIMR 7, 136, 433, 807 Waterpoort (2229 DC), SAIMR 69 Serowe (2228 BB), SAIMR 667 Messina (2230 AC), SAIMR 715, 761, 764 Tshipise (2230 CA), SAIMR 734, 735 Nswatugi Cave (2028 BC), SAIMR 741, 742, 743 Kyle Dam (2031 AA), SAIMR 1070 Mutale (2231 AC), SAIMR 1231, 1293 Blouberg (2328 BB), SAIMR 1242, 1294 Mpapuli Location (2230 DC), SAIMR 1243 Zoutpansberg (2230 BB), SAIMR 1334 Princes Hill Estate (2229 DD), TM 622, 627 Blaukop (2229 DB), TM 615-621, 623-626, 628-666 N'Jelele (2230 CA), TM 667-681 Brakrivier (2229CD), TM 101-109, 2149-2152 Gravelotte (2330 DC), TM 1049-1052 Serowe (2226 BC), TM 2114-2121 Great Saltpan (2330 DA), TM 2122-2129 Shaholle (2330 DC), TM 2135-2137 Silwane (2330 DB), TM 2153 Blackhills (2328 BB), TM 2177 Geelhoutkop (2428 AD), TM 2300, 2301 Messina (2230 AC), TM 2355-2404 Canton (2228 DC), TM 5131 Leibzig

(2328 BB), TM 6431 Skelem (2430 AB), TM 4750-4754 Congo (2229 AD), TM 6421 Middlesex (2130 BD), TM 9041 Umzinto (2228 CB), TM 5277, 9473, 9524, 9587 Waterpoort (2229 DC), TM 9494 Tshipise (2230 CA), TM 9527-9530 Oatlands (2328 BC), TM 9602, 9606 Mateke Hills (2131 CC), TM 2182 Potgietersrus (2131 CC), TM 5686-5690, Fort Victoria (2030 BB), TM 5621 Matoppos (2028 BC), TM 9667, 9669 Birchenough Bridge (1932 CD), TM 2286-2294 Sinkukwe Siding (2029 CA), TM Umtali (1932 BA), TM 5162 Leydsdorp (2431 AA), TM 5862 Mica (2430 BB), TM 10481-10485 Percy Fife Nature Reserve (2429 AA), TM 10421 Weipe (2229 BA), TM 10760, 10761 Crimea (2229 DC), TM 10798 Zimbabwe Ruins (2030 BB), TM 10799, 10800 Fort Victoria (2030 BB), TM 10840 Trevenna (2230 CA), TM 682-695 Magaliesberg (2525 AD), TM 5691-5695 Gaborone (2425 DD), NM 8320, 8321, 8322 Umhlali (2031 CA), NM 8326 Zongoro River Bridge (1932 BA), NM 8331 Pafuri (2331 AD), NM 8342 Bangala Dam (2031 CA), NM 8349 Ngondo (2030 AD), NM 9089 Chipinga (2032 BA), NM 8340 Devuli River Bridge (1932 CD), NM 9942 Driefontein (2028 BC), NM 9943 Mtoko (1732 AC). HPC 316 Lobatsi (2525 BA), HPC 328 Gaborone (2425 DB), HPC 5 Malopo Resort (2626 AA), HPC 45 Sheila (2431 AA), HPC 308 Rochdale (2229 CC), HPC 721 Lukin (2229 DD), HPC 726 Trevenna (2230 CA), KNP Shipandane Picket (2331 CB), UM/S Gwanda (2029 CC), UM/S Bulawayo (2028 BA), UM/S Beit Bridge (2229 BB), UM/S Nyamashati River Bridge (1932 BA), UM/S Messina (2229 DD), UM/S Limpopo River (2229 BB).

Distribution: See fig. 71

Colour: (Freshly preserved specimen SAIMR 1358). Pedipalps bright reddish brown (5YR5/8), carapace dark red (7,5R3/6), tergites dark reddish brown (5YR3/3) and sternites yellowish brown (10YR5/6).

Size: Exceptionally large scorpions measuring between 160 and 210mm in length, making these the longest scorpions in the world. Large females have body masses in excess of 20g.

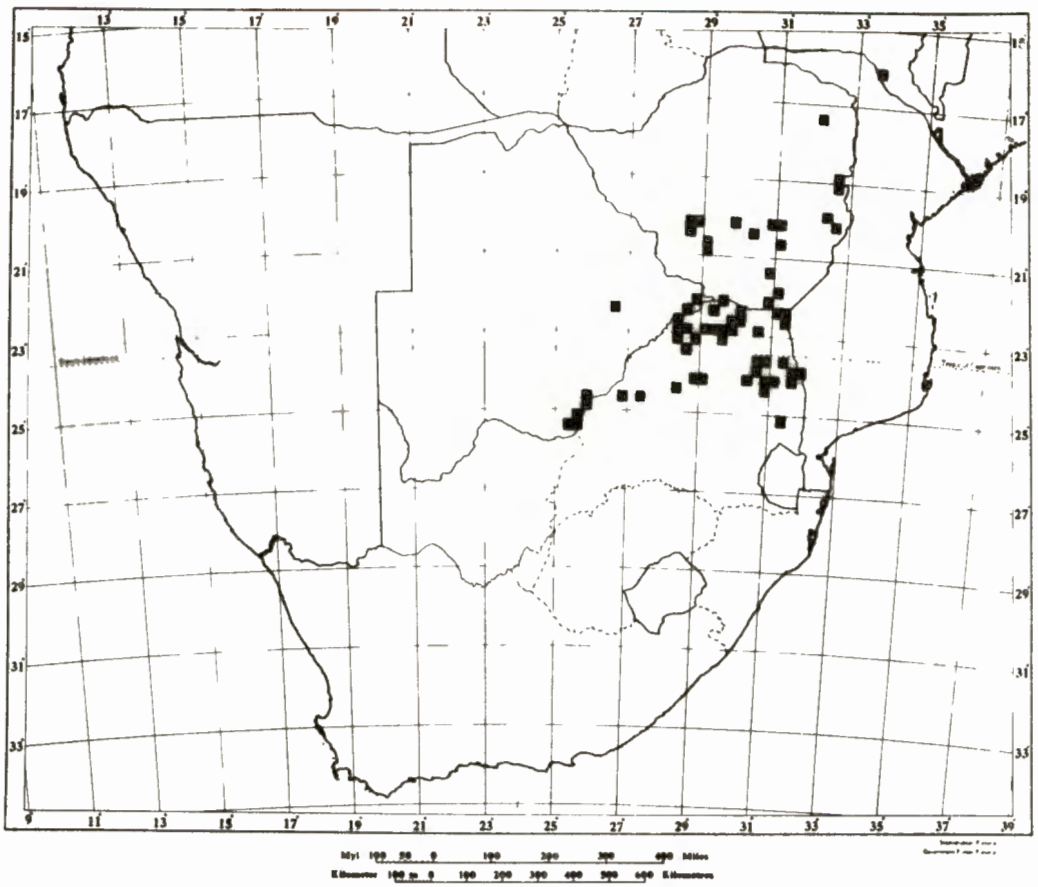


Fig. 71. Map showing the extensive distributional range of *Hadogenes troglodytes* in southern Africa.

Sexual dimorphism: Male with very long metasoma, the dorso-lateral and ventro-lateral keels of which are granular, male chela and mesosoma more slender than those of female. Male with finely granular tergites, higher number of pectinal teeth, divided operculum and genital papillae.

Description: Carapace: Anterior carapace margin straight or very slightly concave, anterior marginal suture present, triangular inset smooth and keelless but slightly longer than wide. Carapace granular all over except for the frontal lobes which are very shiny in the females and of matt appearance in the males. Median ocelli much larger than lateral ocelli. All invaginations present.

Pedipalps: Dorsal surface of femur deeply concave. Keels of all pedipalpal segments very large and prominent and composed of heavily sclerotized granules. Dorsal keel of patella, digital and accessory keels of chela absent or barely discernable. Anterior process of humerus very large, stout and sclerotized. All surfaces finely granular except the dorsal surface of the chela which is weakly reticulated in males. Coxa granular ventrally.

Trichobothria: Neobothriotaxic major, type C. The following counts were obtained: Femur 3, patella 81-95 (average 88) and chela, 77-92 (average 83). The total number of trichobothria per pedipalp varied between 164-188 with an average of 173.

Legs: Coxal endites of legs I and II granular, leg I granular while legs II-IV are less granular. Ventral surface of femur with two granular keels. Ventral surface of patella granular but without distinct keels. Tarsomere II of legs I-IV with 3:3 spines ventrally.

Mesosoma: Tergites of males with very fine granular surface while tergites of females are of a very shiny appearance. Sternites smooth but with a deep oval depression on each side distally. Tergite VII and sternite VII of male as long as wide but wider than long in females.

Pectinal teeth: Males 22-28, females 18-22.

Metasoma: Metasomal segment I positively higher than wide posteriorly. Dorso-lateral keels of females smooth but granular in males. Dorso-lateral keels of segments II and III do not terminate with enlarged spiniform granules.

Telson: Finely granular ventrally in males and weakly granular in females, dorsal profile very straight in both sexes. Vesicle bulbous.

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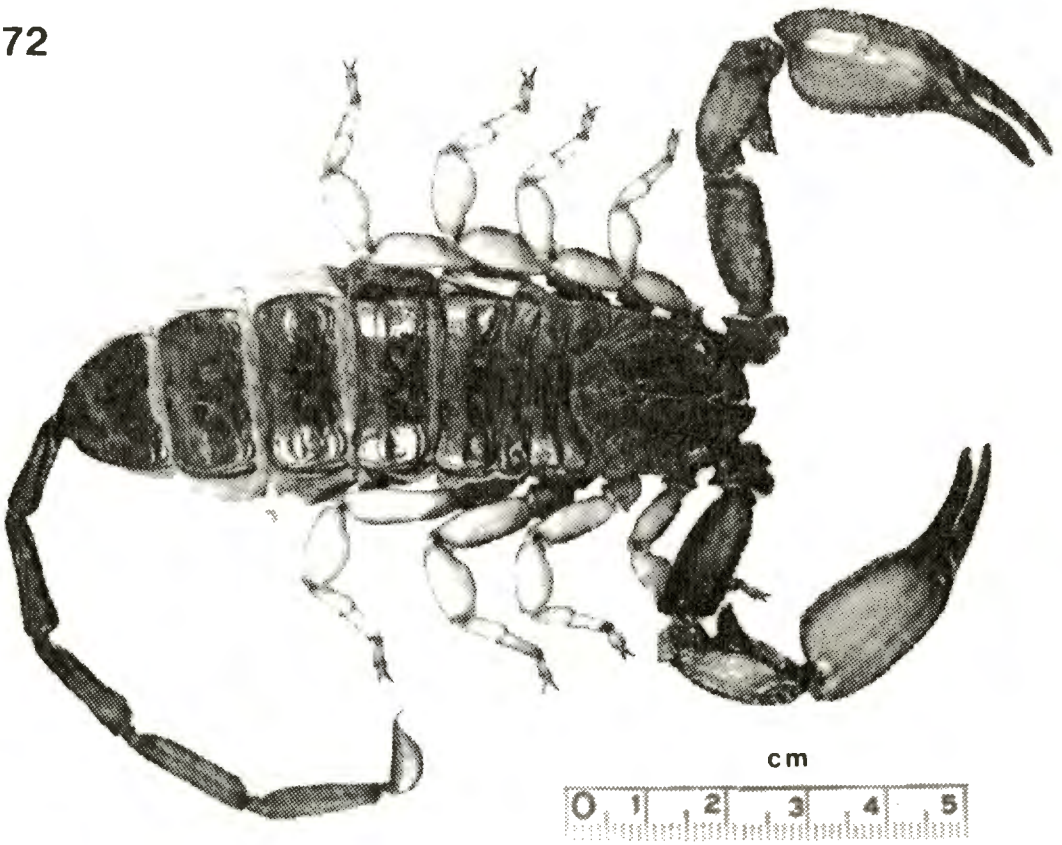

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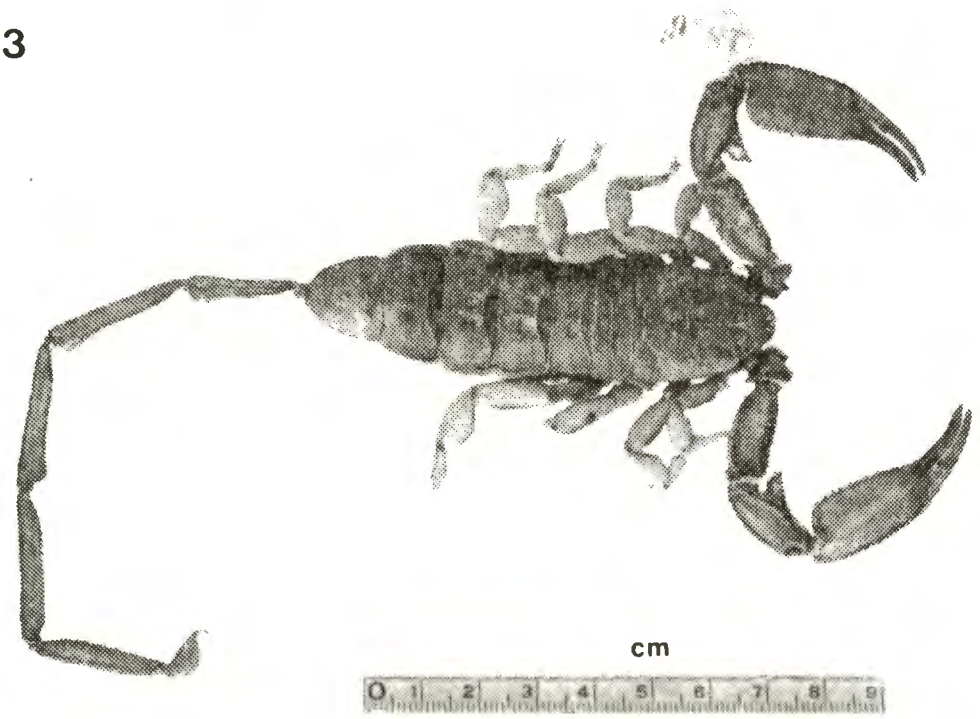


Figs 72-73. *Hadogenes troglodytes* (Peters, 1861). 72. Dorsal view of a female from Waterpoort. 73. Dorsal view of a male from the Zoutpansberg. This specimen (TM 1846) is the longest scorpion ever recorded.

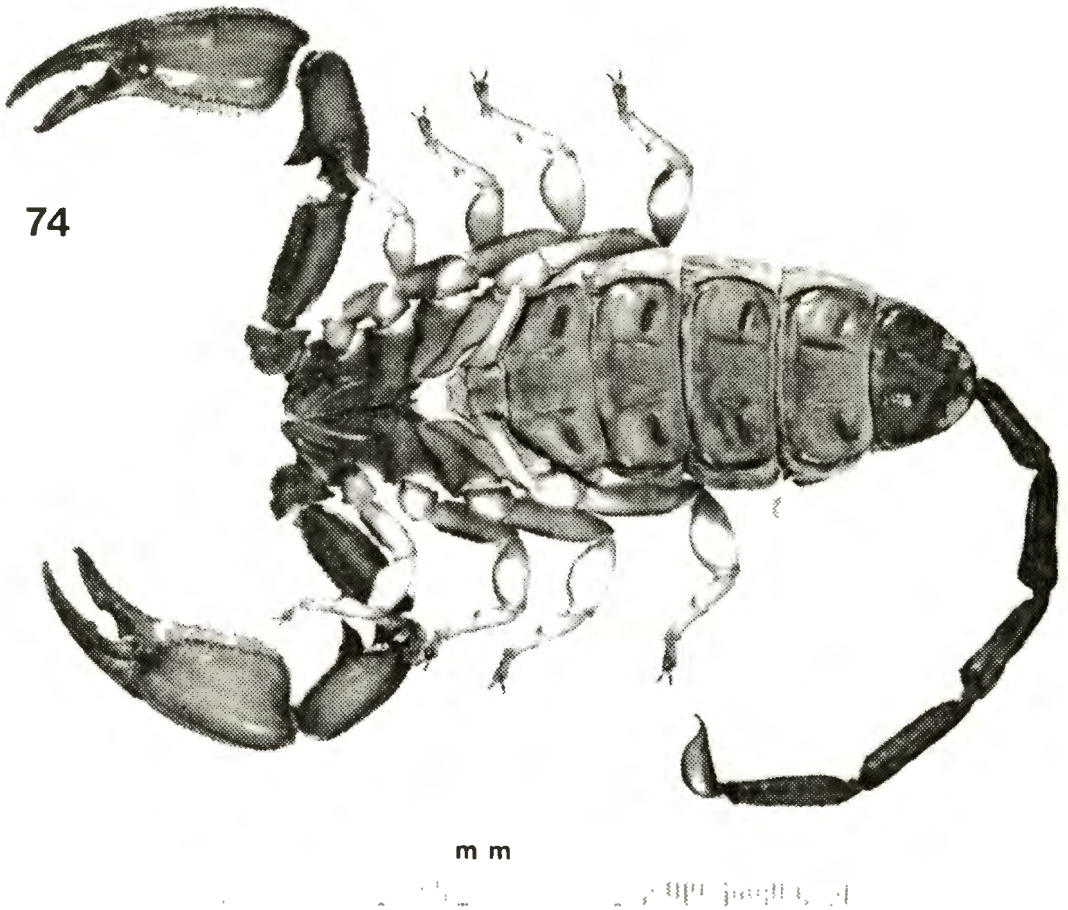
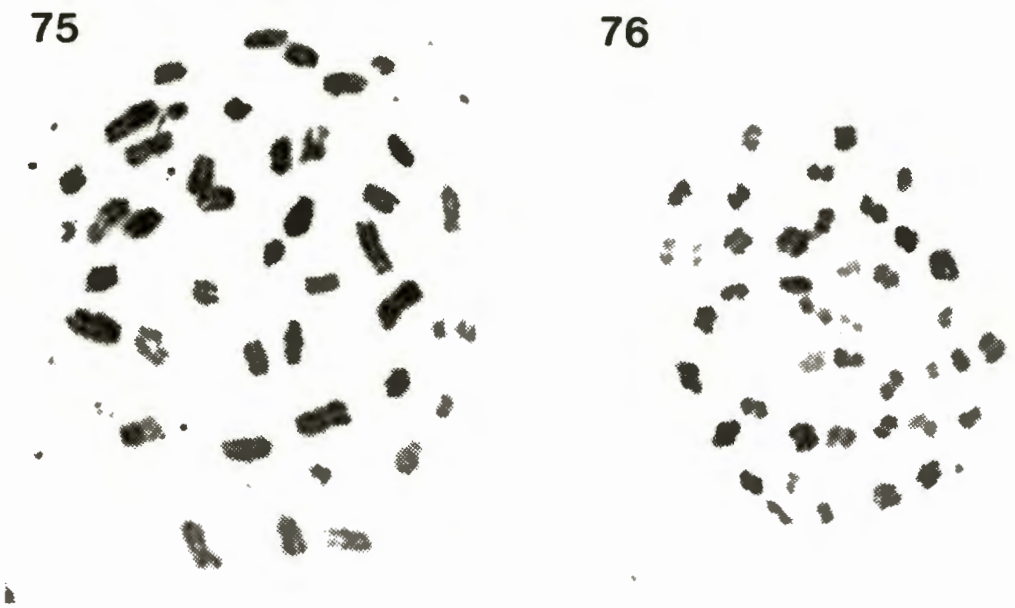


Fig. 74. Ventral view of a female *Hadogenes troglodytes* (Peters) 1861) from Waterpoort.

Measurements: The largest male and female seen were measured. Female (SAIMR 1358): Carapace anterior width, 10,2mm, posterior width, 21,4mm length 20,6mm. Movable finger of chela 19,1mm long, chelal length along the postero-ventral keel 21,9mm, width 13,8mm. Tergite VII, 17,0mm wide, 13,1mm long. Metasomal segment I, 3,6mm wide, 4,9mm high, 13,1mm long. Metasomal segment V, 2,8mm wide, 4,4mm high and 15,9mm long. Telson 11,0mm long, 3,8mm wide and 4,4mm high. Total length of metasoma 89mm. Male (TM 1846): Carapace anterior width 9,9mm, posterior width 20,2mm and length 20,4mm. Movable finger of chela 18,9mm long, chelal length along postero-ventral keel 22,1mm, width of chela 12,1mm. Tergite VII 14,4mm wide and 14,4mm long. Metasomal segment I, 3,8mm wide, 5,2mm high and 19,9mm long. Metasomal segment V, 2,5mm wide, 4,5mm high and 22,2mm long. Telson 10,4mm long, 3,7mm wide and 4,6mm high.

Chromosomes: Specimens from Princes Hill and Mpapuli location consistently yielded chromosome counts of 2n=84. (testicular tissue only).



Figs 75-76. The chromosomes obtained from testicular preparations of northern Transvaal specimens of *Hadogenes troglodytes* (Peters).

Notes: The Transvaal Museum has a very comprehensive collection of this species and this has made it possible to map the distribution with reasonable accuracy as well as to correlate morphological features with geographic location. Hewitt described several "varieties" which have come to be accepted as subspecies over the years. Whether Hewitt meant subspecies or variety we shall never know but in all cases, they are in fact the latter in my opinion. Although the type of *H. troglodytes crassicaudatus* Hewitt 1918 could not be examined, specimens collected in the Tuli Block, Botswana which is near Serowe, were examined and these were in my opinion typical of *H. troglodytes troglodytes* from the Zoutpansberg district. There is probably no break in gene flow between the northern Transvaal populations and the

Serowe populations. According to Hewitt, this variety, based upon a single specimen, has a shorter metasoma and a more rounded first metasomal segment than the typical form. In *H. troglodytes* considerable individual variation in the proportions of the metasomal segments has already been demonstrated (Newlands, 1970).

The variety *H. troglodytes matoppoanus* Hewitt 1918 was said to differ from the typical form in that it lacked granulation on the ventral and lateral vesicle surfaces. In all species of the genus, this characteristic differed at the individual level and when used as the sole distinguishing feature of a new taxon, the validity of the latter must be suspect. Only one of Hewitt's 1918 varieties was significantly different from the typical form, viz *H. troglodytes dentatus*. This "variety" based on a single male from Vliegenpoort near Thabazimbi, differs in being much smaller than the typical male specimens from the northern Transvaal. The legs are the same colour as the tergites and the ventral and dorsal metasomal keels are certainly more granular. As far as I can judge from the geomorphology of the area, there is no break in the gene flow between this "variety" and the typical form in the northern Transvaal. Accordingly, these differences may be clinal which will be proved only if intermediate specimens can be collected.

Werner (1933) described a new subspecies *H. troglodytes letabensis* from a female collected at Letaba Rest Camp in the Kruger National Park. The specimen was examined and found to fit Werner's description accurately but whether it is a valid subspecies is certainly very questionable. In my opinion it does not differ from northern Transvaal specimens of the same size.

The above decisions are based solely upon morphological considerations and it would not be surprising if a detailed study revealed that *H. troglodytes* is a species complex

consisting of several sibling species. The morphology of the specimens seen suggests that there are clinal differences over the distritubional range. There are also cases where gene flow has been interrupted as in the case of the Blouberg, Zoutpansberg district. The Blouberg is separated from the Zoutpansberg by a 15km sandy plain. Specimens in the Transvaal Museum from Blouberg and Zoutpansberg are morphologically identical but the possibility exists that they are sibling species as in the case of *H. lawrencei* and *H. tityrus*. The same may prove to be the case in *H. troglodytes crassicaudatus*. In this case gene flow may occur along the Chawapong Hills which stretch between Serowe and the Tuli Block. As gauged from topographical maps, the Chawapong Hills appear to be disjunct and badly erroded but as I have not seen them their suitability as habitats for these scorpions is conjectural.

5.2.12 *Hadogenes gracilis* Hewitt, figs 77-82
H. gracilis Hewitt, 1909 p. 41-42.

Type specimens: Collected at De Kroon near Brits (2527 DB) and housed in the Transvaal Museum (♂) TM 1832 (♀) TM 1833.

Material examined: SAIMR 189 Rosslyn (2528 CA), SAIMR 614 Garankuwa (2528 CA), SAIMR 1051-1053 Vasval (2527 DA), SAIMR 1106-1121, 1165 Brits (2527 DB), TM 833-854, 933-1021, 1025-1029, 1037-1046, 1832, 4775 De Kroon (2527 DB), TM 855-864, 1023, 1024, 1031 Rosslyn (2528 CA), TM 865, 866, 1022 Bon Accord (2528 CA), TM 867-872, 879, 880 Swartkoppies (2527 DB), TM 873-878 Samboklokasie (2527 DB), TM 881-932, 1047, 1048 Bleskop (2527 CB), TM 1033-1036 Wolhuterskop (2527 DC).

Distribution: See fig. 77.

Colour: (Alcohol preserved type specimens). Pedipalps dark red (7,5R3/6), carapace and tergites dark reddish brown

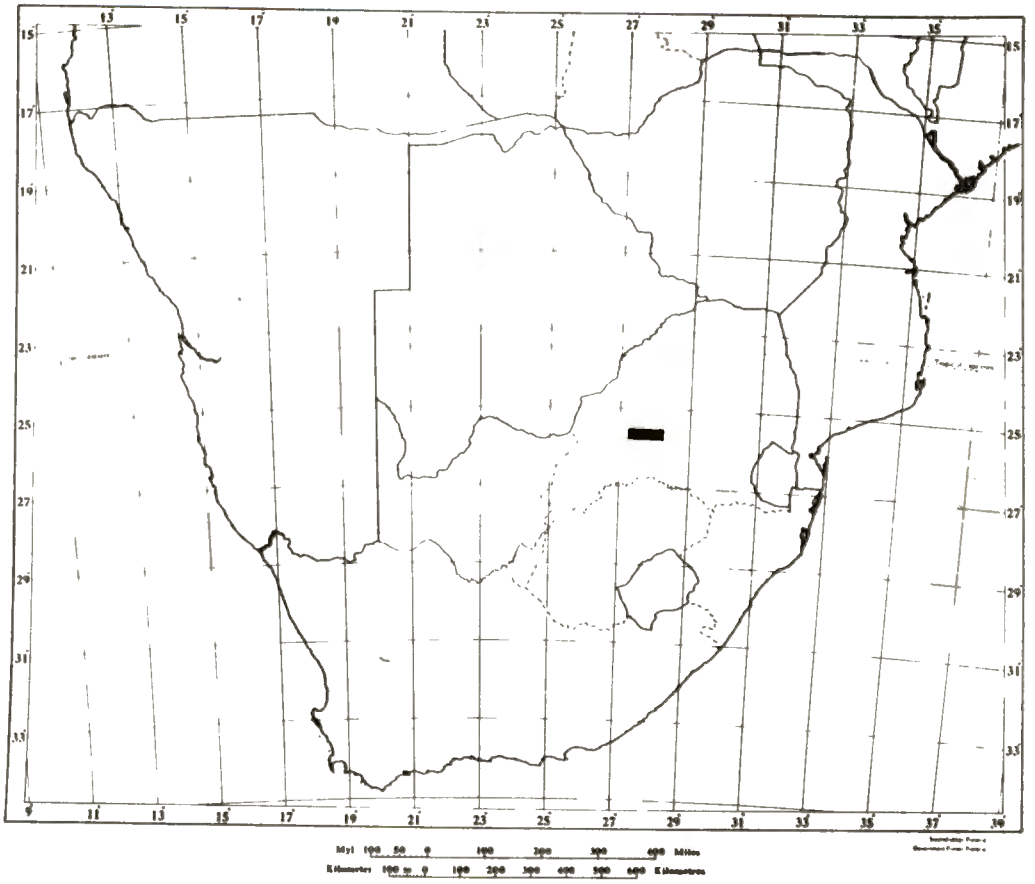


Fig. 77. Map showing the very restricted distribution of *Hadogenes gracilis*. Although this species is found in the same quarter degree square as *H. gunningi* (see fig. 55) these species have never been found sympatrically.

(2,5YR3/6) and sternites light reddish brown (5YR5/6).

Size: Large scorpions, the types measuring 134mm (♀) and 194mm (♂). Other males examined measured between 148 and 190mm.

Sexual dimorphism: Male mesosoma very slender, tergite VII and sternite VII longer than wide in male and wider than long in female. Male metasoma considerably elongated. Chela of male narrower proximally than that of female. The male has a higher number of pectinal teeth, genital papillae and a divided genital operculum.

Description: Carapace: Anterior marginal suture absent, anterior margin concave with large keelless triangular inset which is set well back. Finely granular over whole surface except mesially where the granulation is coarser. All invaginations present.

Pedipalps: Interface pedipalp keels prominent and composed of large heavily sclerotized granules. Anterior dorsal keels of femur composed of 14-15 large granules. Patella with large anterior process. All surfaces of pedipalps finely granular. Movable finger longer than length of chela measured along the postero-ventral keel.

Trichobothria: Neobothriotaxic major type C. Femur 3, patella 86-106 (average 94), chela 83-95 (average 89). Total number of trichobothria per pedipalp 174-204 (average 185).

Legs: Granular ventral keels on femur and patella. Tarsomere II with 3:3 spines on all legs.

Pectinal teeth: ♂ 18-20; ♀ 16-18.

Mesosoma: All tergites evenly and very finely granular in male. Sternites smooth and shiny in male. In female, tergites and sternites smooth and shiny.

Metasoma: Segment I narrower than high in female, dorso-lateral keels of segments II and III each terminate posteriorly with an enlarged spiniform granule. Keels weakly granular. In males all segments are extremely long and slender. Metasoma averages 8 times as long as the carapace in males.

Telson: In females, smooth and shiny while finely granular in males.

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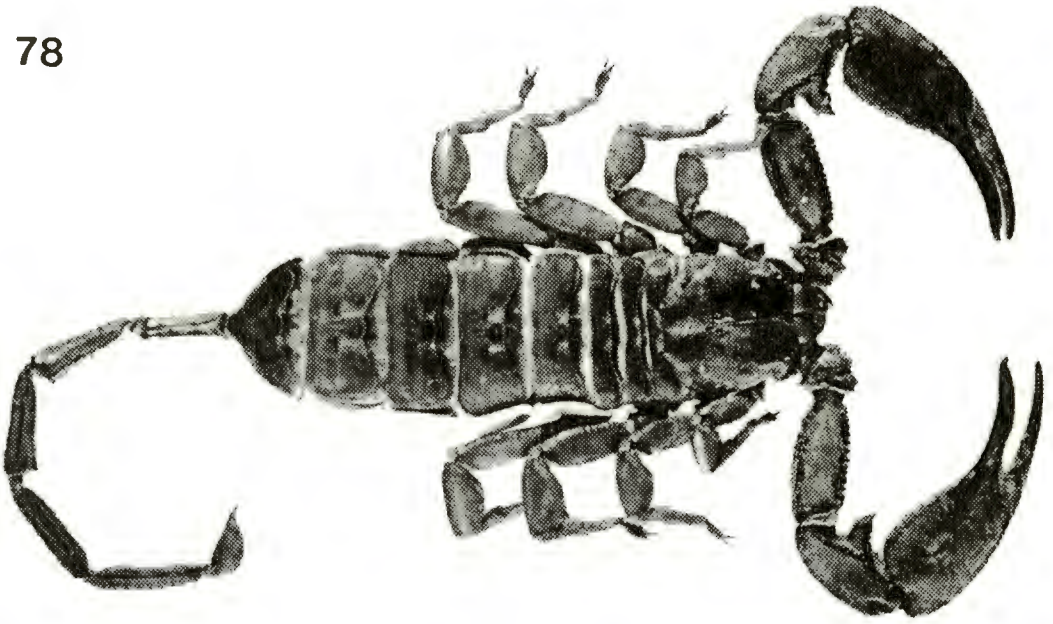

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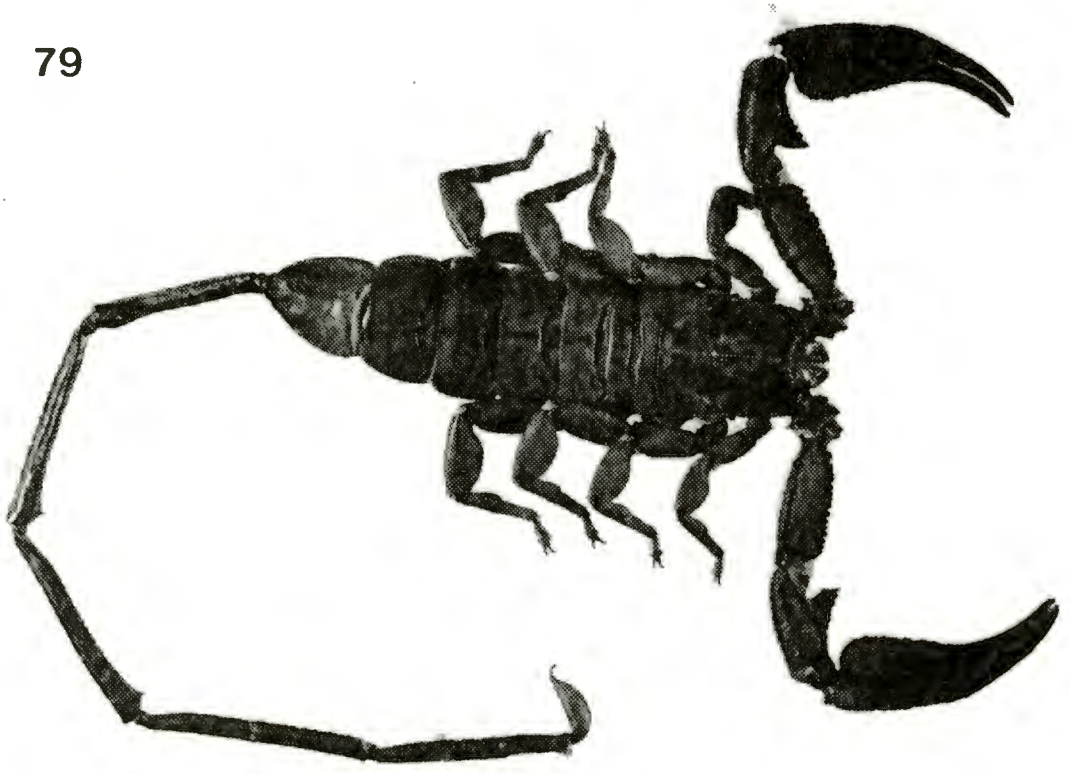


Figs 78-79. *Hadogenes gracilis* Purcell 1909. 78. Dorsal view of the female type specimen (TM 1833). 79. Dorsal view of the male type specimen (TM 1832).

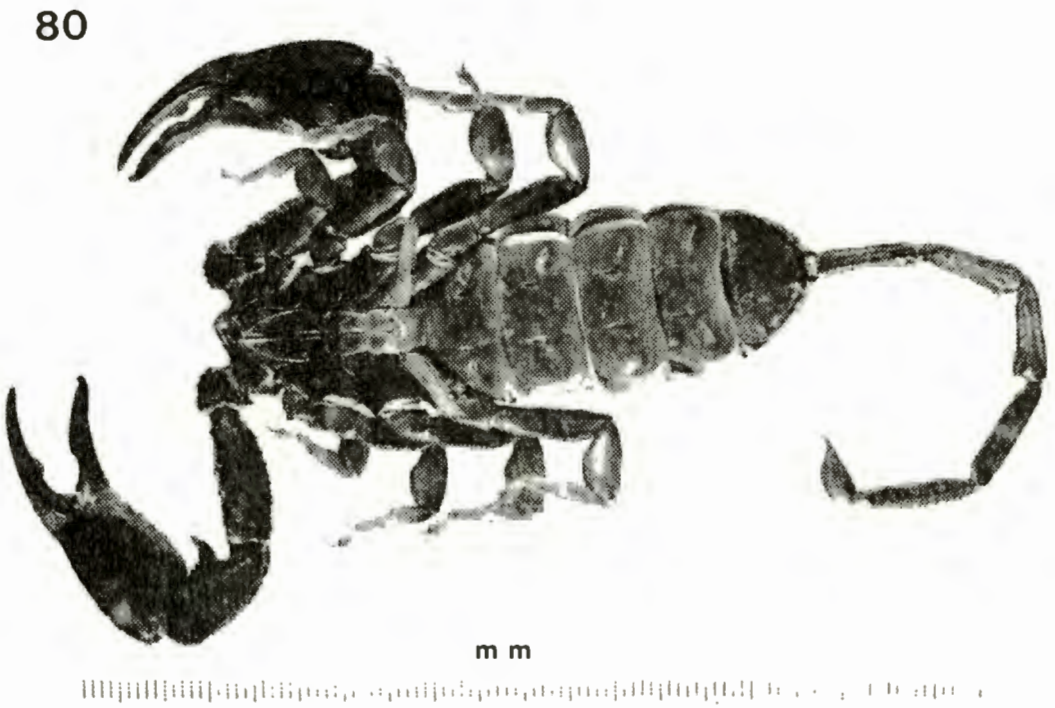
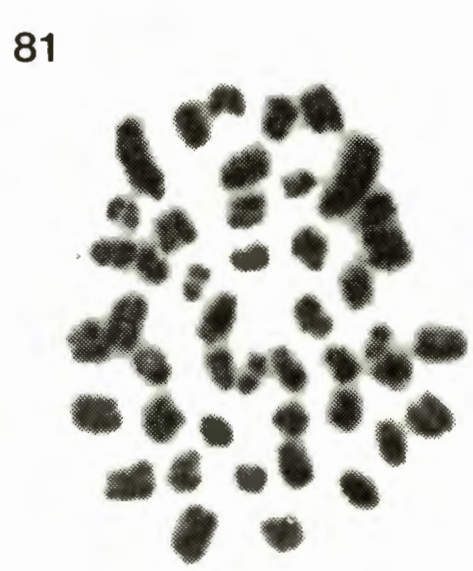


Fig. 80. Ventral view of the female type of *Hadogenes gracilis* Purcell (TM 1833).

Measurements: Types: Female TM 1833. Carapace anterior width 7,8mm, posterior width 15,8mm, length 16,1mm. Movable finger of chela 17,5mm, chelal length along the postero-ventral keel 15,7mm, chela width 10,4mm. Metasomal segment I, 2,9mm wide, 3,7mm high 10,0mm long, metasomal segment V, 2,2mm wide, 3,1mm high and 12,3mm long. Telson 9,3mm long, 2,8mm wide and 3,4mm high. Male TM 1832. Carapace anterior width 7,2mm, posterior width 15,3mm, length 15,2mm. Movable finger of chela 16,2mm, chelal length along the postero-ventral keel 15,7mm, chela width 8,6mm. Metasomal segment I, 2,7mm wide, 3,9mm high and 20,4mm long. Metasomal segment V, 1,9mm wide, 2,5mm high and 23,2mm long. Telson 9,7mm long, 2,5mm wide and 3,0mm high. Total length of metasoma 132mm.

Chromosomes: The testicular tissue of two males from Brits

yielded counts of 2n=80.



Figs 81-82. Chromosome spreads from the testicular tissue of specimens of *Hadogenes gracilis* Hewitt from Brits.

Notes: In the specimens examined, the degree of granulation varied slightly as did the exact ratios of the segments relative to each other. However, as the distribution is relatively restricted, the specimens seen were all easily identified by virtue of the above characteristics. A far more complex problem was exposed when the described subspecies were examined. Three subspecies of *H. gracilis* have been described, one of which, *H. gracilis rhodesianus* Hewitt has already been synonymised with *H. troglodytes* (Peters) Newlands, 1970. Hewitt's types of *H. gracilis rhodesianus* (TM 5618-5619) were re-examined and the synonymy was confirmed upon morphological grounds. In 1918, Hewitt described *H. gracilis namaquensis* and in the concluding remarks of the species description said that Purcell was of the opinion that *H. gracilis namaquensis* was conspecific with *H. phyllodes* Thorell. Unfortunately the types of *H. phyllodes* and *H. gracilis namaquensis* could not be obtained for examination.

A third subspecies, *H. gracilis fluvialis* was described by Lawrence (1955) based upon one male and two females. Now that a very large sample of specimens from the N.W. Cape have been examined and compared I am fairly confident that the subspecies *H. gracilis namaquensis* and *H. gracilis fluvialis* are conspecific from a morphological point of view as well as electrophoretically (figs 110-111) and on account of chromosome number. These subspecies are in turn conspecific with *H. phyllodes* (see 5.2.13). Numerous specimens of *H. phyllodes* from various localities in the north western Cape were examined and found to have a chromosome number of 2n=36 while *H. gracilis* specimens from Brits yielded chromosome counts of 2n=80. The subspecies *H. gracilis namaquensis* and *H. gracilis fluvialis* are separated geographically from the typical form by more than 800 kilometres of plateau.

5.2.13 *Hadogenes phyllodes* (Thorell), figs 83-88
Ishnurus taeniurus phyllodes Thorell, 1877 p. 254-258.
Hadogenes phyllodes Hewitt, 1918 p. 163
H. gracilis namaquensis Hewitt, 1918 p. 162 syn. nov.
H. gracilis fluvialis Lawrence, 1955 p. 222-223 syn. nov.

Type specimen: Allegedly housed in the Goteborg Museum, Sweden. The museum would not make their type specimens available for study in South Africa. Type locality unknown, but according to Lawrence (1955), the specimen was probably from Namaqualand.

Material examined: SAIMR 70, 71, 72, 317, 318 N. Garies (3017 BD), SAIMR 73, 1215, 1216, 1221, 1351 N. Steinkopf (2917 BB), SAIMR 780 Sandmund (2518 CA), SAIMR 963, 964, 965, 1239-1241, 1251 Keimoes (2820 DB), SAIMR 1103, 1162, 1170, 1244-1246 Louisvale (2821 CA), SAIMR 1123, 1054-1056 Limewell (2822 DC), SAIMR 1156-1161 Keimoes (2820 DB), SAIMR 1163, 1237, 1238 Leerkrans (2821 BC), SAIMR 1164, 1057 Zeekoebaard Nek (2922 AB), SAIMR 1235 Springbok (2918 DA), SAIMR 1256 Upington (2821 AC), SAIMR 1112 Ezelsfontein

(2917 DA), SAIMR 1145 Brakfontein (2917 DA), TM 9415 N.E. Pofadder (2919 AB), TM 9498 Marydale (2922 AA), TM 9499 W. Kenhardt (2920 BD), TM 1059, 1060 Kraaikluft (2718 BC), TM 1061 Narudas (2718 BD), TM 9523 Eendoorn (2818 DD), TM 9400 Spektakel Pass (2917 DA), TM 9495 S. Kenhardt (2921 AC), TM 10153-10156 Kamieskroon (3017 BD), TM 10162-10167 Bitterfontein (3118 AB), TM 10001-10004 N. Diemansputs (2921 DA), TM 10407 Hondeklipbaai (3017 AD). NM Steinkopf (2917 BA), NM 11351 Horingsgat (3018 AC), SAM C57 Kamieskroon (3017 BD), SAM Garies (3017 DB), SAM Tsabis (2215 DB), SAM Spitzkop (2115 CC), SAM Concordia (2717 DB), SAM Klipfontein (2917 AB), SAM Narsep (2818 DC), SAM Port Nolloth (2916 BB), SAM Bitterfontein (3118 AB), SAM Kamieskroon (3017 BB), SAM Steinkopf (2917 BB), SAM Namies (2919 AC), AM Bitterfontein (3118 AB), AM Rietpoort (3026 AA), AM Marydale (2922 AC), AM Onseepkans (2819 CC), HPC 341 N.N.E. Upington (2821 AD).

Distribution: See fig. 83.

Colour: Two main colour varieties through the distribution range typical examples of which are as follows: The light form typical from Springbok in Namaqualand to Upington. Coloration of freshly preserved specimen (SAIMR 1244) from Upington: Pedipalps dark reddish brown (5YR3/6), carapace dark reddish brown (5YR3/6), tergites brown (7,5YR4/4), sternites brown (10YR4/4) and legs bright yellowish brown (10YR6/8). The dark form characteristic of the more southern parts is typified in a freshly preserved specimen from the farm Limewell in the Hay district (SAIMR 1054). Pedipalps very dark reddish brown (10R2/3), carapace reddish black (10R2/1), tergites very dark reddish brown (10R2/2), sternites dark reddish brown (10R3/3) and legs very dark reddish brown (10R2/3).

Size: A very large species measuring from 130 to 170mm in length.

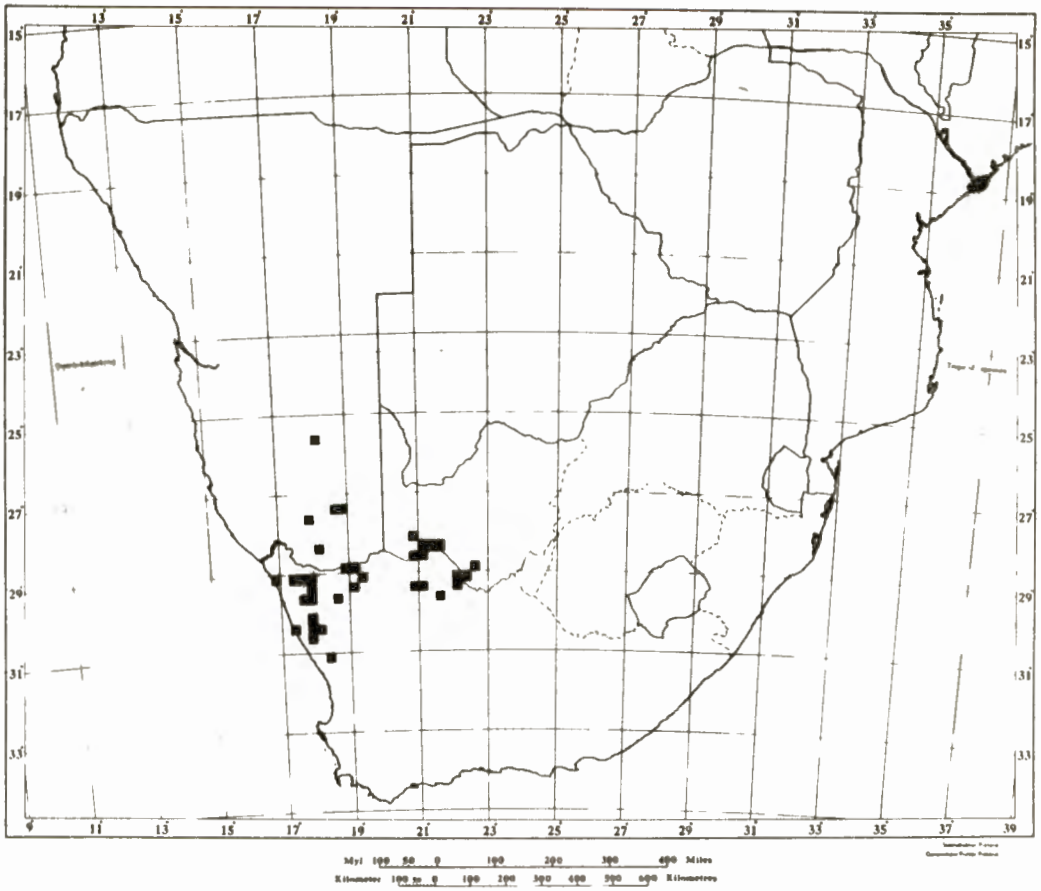


Fig. 83. Map showing the extensive distributional range of *Hadogenes phyllodes* Thorell.

Sexual dimorphism: Chela of male slightly more slender than that of female, carapace of male granular while that of the female is sparsely granular except immediately anterior to the median ocelli where the granulation is fairly dense. Male mesosoma more slender than that of female, male metasoma more than six times carapace length while metasoma of female roughly four times the carapace length. Male with greater number of pectinal teeth, divided genital operculum and genital papillae.

Description: Carapace: Anterior carapace margin slightly concave, anterior marginal suture absent, in some males antero-lateral, antero-median and postero-median invaginations obsolete or difficult to detect. Median ocelli much larger than lateral ocelli. Triangular inset distinctly wider than long.

Pedipalps: Dorsal surface of chela reticulated in peripheral areas in females and either reticulated or granular in males. All other interkeel surfaces granular. Dorsal keel of patella present in vestigial form in some females but absent in males. Anterior process of patella very large. Movable finger of the chela much shorter than length of chela measured along the postero-ventral keel.

Trichobothria: Neobothriotaxic major type C. Trichobothrial counts of nine specimens were as follows: femur 3, patella 71-94 (average 81), chela 63-87 (average 74) and a total number of trichobothria of 141-184 (average 158) per pedipalp. The number of trichobothria are quite variable in this species, even amongst specimens from the same locality.

Legs: Tarsomere II ventrally with 3:3 spines on all legs. Femur and patella of all legs with a pair of granular keels on venter.

Mesosoma: Tergites of male very finely and evenly granular imparting a matt appearance to the sclerites. In female tergites are smooth. Last tergite and sternite of female much wider than long while marginally longer than wide in the males.

Pectinal teeth: ♂:16-18, ♀:14-16.

Metasoma: Somewhat variable, depending upon geographic factors. Specimens from the Gordonia, Kenhardt and Namaqualand districts south of Nababeep have a spine-like terminal granule on the dorso-lateral keel of metasomal segments II and III. In specimens from the southern Richtersveld, parts of Hay and Postmasburg districts, these metasomal terminal granules are either weakly spiniform or absent and generally vary in prominence amongst

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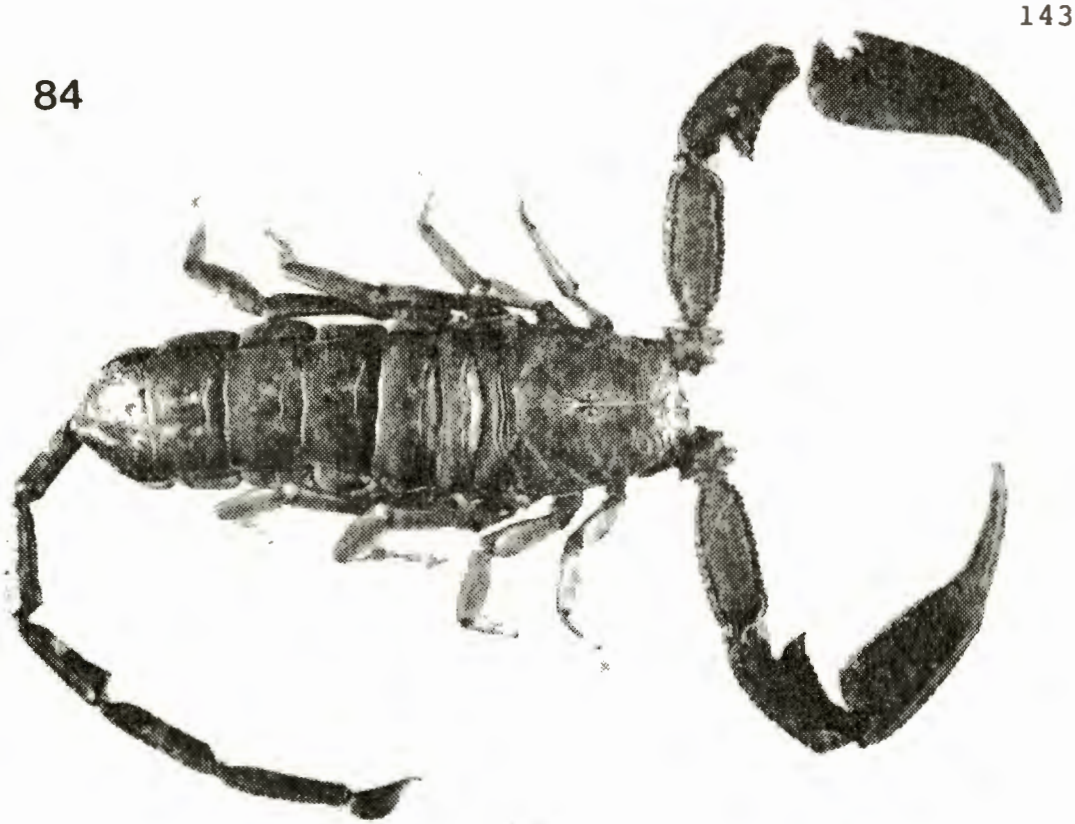

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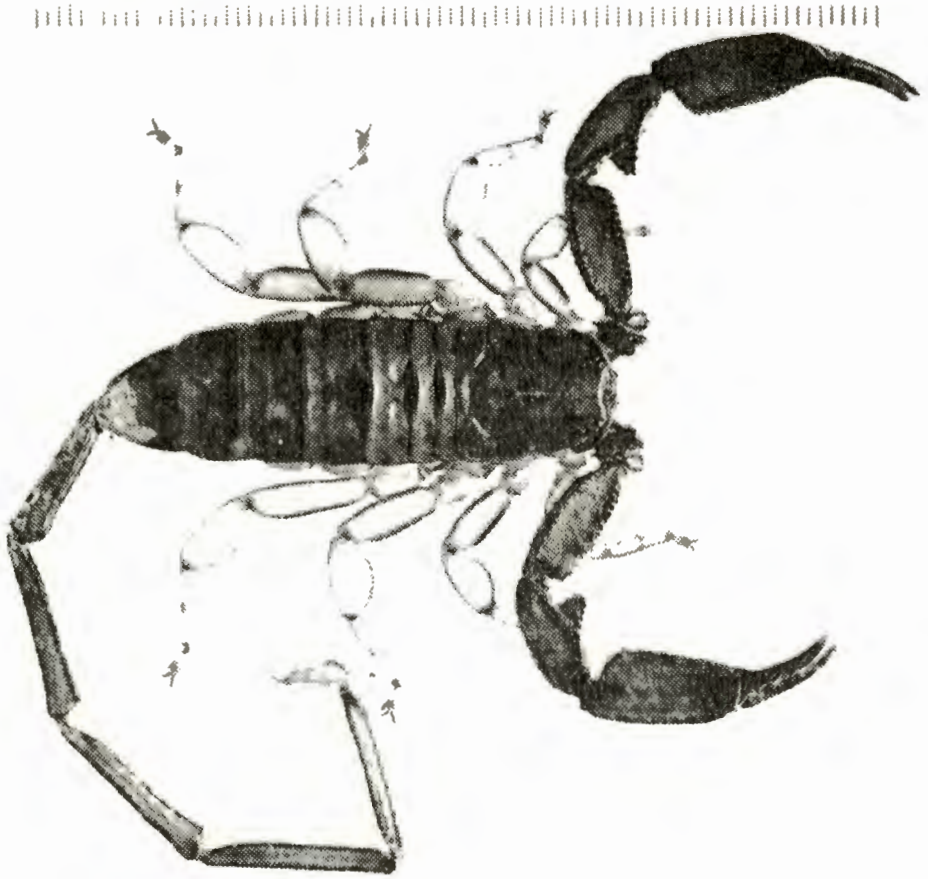

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Figs 84-85. *Hadogenes phyllodes* Thorell 1877. 84. Dorsal view of a female from the Namaqualand District. 85. Dorsal view of a male from Keimoes.

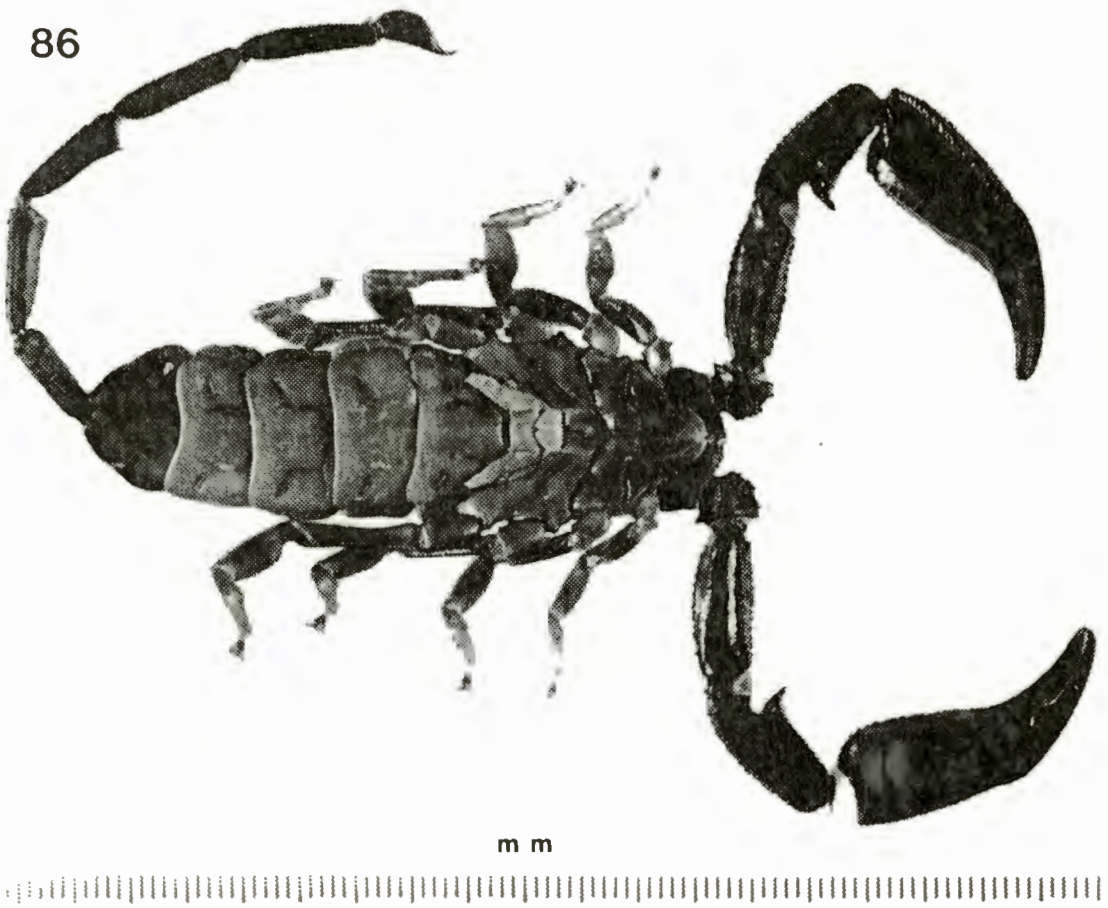
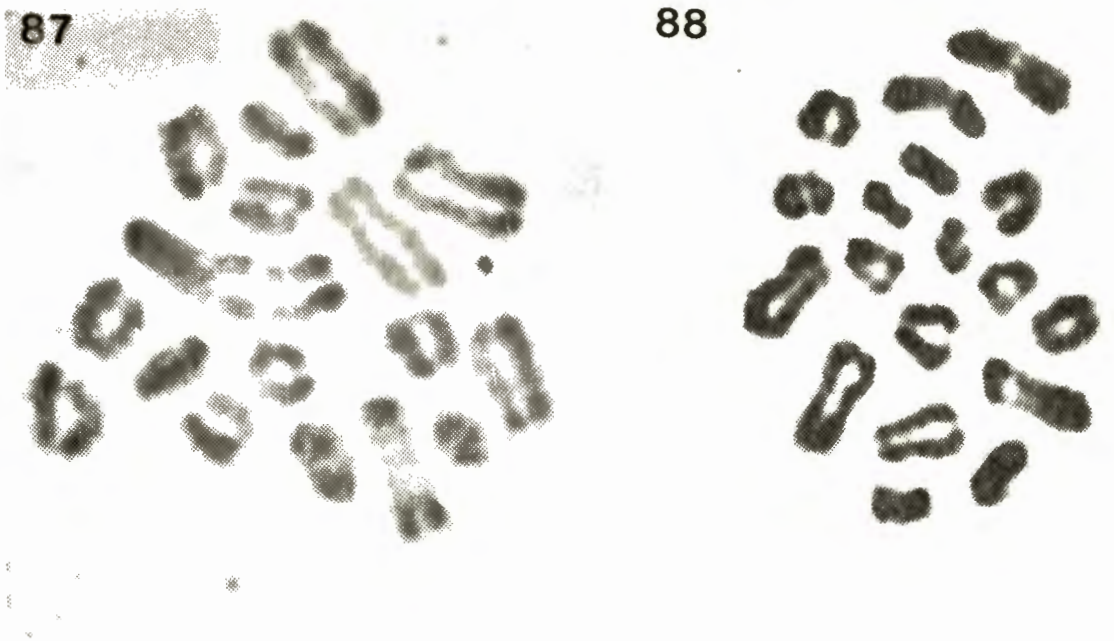


Fig. 86. Ventral view of a female *Hadogenes phyllodes* Thorell from the Namaqualand District.

individuals from the same location. The metasomal segments are very long and slender with distinctly granular keels in all male specimens. In females, the metasomal keels are weakly granular and the metasoma is rather short.

Telson: The straightness or slight concavity of the vesicle upper margin varies at an individual level as well as geographically with specimens from the western half of the distributional range tending to have a concave upper vesicle margin. The vesicle is weakly granular in most males and smooth in females.

Chromosomes: Testicular tissue of this species regularly yielded chromosome counts of 2n=36. Occasional polyploid spreads yielding 2n=72 were also seen (figs 87-88).



Figs 87-88. Chromosome preparations obtained from the testicular tissue of a *Hadogenes phyllodes* (Thorell) from Spektacle Pass in Namaqualand.

Measurements: Female, SAIMR 1244; carapace anterior width 8,8mm, posterior width 16,9mm and length 16,2mm. Length of chelal movable finger 16,7mm, length of chela along postero-ventral keel 18,0mm and width 9,7mm. Metasomal segment I, 3,5mm wide, 3,6mm high and 9,9mm long. Metasomal segment V, 2,2mm wide, 3,1mm high and 14,6mm long. Telson 8,6mm long, 3,1mm high and 2,7mm wide. Male SAIMR 1239; carapace anterior width 8,0mm, posterior width 15mm and length 14,9mm. Movable finger of chela 14,0mm long, length of chela along postero-ventral keel 16,7mm and width 8,3mm. Metasomal segment I, 3,0mm wide, 3,7mm high and 15,0mm long. Metasomal segment V, 1,6mm wide, 2,9mm high and 21,8mm long. Telson 8,3mm long, 3,5mm high and 2,7mm wide.

Notes: The two subspecies, *H. gracilis namaquensis* Hewitt and *H. gracilis fluvialis* Lawrence have been placed in tentative synonymy with *H. phyllodes* for the following reasons. The morphological grounds oiginally used to distinguish the

subspecies from the typical form, viz the profile of the vesicle, granularity of the vesicle, presence of terminal spiniform granules on the dorsal keels of metasomal segments II and III and the granularity of the pedipalpal patella have proved to vary at the individual level as well as with geographic location. Furthermore, specimens collected from the type localities of the two subspecies were found to differ from *H. gracilis* sufficiently to be regarded as specifically distinct in terms of their chromosome counts. However, *H. gracilis namaquensis* and *H. gracilis fluvialis* did not prove to differ from each other in terms of their chromosome number and electrophoretic banding patterns. That *H. phyllodes* bears little or no relation to *H. gracilis* is clear from the chromosome numbers, morphological, geographical and electrophoretic considerations. Careful comparison of electrophoretogram samples 3-12 (fig. 110) clearly show that *H. gracilis* and the N.W. Cape specimens of *H. phyllodes* bear no relationship. The characters used to separate these subspecies from *H. gracilis* bear no relation to those which would separate them from *H. phyllodes* and that while there are minor differences between the bands of specimens from the N.W. Cape area, these band differences are certainly not more than the individual band variations seen between duplicate specimens from the same locality.

Unfortunately the chromosome evidence was found to be unreliable. A single specimen from the type locality area (Keimoes) of *H. gracilis fluvialis* only yielded two very poor spreads amongst several prepared microscope slides which yielded counts of 2n=36. Specimens from 30km west of Springbok (SAIMR 1112) consistently yielded spreads with 2n=36 and several with 2n=72, suggesting occasional polyploidy which is common in scorpions. A specimen from Horingsgat (NM 11351) and specimens from Steinkopf which had been injected with PHA and colchicine for several days prior to dissection yielded counts of 2n=72 with one or two

spreads of 2n=36. Now experiments conducted with *H. tityrus* proved conclusively that this PHA-colchicine treatment increased the number of spreads obtained per preparation by several hundred percent but it also induced polyploidy. Accordingly, it is by no means certain whether the actual count should be 2n=36 or if there are two morphologically identical species with counts of 2n=36 and 2n=72 respectively. The chromosomal evidence in this case is thus very unreliable but I suspect that it will be proved that all of these populations will be shown to be 2n=36. Obviously different species need not have different chromosome counts but where there are differences which are not obvious multiples of each other, there can be no question of conspecificity.

In order to solve this problem it would be necessary to re-examine the chromosomes of specimens from a wide area and also to get Thorell's type of *H. phyllodes* for examination. Because the problem cannot be solved without any element of doubt at present, I have decided to place the species in provisional synonymy for the reasons stated above.

5.2.14 *Hadogenes zumpti* spec. nov., figs 89-103.

Type specimens: Holotype ♂ SAM collected by R. Smithers at Kuboos, Richtersveld (2817 AC), circa 1956. Paratypes: TM 11866, 11867 ♂♂ (imm) collected by W.D. Haacke at a site 3,4km west of Numees Mine, Richtersveld (2816 BD) on 26 November, 1962; SAIMR 1340 (nymph) collected at Tatasberg, Richtersveld by G. Newlands on 05 April 1979, and SAIMR 1365, 1366 collected by A. Harington at Swartrant, Aughrabies National Park on the 20 December 1978.

The holotype SAM is in the South African Museum, Cape Town, the paratypes TM 11866 and 11867 are housed in the Transvaal Museum, Pretoria and the remaining paratypes are kept at the South African Institute for Medical Research in Johannesburg.

Distribution: See fig. 89.

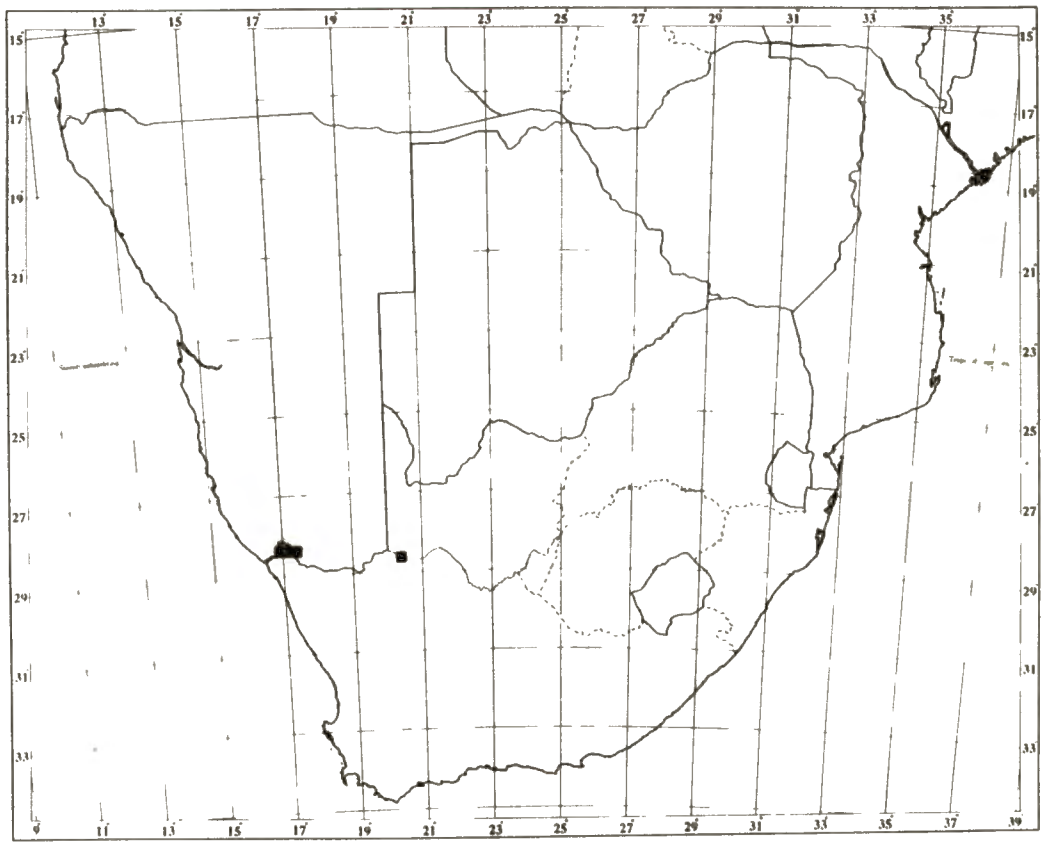


Fig. 89. Map showing the distribution of *Hadogenes zumpti* spec. nov. in the Richtersveld and Kenhardt district of the north western Cape.

Diagnosis: This species can be distinguished from all other species of the genus by adult male having no basal lobe in the proximal region of the chela tarsus and by the following combination of features: (males) pedipalps extremely long and slender, the chela being 5,5 times as long as wide, metasoma twice the length of the prosoma and mesosoma combined and pectinal teeth 16-17. The only other species which has a very long, slender pedipalp, *H. lawrencei* has a low pectinal tooth count of less than 11 and the metasoma is shorter than the mesosoma and prosoma combined. The dorsal surface of the pedipalpal patella

only has two trichobothria in the new species.

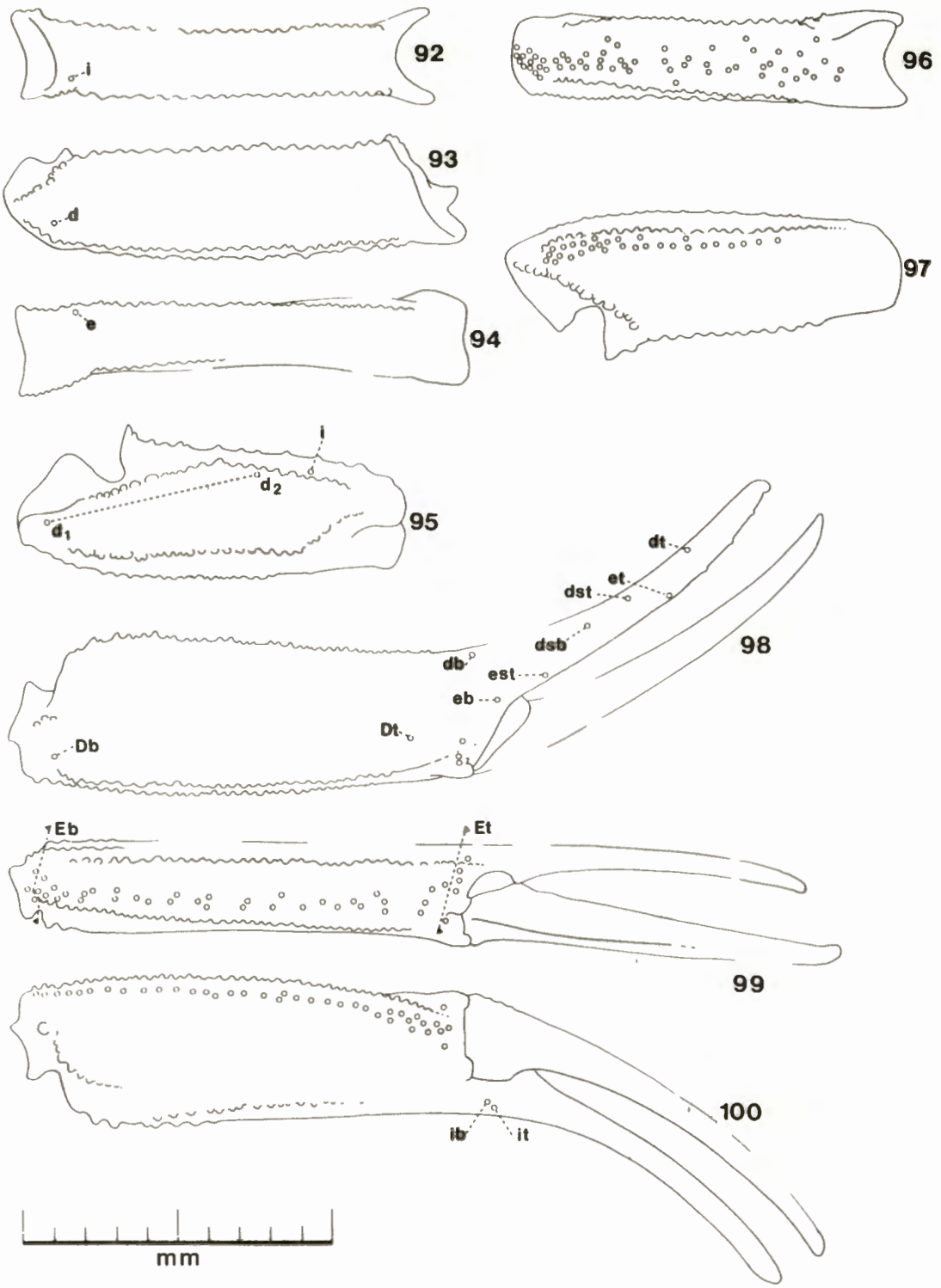
Sexual dimorphism: Adult female unknown. In all other species of the genus, nymphal males resemble females very closely until the final ecdysis. Nymphal males of this new species differ from adult males in having a shorter metasoma without the terminal spiniform granule on the dorso-lateral keels of segments II and III. An early instar nymphal female has 12/12 pectinal teeth. The males have a divided genital operculum and genital papillae.

Description of the holotype: Colour: Chela dark red (10R3/6), carapace dark red (10R3/6), tergites dark reddish brown (10R3/3), sternites dull reddish brown (5YR5/4) and legs bright brown (7,5YR5/8)

Carapace: Anterior margin deeply concave, triangular inset situated far back and much wider than long. Triangular inset granular and with an uneven surface. The entire carapace area is granular except for a small patch on each frontal lobe. A sparse row of fine setae arise from the anterior edge of the carapace. Median ocelli only slightly larger than the lateral ocelli. All invaginations present but anterior keel and anterior marginal suture absent.

Pedipalps: Segments extremely elongate and exceptionally slender. Chela 6,5 times as long as wide. Dorsal keel of patella absent and without vestigial trace, all other keels present. Finger keel and dorsal accessory keels of chela very prominent although only weakly granular. All pedipalpal surfaces granular and without any sign of reticulation. Anterior process of humerus almost obsolete. Adult males (assessed as being adult by the presence of fully developed paraxial organ and testes) without basal lobe of chela tarsus.

Figs 90-91. Male holotype of *Hadogenes zumpti* spec. nov. from Kuboos, Richtersveld. 90. Dorsal view. 91. Ventral view.



Figs 92-100. Distribution of trichobothria on the right-hand pedipalpal segments of *Hadogenes zumpti* spec. nov. Trichobothrial notation after Vachon (1973). 92. Anterior view of the femur. 93. Dorsal view of the femur. 94. Posterior view of the femur. 95. Dorsal view of the patella. 96. Posterior view of the patella. 97. Ventral view of the patella. 98. Dorsal view of the chela. 99. Posterior view of the chela. 100. Ventral view of the chela.

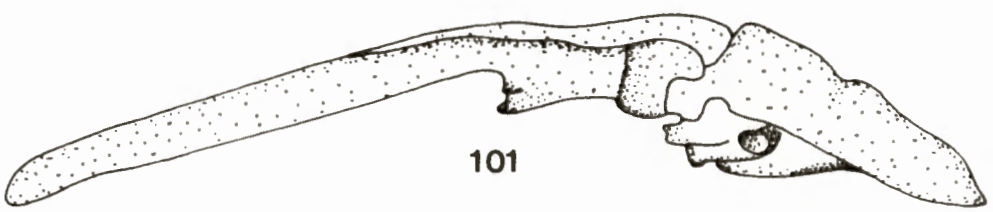
Trichobothria: Neobothriotaxic major, type C (figs 92-100) with the following segment total; femur 3, patella 93 and chela 91. Total number of trichobothria per pedipalp, 187. There are only trichobothria on the dorsal surface of the patella d_1 and d_2, (fig. 95).

Legs: Femur of all legs with lightly sclerotized pair of granular keels on ventral surface; ventral surface of patella with irregular granulation, tarsomere II of all legs with 3:3 spines ventrally. Coxal endites of legs I and II sparsely but coarsely granular on ventral surfaces.

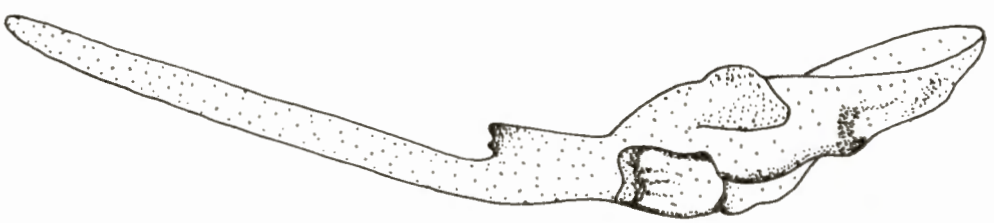
Mesosoma: Tergites with very fine and even granulation which imparts a matt appearance to these sclerites. Sternite VII and tergite VII slightly longer than wide.

Pectinal teeth: Left 16, right 17.

Paraxial organ: See figs 101-102.



101



102

Figs 101-102. Left paraxial organ of *Hadogenes zumpti* spec. nov. 101. Dorsal view. 102. Ventral view.

Metasoma: Metasomal segment I higher than wide, dorso-lateral keel of metasomal segment II terminates distally

with a spiniform granule on each side; all other metasomal segments lack this characteristic. Metasomal segment V has weakly granular keels. Ventral surface of vesicle covered with barely discernible granulation; profile of vesicle dorsal surface virtually straight.

Measurements of holotype: Carapace anterior width 6,8mm, posterior width 11,4mm and length 12,0mm. Chela width 4,7mm, total length, 25,0mm, length along postero-ventral keel 14,0mm and length of movable finger 13,4mm. Metasomal segment I, 2,3mm wide, 12,1mm long and 2,8mm high; metasomal segment II, 2,2mm wide, 15,7mm long and 3,4mm high; metasomal segment III, 2,0mm wide, 14,5mm long and 3,0mm high, metasomal segment V, 1,8mm wide, 16,7mm long and 2,2mm high and telson 7,7mm long, 1,9mm wide and 2,7mm high. Total length of metasoma 84mm, of prosoma and mesosoma together 42,3mm and width across pedipalps 128mm.

Paratypes: The paratypes differ from the holotype in the following characteristics: TM 11866 (♂) with triangular inset having the same width as length, dorso-lateral keels of both metasomal segments II and III terminating in a large spiniform granule distally.

Pectines: 16:17 TM 11867 (♀ nymph) with shorter metasoma lacking spiniform granules on the dorso-lateral metasomal keels and with 12:12 pectinal teeth. Two specimens from the Aughrabies Falls area, SAIMR 1365, 1366 almost certainly belong to the new species but differ from the holotype in the following characteristics: chela slightly more robust than the holotype, the ventral keels on the femur of the legs are slightly more granular and pronounced, dorso-lateral keels of metasomal segment I terminate with a weak tooth-like granule, dorso-lateral keels of segments II and III have very distinct enlarged spiniform granules. Immature male similar to female paratype in general morphological features. Pectinal teeth: 16:16.

Chromosomes: 2n=60 (see fig. 103)

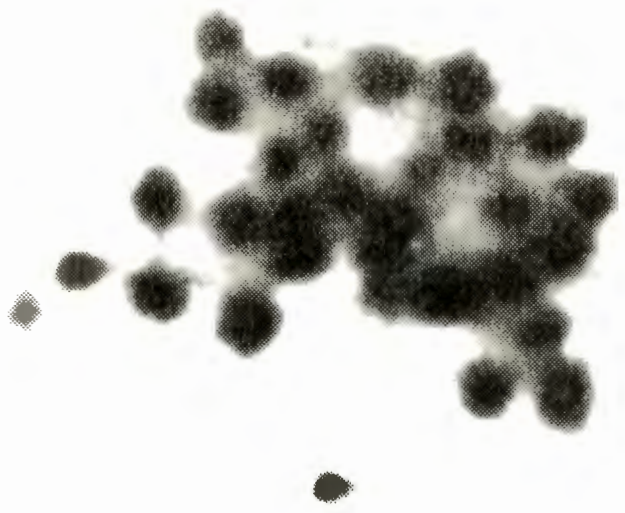


Fig. 103. Photomicrograph of the only chromosome spread obtained from a dead nymph of *Hadogenes zumpti* spec. nov.

Notes: The new species is named in honour of Prof. F.K.E. Zumpt who initially made the present study possible. Prof. Zumpt has published a great many papers on African arachnida of the orders Acari, Araneae and Scorpiones.

Electrophoretic results suggest that the nearest relative of the new species is *H. phyllodes* (Thorell) but although it has approximately the same banding sequence, the position of six bands differs distinctly from the equivalent bands of *H. phyllodes*, suggesting definite differences in molecular weight (fig. 111).

Chromosomal preparations were attempted with two nymphal specimens as well as with the testes of the preserved holotype. The first nymphal specimen (SAIMR 1312) was killed and nerve and glandular tissue removed for spread preparations but with totally negative results. I decided

to inject the second specimen (SAIMR 1340) with a PHA-colchicine mixture to induce mitosis and arrest the process at metaphase. Unfortunately the specimen died in the night and although developing testicular and other tissue was examined, only one chromosome spread was found (fig. 92). Examination of testicular tissue of the preserved holotype yielded negative results. The chromosome number of 2n=60 determined from a single poor spread should be regarded with some caution.

The new species is probably restricted to the northern Richtersveld and the adjacent very arid areas of the Kenhardt District. It occurs sympatrically with *H. tityrus* (Simon) in the Richtersveld. In the southern Richtersveld, *H. phyllodes* occurs sympatrically with *H. tityrus* but probably not with *H. zumpti*.

5.3 Key's to species of *Hadogenes*

5.3.1 Key to the species of *Hadogenes* based on morphological characteristics

The following key is intended to enable non-specialists to identify adult specimens of the genus. Once a specimen has been classified by means of the key, the identity should be confirmed by the geographic key (see 5.3.2) and the distributional range of the relative species. Obviously range extensions are possible, but a species restricted to the southern Cape for example, could not occur in the Transvaal.

1. Movable finger of chela longer than length of chela as measured along the postero-ventral keel..... 2.
- Movable finger of chela shorter than length of chela as measured along the postero-ventral keel... 3.

2. Chela with 1-3 accessory trichobothria between *it* and *ib* on the anterior surface (= interior surface of Vachon, 1973) of chela; anterior margin of carapace deeply excavated with well-rounded frontal lobes. Males with terminal spiniform granules on the dorso-lateral keels of metasomal segment IV.....*H. zuluanus* Lawrence
- Chela without accessory trichobothria between *it* and *ib* on anterior surface of chela; anterior carapace margin almost straight or weakly concave, males without spiniform granules on dorsal surface of metasomal segment IV.....*H. gracilis* Hewitt

3. Metasoma considerably shorter than mesosoma and prosoma combined. Total number of trichobothria less than 140 per pedipalp and diploid chromosome number in excess of 130.....4.
- Metasoma longer than mesosoma and prosoma combined, more than 150 trichobothria per pedipalp. Diploid chromosome number less than 120.....5.

4. Length of pedipalpal patella shorter than carapace length, length of pedipalpal femur equal to the carapace length. Pectinal teeth: ♀, 9-13; ♂ , 13-16. Diploid chromosome number 168 .....*H. tityrus* Simon
- Length of pedipalpal patella longer than the carapace length, length of pedipalpal femur 1,3 times the carapace length. Pectinal teeth: ♀, 6; ♂ 11. Diploid chromosome number:132...*H. lawrencei* Newlands

5. Adult males and females without basal lobe on the chela tarsus, length of the chela more than five times its width. Dorsal surface of the pedipalpal patella with two trichobothria.....*H. zumpti* Newlands
- Adult males and females with basal lobe on the chela tarsus, length of chela less than four times the width. Dorsal surface of pedipalpal patella with at least

four trichobothria.....6.

6. Triangular inset positioned well back on carapace such that the frontal lobes are exposed as a pair of well-rounded protruding structures.....7.
- Triangular inset positioned anteriorly on the carapace such that the anterior margin is straight or slightly concave and that the frontal lobes do not protrude....8.

7. Dorsal keel of patella distinct and granular. Lateral ocelli slightly smaller in size than the median ocelli. Metasoma of adult male not elongated...*H. bicolor* Purcell.
- Dorsal keel of patella absent, lateral ocelli distinctly larger than the median ocelli; metasoma of adult male considerably elongated.....
.....*H. trichiurus* (Gervais).

8. Metasomal segment I wider than high.....9.
- Metasomal segment 2 higher than wide.....12.

9. Subspiniform granules present on the venter of metasomal segment II of equal size or larger than those present on the venter of metasomal segment V.....10.
- If present, weak or subspiniform granules on the venter of metasomal segment II considerably smaller than those on the venter of metasomal segment V.....11.

10. Legs and sternite much lighter in colour than tergites. Carapace length of female distinctly shorter than the combined length of metasomal segment I and II.....
.....*H. taeniurus* (Thorell).
- Legs and sternites the same colour as the tergites. Carapace length of female equal in length to the combined length of metasomal segments I and II. Male unknown.....*H. paucidens* Pocock.

11. Species small (80-130mm), more than 230 trichobothria

per pedipalp. Female with less than 12 pectinal teeth. Granules of dorso-lateral and ventro-lateral keels of metasomal segment V larger than those of the antero-dorsal keel of the pedipalpal femur.....
.....*H. minor* Purcell.

- Species large (140-180mm), less than 200 trichobothria per pedipalp. Female with more than 14 pectinal teeth. Granules on dorso-lateral and ventro-lateral keels of metasomal segment V much smaller than those of the antero-dorsal keel of the pedipalpal femur.....
.....*H. granulatus* Purcell.

12. Dorso-lateral keels of metasomal segments II and III without an enlarged terminal granule distally.....
.....*H. troglodytes* (Peters).

- Dorso-lateral keels of metasomal segments II and III terminate distally with an enlarged granule or spiniform granule.....13.

13. Female with pair of deep oval depressions distally on sternite VII, metasomal segment V shorter than the carapace. In male, metasomal segment V less than 1,25 times the carapace length.....*H. gunningi* Purcell.

- Female without distal, oval depressions on sternite VII, metasomal segment V equal in length to carapace length. In male, metasomal segment V more than 1,5 times the carapace length.....*H. phyllodes* (Thorell).

5.3.2 Key to the species of *Hadogenes* in terms of their geographic occurrence.

The key below makes use of distributional data in order to help confirm identifications determined by the key utilizing morphological characteristics. It can also be used to establish the species likely to occur in a given area and in so doing, speed up the process of identification. This key

is valid for southern Africa, south of 15°S and the only species likely to fall outside this range are *H. taeniurus* (Thorell) which may occur north of 15°S between 12°E and 17°E and the west African species, *H. paucidens* Pocock for which no precise locality records are known.

For the purpose of this key, southern Africa has been divided into a series of 97 squares, each being 2° latitude by 2° longitude. Species which are very likely to occur in a square where they have not yet been recorded are listed as probable occupants while species which may occur in the area are referred to as possible occupants. Areas for which no species whatever are recorded are those where they have never been found and which I consider to be ecologically unsuitable for habitation by species of the genus.

The fact that two or more species are listed for some squares does not necessarily mean that these species occur sympatrically. The only two species known to occur sympatrically thus far are *H. phyllodes* and *H. tityrus*.

LATITUDE	LONGITUDE	SPECIES
15°S-17°S:	11°E-13°E	*Hadogenes taeniurus* (Thorell)
15°S-17°S:	13°E-15°E	*Hadogenes taeniurus* (Thorell)
15°S-17°S:	15°E-17°E	Probably *Hadogenes taeniurus* (Thorell)
15°S-17°S:	17°E-19°E	None
15°S-17°S:	19°E-21°E	None
15°S-17°S:	21°E-23°E	None
15°S-17°S:	23°E-25°E	None
15°S-17°S:	25°E-27°E	None
15°S-17°S:	27°E-29°E	*Hadogenes granulatus* Purcell
15°S-17°S:	29°E-31°E	*Hadogenes granulatus* Purcell
15°S-17°S:	31°E-33°E	*Hadogenes granulatus* Purcell and probably *H. troglodytes* (Peters)
15°S-17°S:	33°E-35°E	*Hadogenes troglodytes* (Peters)
15°S-17°S:	35°E-37°E	None
17°S-19°S:	11°E-13°E	*Hadogenes taeniurus* (Thorell)
17°S-19°S:	13°E-15°E	*Hadogenes taeniurus* (Thorell)
17°S-19°S:	15°E-17°E	Probably *Hadogenes taeniurus* (Thorell)
17°S-19°S:	17°E-19°E	Probably *Hadogenes taeniurus* (Thorell)
17°S-19°S:	19°E-21°E	None

LATITUDE	LONGITUDE	SPECIES
17°S-19°S:	21°E-23°E	None
17°S-19°S:	23°E-25°E	None
17°S-19°S:	25°E-27°E	*Hadogenes granulatus* Purcell
17°S-19°S:	27°E-29°E	Probably *Hadogenes granulatus* Purcell
17°S-19°S:	29°E-31°E	*Hadogenes granulatus* Purcell
17°S-19°S:	31°E-33°E	*Hadogenes granulatus* Purcell and *H. troglodytes* (Peters)
17°S-19°S:	33°E-35°E	None
17°S-19°S:	35°E-37°E	None
19°S-21°S:	13°E-15°E	*Hadogenes taeniurus* (Thorell)
19°S-21°S:	15°E-17°E	Probably *Hadogenes taeniurus* (Thorell)
19°S-21°S:	17°E-19°E	*Hadogenes taeniurus* (Thorell) and *H. tityrus* Simon
19°S-21°S:	19°E-21°E	None
19°S-21°S:	21°E-23°E	None
19°S-21°S:	23°E-25°E	None
19°S-21°S:	25°E-27°E	*Hadogenes granulatus* Purcell
19°S-21°S:	27°E-29°E	*Hadogenes granulatus* Purcell and *H. troglodytes* (Peters)
19°S-21°S:	29°E-31°E	*Hadogenes granulatus* Purcell and *H. troglodytes* (Peters)
19°S-21°S:	31°E-33°E	*Hadogenes granulatus* Purcell and *H. troglodytes* (Peters)
19°S-21°S:	33°E-35°E	None
21°S-23°S:	13°E-15°E	*Hadogenes taeniurus* (Thorell) and *H. tityrus* (Simon)
21°S-23°S:	15°E-17°E	*Hadogenes tityrus* (Simon) and probably *H. taeniurus* (Thorell)
21°S-23°S:	17°E-19°E	*Hadogenes taeniurus* (Thorell) and probably *H. tityrus* (Simon)
21°S-23°S:	19°E-21°E	None
21°S-23°S:	21°E-23°E	None
21°S-23°S:	23°E-25°E	None
21°S-23°S:	25°E-27°E	*Hadogenes troglodytes* (Peters)
21°S-23°S:	27°E-29°E	*Hadogenes troglodytes* (Peters)
21°S-23°S:	29°E-31°E	*Hadogenes troglodytes* (Peters) and possibly *H. granulatus* Purcell
21°S-23°S:	31°E-33°E	*Hadogenes troglodytes* (Peters) and *H. granulatus* Purcell
21°S-23°S:	33°E-35°E	None
23°S-25°S:	13°E-15°E	Probably *Hadogenes tityrus* (Simon)
23°S-25°S:	15°E-17°E	*Hadogenes tityrus* (Simon)
23°S-25°S:	17°E-19°E	Probably *Hadogenes tityrus* (Simon)
23°S-25°S:	19°E-21°E	None
23°S-25°S:	21°E-23°E	None
23°S-25°S:	23°E-25°E	None
23°S-25°S:	25°E-27°E	*Hadogenes troglodytes* (Peters)
23°S-25°S:	27°E-29°E	*Hadogenes troglodytes* (Peters)
23°S-25°S:	29°E-31°E	*Hadogenes bicolor* Purcell and *H. troglodytes* (Peters)
23°S-25°S:	31°E-33°E	*Hadogenes troglodytes* (Peters) and *H. bicolor* Purcell
23°S-25°S:	33°E-35°E	None
25°S-27°S:	15°E-17°E	*Hadogenes lawrencei* Newlands and *H. tityrus* (Simon)
25°S-27°S:	17°E-19°E	*Hadogenes tityrus* (Simon) and *H. phyllodes* (Thorell)
25°S-27°S:	19°E-21°E	None
25°S-27°S:	21°E-23°E	None
25°S-27°S:	23°E-25°E	None
25°S-27°S:	25°E-27°E	*Hadogenes troglodytes* (Peters)
25°S-27°S:	27°E-29°E	*Hadogenes gracilis* Hewitt and *H. gunningi* Purcell
25°S-27°S:	29°E-31°E	*Hadogenes bicolor* and probably *H. gunningi* Purcell
25°S-27°S:	31°E-33°E	Possibly *Hadogenes zuluanus* Lawrence
27°S-29°S:	15°E-17°E	*Hadogenes sumpti* spec. nov and *H. tityrus* (Simon)
27°S-29°S:	17°E-19°E	*Hadogenes sumpti* spec. nov., *H. tityrus* Simon and *H. phyllodes* (Thorell)

LATITUDE LONGITUDE	SPECIES
27°S-29°S:19°E-21°E	*Hadogenes zumpti* spec. nov., *H. phyllodes* (Thorell) and probably *H. tityrus* (Simon)
27°S-29°S:21°E-23°E	*Hadogenes phyllodes* (Thorell)
27°S-29°S:23°E-25°E	None
27°S-29°S:25°E-27°E	None
27°S-29°S:27°E-29°E	None
27°S-29°S:29°E-31°E	*Hadogenes trichiurus* (Gervais)
27°S-29°S:31°E-33°E	*Hadogenes zuluanus* Lawrence
29°S-31°S:17°E-19°E	*Hadogenes tityrus* (Simon) and *H. phyllodes* (Thorell)
29°S-31°S:19°E-21°E	*Hadogenes phyllodes* (Thorell)
29°S-31°S:21°E-23°E	*Hadogenes phyllodes* (Thorell)
29°S-31°S:23°E-25°E	Possibly *Hadogenes trichiurus* (Gervais)
29°S-31°S:25°E-27°E	*Hadogenes trichiurus* (Gervais)
29°S-31°S:27°E-29°E	Probably *Hadogenes trichiurus* (Gervais)
29°S-31°S:29°E-31°E	*Hadogenes trichiurus* (Gervais)
31°S-33°S:17°E-19°E	*Hadogenes phyllodes* (Thorell) and *H. minor* Purcell
31°S-33°S:19°E-21°E	*Hadogenes minor* Purcell
31°S-33°S:21°E-23°E	*Hadogenes trichiurus* (Gervais)
31°S-33°S:23°E-25°E	*Hadogenes trichiurus* (Gervais)
31°S-33°S:25°E-27°E	*Hadogenes trichiurus* (Gervais)
31°S-33°S:27°E-29°E	*Hadogenes trichiurus* (Gervais)
31°S-33°S:29°E-31°E	Probably *Hadogenes trichiurus* (Gervais)
33°S-35°S:17°E-19°E	None
33°S-35°S:19°E-21°E	*Hadogenes trichiurus* (Gervais)
33°S-35°S:21°E-23°E	Probably *Hadogenes trichiurus* (Gervais)
33°S-35°S:23°E-25°E	Probably *Hadogenes trichiurus* (Gervais)
33°S-35°S:25°E-27°E	*Hadogenes trichiurus* (Gervais)
33°S-35°S:27°E-29°E	Probably *Hadogenes trichiurus* (Gervais)

6.0 DISCUSSION

6.1 Taxonomic considerations

Many of the taxonomic problems I had hoped to solve during the course of this study could not be resolved. These unresolved problems can be divided into two categories, viz those caused by an inability to obtain certain type specimens for examination and the discovery that some species are almost certainly species complexes, the study of which were beyond the scope of this account. Most local and overseas museums approached for the loan of type and other specimens were very co-operative (see acknowledgements). However, two museums were either unable or unwilling to loan crucial material in their possession. The Albany Museum failed to respond to two letters requesting the types of species described by Hewitt and especially *H. gracilis namaquensis* and the various subspecies of *H. trichiurus*. It is thought that these specimens may have been destoryed during the two fires which gutted the museum in the early years of its existence. The Goteborg Museum in Sweden was unco-operative. Accordingly, decisions reached on the synonymy of *H. gracilis fluvialis* and *H. gracilis namaquensis* with *H. phyllodes* are tentative and based solely on the original descriptions and specimens I was able to collect. Specimens of the two subspecies were collected at the type localities but as the type locality of *H. phyllodes* is unknown, (except that it was probably in Namaqualand, (Lawrence, 1955)) comparison was impossible.

Another problem species is *H. trichiurus*, the whereabouts of the type of which is unknown. The original description is totally inadequate and the type locality simply stated as "La Cafrerie". Fortunately the only species which occur in Caffria is *H. trichiurus*. As early taxonomists did not know what the typical form looked like, they solved the

problem by ignoring the typical form completely and describing six subspecies, the distributional ranges of which overlapped in most cases. Of the six subspecies described between 1898 and 1937, only one appears valid, not as a subspecies, but as a species. The electrophoretic differences between *H. trichiurus zuluanus* from Magudu and *H. trichiurus* from Rooinek Pass are great and so are the morphological differences and sexual dimorphism. This subspecies was thus raised to full species status

Another problem species is *H. tityrus* which appears to be a species complex.. A closely allied species, *H. lawrencei* is very distinctly different in terms of morphology, electrophoretic profile and chromosome number. Three forms of *H. tityrus* are known to me viz a very small yellow form found only at Awasib Mountain, South West Africa, a slightly larger darker yellow form found from Windhoek to the Richtersveld and a large dark brown form which has approximately the same distribution as the latter species. In this study, these forms have not been differentiated as they could not be satisfactorily separated by relatively crude cytogenetic methods used. Whether these are polymorphic forms of the same species or sibling species is not known at this stage and will hopefully form the subject of a more detailed dissertation.

The distributional range of each species as plotted on the maps included with the species descriptions represent all the acceptable literature records to-date, the collections of all the local and several overseas museums and the results of over 100 days of intensive field work. As most species of *Hadogenes* appear so similar, many of the early published records are based upon incorrectly identified specimens. Accordingly, all doubtful literature records which could not be checked by reference to the actual specimens, were omitted from the distribution maps presented in this account. In virtually all cases where locality data

was in question and the specimens could be re-examined, the identity of the species was found to be in error. In a few cases where the identity was found to be correct, the labels had not been attached to the specimens and it is fairly certain that museum curators must have mixed specimens and their labels. In some museums, such as the British Museum (Natural History) and the South African Museum, labels are not physically attached to the specimens but merely placed in the specimen jar. This practise does lend itself to accidental mixing of specimens and labels. In one or two cases where label swopping was suspected, the localities were omitted from the distribution maps, for example, specimens of *H. troglodytes* from Lesotho (South African Museum).

The need to check carefully the identity of all catalogued museum specimens can be further illustrated by the new species, *H. zumpti*, which is described in this work. The holotype from the South African Museum had been identified as *H. phyllodes* and two paratypes from the Transvaal Museum collection were identified by the same authority as *H. gracilis fluvialis*.

6.2 Results of the chromosome study

The chromosome studies which were only started half way through the project, proved very interesting and eleven of the fourteen species were karyotyped in terms of chromosome number. Those which were not examined were *H. paucidens* which is known from a single specimen collected in West Africa, *H. taeniurus* from the Kaokoveld, *H. trichiurus* from the south eastern Cape and *H. zuluanus* from Natal. Many tissues were investigated as a source of somatic chromosomes to avoid total reliance on testicular tissue. Tissues used repeatedly were the digestive gland, ganglia, muscle, coxal glands, gonads and developing embryos. However, spreads were found with such low frequency in all except testicular tissue, that

other tissues were not a practical proposition. For example, it took an average of 30 minutes to scan a microscope slide for spreads at a magnification of 100 times which is the minimum at which spreads can be dectected. Slides prepared from testicular tissue yield an average of 5 to 50 or more spreads, while embryonic tissue yields an average of 1 spread per slide. All other tissues yielded less than 1 spread per 10 slides and only a small proportion of the spreads were countable. The reason for the low yield is almost certainly due to the low metabolic rate of scorpions which take at least eight years to reach maturity. Accordingly, cell division is a rarer event per unit time than in other biological systems. Attempts to induce more rapid cell division by injecting the animals with PHA and arresting cell division with colchicine were partly successful and most certainly increased the number of spreads per slide in the case of testicular and embryonic tissues.

In the taxonomic section (section 5.0), the species were arranged according to general morphological similarity and it was thus interesting that this order corresponded fairly accurately with the chromosome numbers for each species when arranged in descending order. The diploid chromosome numbers were as follows: *H. tityrus:* 168, *H. lawrencei:* 132, *H. minor:* 108, *H. bicolor:* 96, *H. granulatus:* 96, *H. gunningi:* 88, *H. troglodytes:* 84, *H. gracilis:* 80, *H. zumpti:* 60 and *H. phyllodes:* 36. Only two pairs of species were differently placed in the morphological section, viz *H. granulatus* - *H. gunningi* and *H. phyllodes* - *H. zumpti*.

One very important result of the chromosome study was the categorical proof that minor but distinct morphological differences should not be ignored. Many modern taxonomists might well have been tempted to synonymise species such as *H. lawrencei* with *H. tityrus*, *H. bicolor* with *H. gunningi* and *H. gracilis* with *H. troglodytes*. However, the differences in

chromosome number in all these cases prove that such synonymization would be totally unjustified.

Although no effort was spared to obtain accurate chromosome counts for each species, this was very difficult, especially in those species with exceptionally high diploid numbers. As many spreads as possible were counted and the modal number which appeared most frequently was accepted. In species which yielded two numbers consistantly, the one being twice the other, the lowest number was taken as it was found that the injection of colchicine definitely induced polyploidy. Only one species yielded two numbers with equal frequency, viz *H. phyllodes*. The counts obtained for this latter species were 2n=36 and 2n=72. The only specimen which was not injected with colchicine (SAIMR 1112) constantly yielded counts of 2n=36 while all the other specimens examined yielded counts of 2n=36 and 2n=72 at approximately equal frequency.

Because *Hadogenes* species chromosomes are so small and apparently telocentric, attempts at G and C banding met with little success. If the chromosomes could be G-banded, it would probably be possible to identify the individual chromosomes and arrange them karyogrametically. Possible sibling species could also be detected if the chromosomes could be properly karyotyped.

6.3 Results of the electrophoretic study

One of the first electrophoretic experiments conducted was to establish how constant the banding patterns were for different individuals from the same and different geographic localities. Provided animals of the same sex were chosen, no individual variation could be detected in most species, even when the individuals were separated by hundreds of kilometres. Reference to figs 103-104 reveal the high level of reproductability obtained. Even when specimens

were re-milked a week later there was no change in the banding pattern except for a slightly lower protein concentration in the crude venom (fig. 103). In all species in which both male and female specimens were available for electrophoretic analysis, sexual differences were detected in the positions of certain bands (fig. 103).

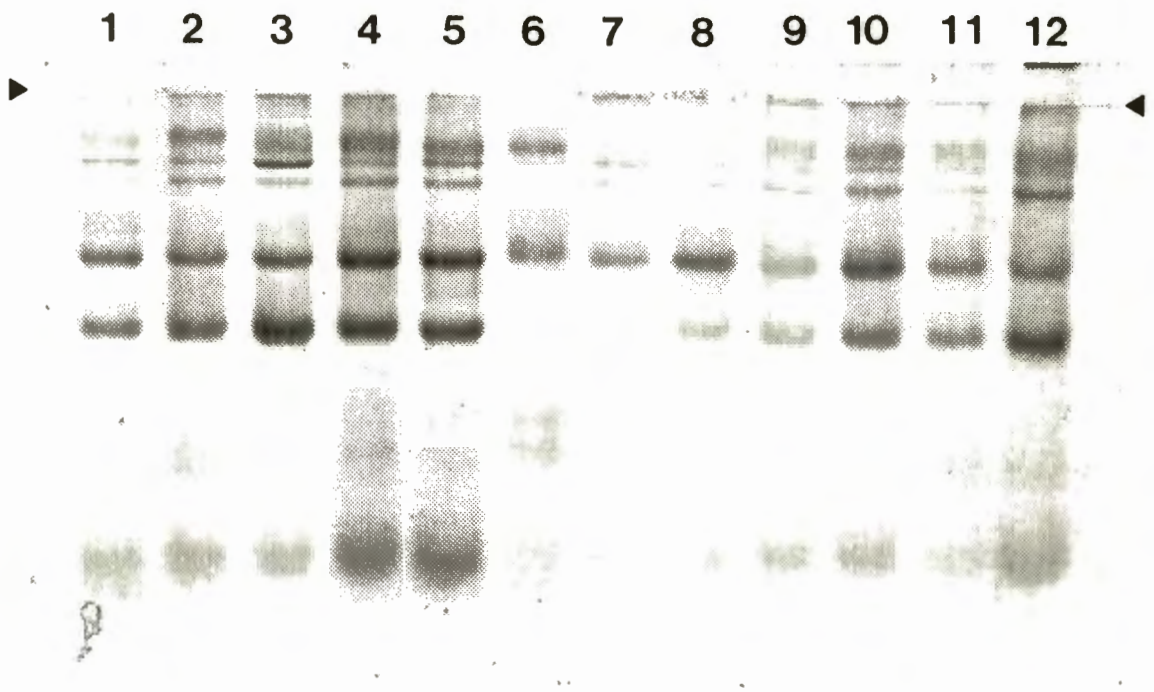


Fig. 103. Electrophoretic separation of *Hadogenes gracilis* Hewitt venom proteins on an acrylamide gel slab. Samples 1-5 were different female specimens from the same koppie. A male from the same locality is represented by sample 6. Samples 7-12 are females which were re-milked a week later showing similar banding patterns but a lower protein concentration.

In general, species which were morphologically similar were found to be the most similar electrophoretically. Chromosome counts (see 6.2) also fitted in this general scheme of morphological similarity. The electrophoretic results were

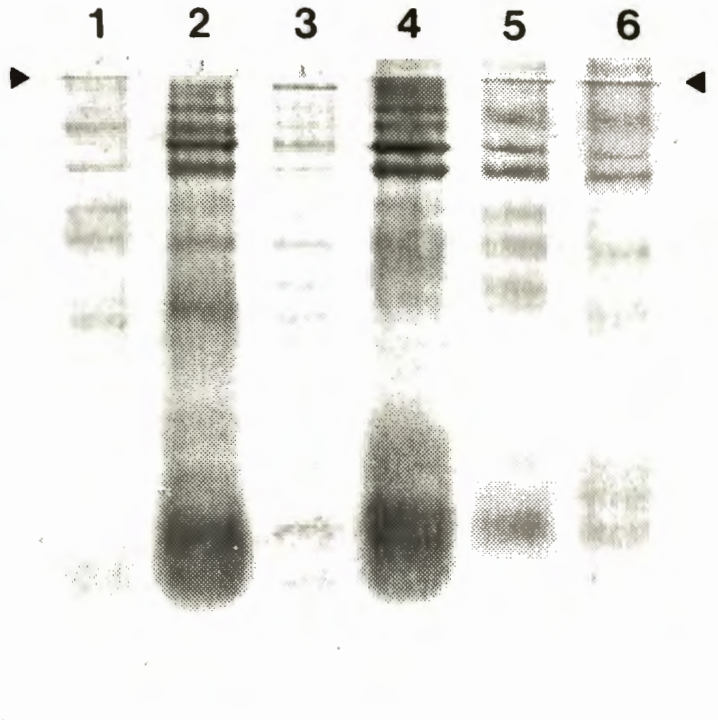


Fig. 104. Electrophoretic separation of the venom proteins of male specimens of the *Hadogenes tityrus* Simon group. Samples 1 and 6 were specimens from Helskloof representing the typical form of the species. A larger dark form of the species which differs electrophoretically is represented in two samples (2 and 3) from Windhoek and two samples (4 and 5) from Lekkersing, some 800km south of Windhoek.

only used as a taxonomic aid and no attempt was made to assess the number of components present and their molecular weight or the genetic distance between the species.

The electrophoretic analysis of venom proteins of the *H. tityrus* - *H. lawrencei* species complex demonstrated that this complex comprises at least four sibling species, two of which are named, viz *H. tityrus* and *H. lawrencei*. Reference to figs 104-106 will show how a larger dark form (see 5.2.1) differed considerably from the typical yellow form as represented by specimens from Helskloof in the Richtersveld and how these in

turn differ from *H. lawrencei*. The fourth form is a small light yellowish scorpion from Awasib in the Namib known from one adult female and a nymphal specimen, the venom proteins of which differ considerably from all other members of the species complex. Morphologically, the closest relative of the *H. tityrus* - *H. lawrencei* complex is *H. minor* from the Clanwilliam district and the electrophoretic analysis of the venom proteins bear this out in that there are only slight differences in the relative band positions of these scorpions (figs 105 and 106).

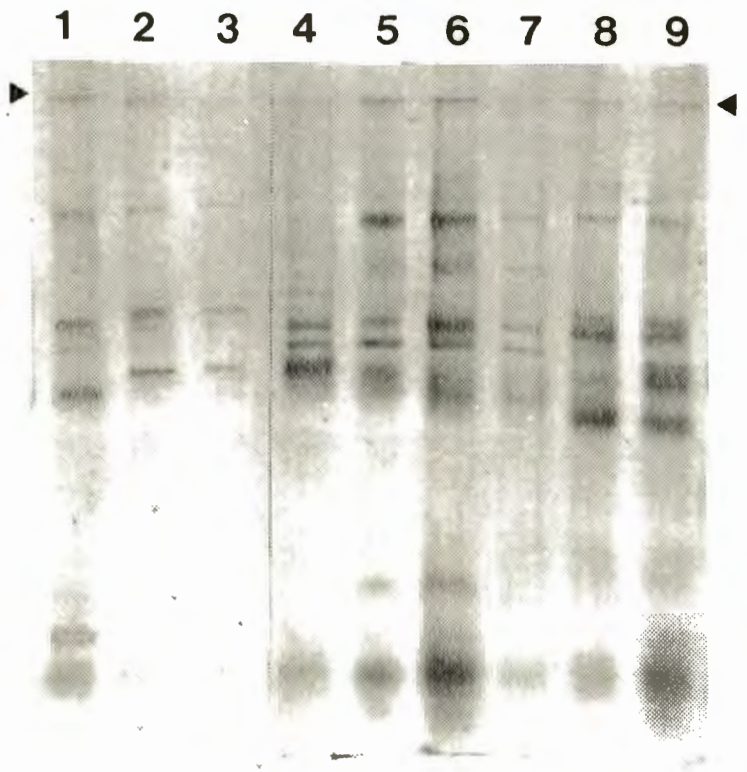


Fig. 105. Electrophoretic separation of the venom proteins of female specimens of the *Hadogenes tityrus* Simon species complex (1-7) and *H. minor* Purcell (8-9). Sample 1 is a specimen from Helskloof representing the typical form. Samples 2-3 represent a small light yellow form from Awasib which differ quite markedly, the concentration of sample 3 was too low. Sample 4 was a specimen of *H. lawrencei* from the Hauchab Mountain and samples 5-7 the large dark form of *H. tityrus* from Tierhoek in the Ploegberg. Samples 8 and 9 are specimens of *H. minor* from Clanwilliam.

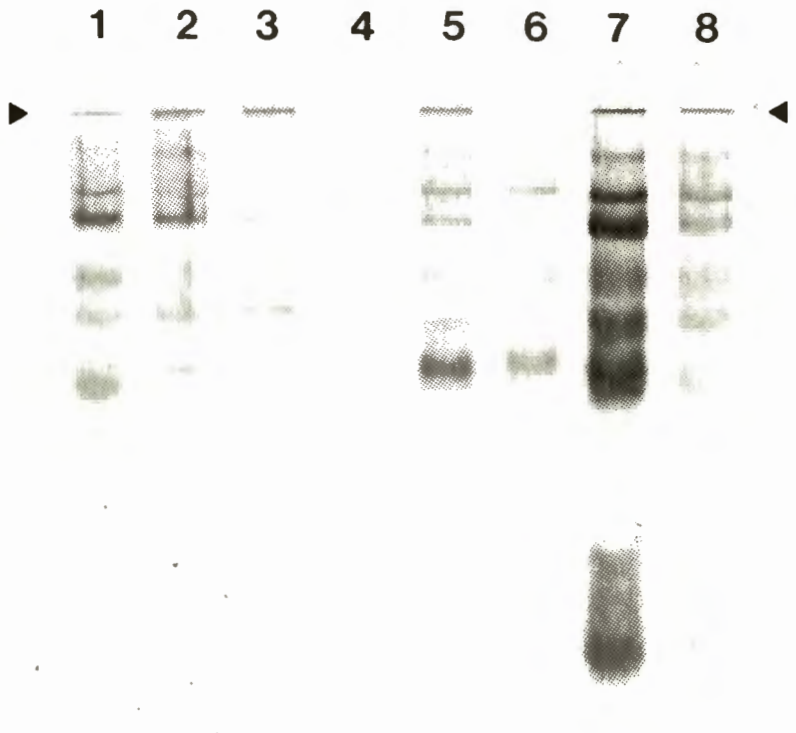


Fig. 106. Electrophoretogram showing the differences in banding pattern displayed by venom proteins of *H. lawrencei* (samples 1,7,8), the dark form of *H. tityrus* from Tierhoek (samples 4-6) and *H. minor* (samples 2-3).

Support for the decision based on morphological characteristics to raise *H. zuluanus* to full species status is obtained from the electrophoretic differences of their venom proteins (fig. 107). There are six obvious differences in the protein components of the venom of the specimens of these two species studied. It must be remembered when interpreting these results that only one specimen of *H. trichiurus* (Rooinekpass) was available for study and as this species has a wide geographic distribution and may even be a species complex, these differences, although very distinct, should be considered with reserve.

The species *H. zuluanus, H. bicolor, H. gunningi* and *H. granulatus* were considered to be related based upon morphological similarities.

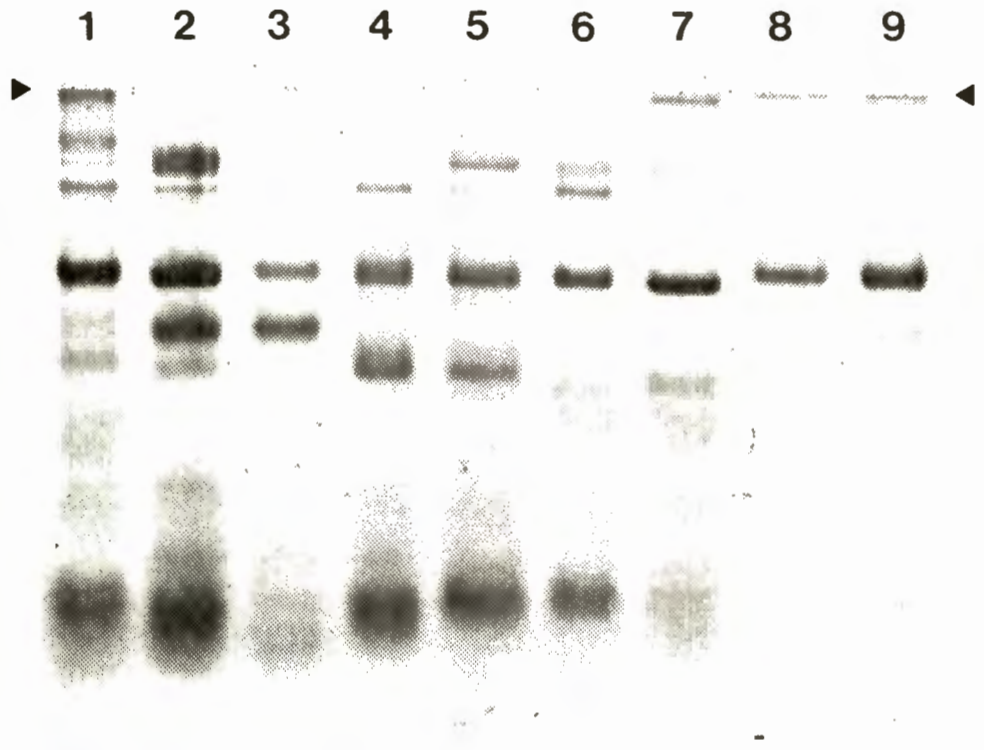


Fig. 107. Electrophoretogram showing differences in the venom proteins of female specimens of several related species. Sample 1, *Hadogenes gunningi* Purcell from Johannesburg. Samples 2-3, *H. bicolor* Purcell from Zusterstroom, 4-5, *H. bicolor* from Haffenden Heights, 6-7, *H. zuluanus* Lawrence from Magudu, 8-9, *H. trichiurus* (Gervais) from Rooinekpass.

Similarities were also seen in the general electrophoretic banding patterns but in each case the species were nevertheless distinct. An examination of figs 107-109 will clearly show the electrophoretic differences and similarities amongst these species. The venom proteins of *H. zuluanus* are more similar to those of *H. bicolor* than they are to *H. trichiurus* but specimens of *H. bicolor* from Zusterstroom in the Bronkhorstspruit district have a protein component which is absent in specimens from Haffenden Heights in the Pietersburg district (fig. 107, samples 2 and 3). Specimens of this species from Lillie and Leopards Crag do have the band which

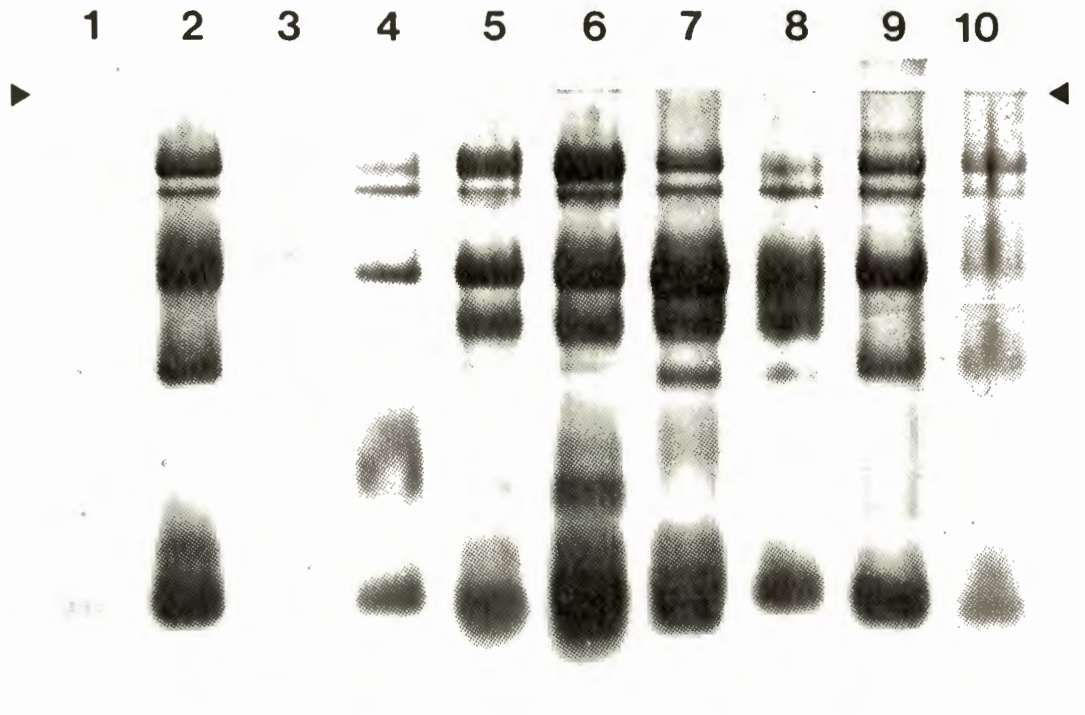


Fig. 108. Electrophoretogram showing venom protein relationships amongst several related species. 1. *Hadogenes gunningi* Purcell from Hekpoort, 2. *H. bicolor* Purcell from Haffenden Heights, 3. *H. granulatus* Purcell from Salisbury, 4. *H. zuluanus* Lawrence from Magudu, 5-6. *H. bicolor* from Zusterstroom, 7-8. *H. bicolor* from Lillie and 9-10. *H. bicolor* from Leopards Crag.

is absent in the Haffenden Heights specimens (fig. 108, samples 5-10) but differ in turn amongst themselves slightly with regard to the concentrations and banding profiles. Six specimens of *H. bicolor* from Haffenden Heights (fig. 109, samples 1-6) do not differ except with regard to concentration which suggests that *H. bicolor* venom composition does differ with geographic distribution. It is possible that sibling species are involved but no morphological differences could be found amongst individuals from the three localities in question. A venom sample from *H. granulatus* (although of a low concentration) does show that this species is similar to

H. bicolor (fig. 108). Morphologically *H. bicolor* and *H. gunningi* are very similar but the venom proteins of these species differ markedly (see figs 107-108).

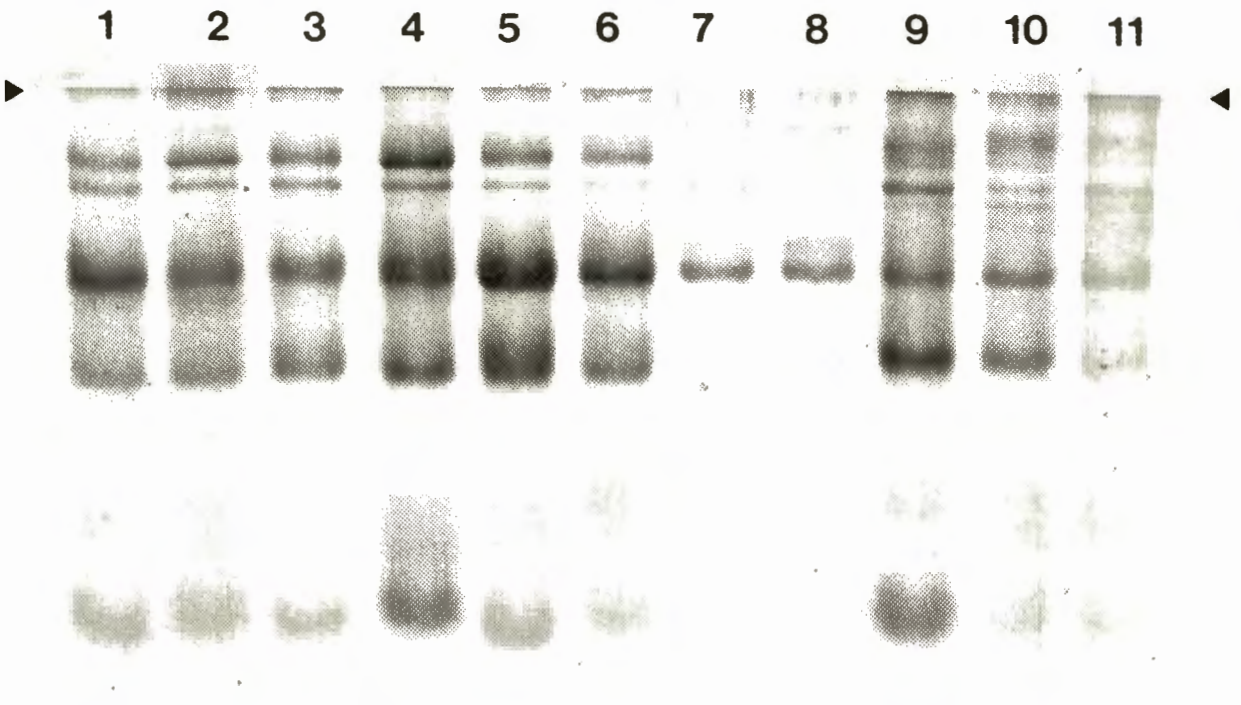


Fig. 109. Electrophoretogram showing the similarity between samples of *Hadogenes bicolor* Purcell from Haffenden Heights (samples 1-6) and their relationship to the banding patterns of *H. troglodytes* (Peters) (samples 7-8) and *H. gracilis* Hewitt (samples 9-11).

An important group of species which I here term the *H. troglodytes* group because they are morphologically similar, consist of *H. troglodytes*, *H. gracilis*, *H. phyllodes* and *H. zumpti*. Morphologically *H. troglodytes* and *H. gracilis* are so similar that I initially thought they might be conspecific. However, they differ in that at least three of the major venom protein components are of different molecular weight (figs 109-110). Likewise *H. phyllodes* and *H. zumpti* are very similar morphologically but

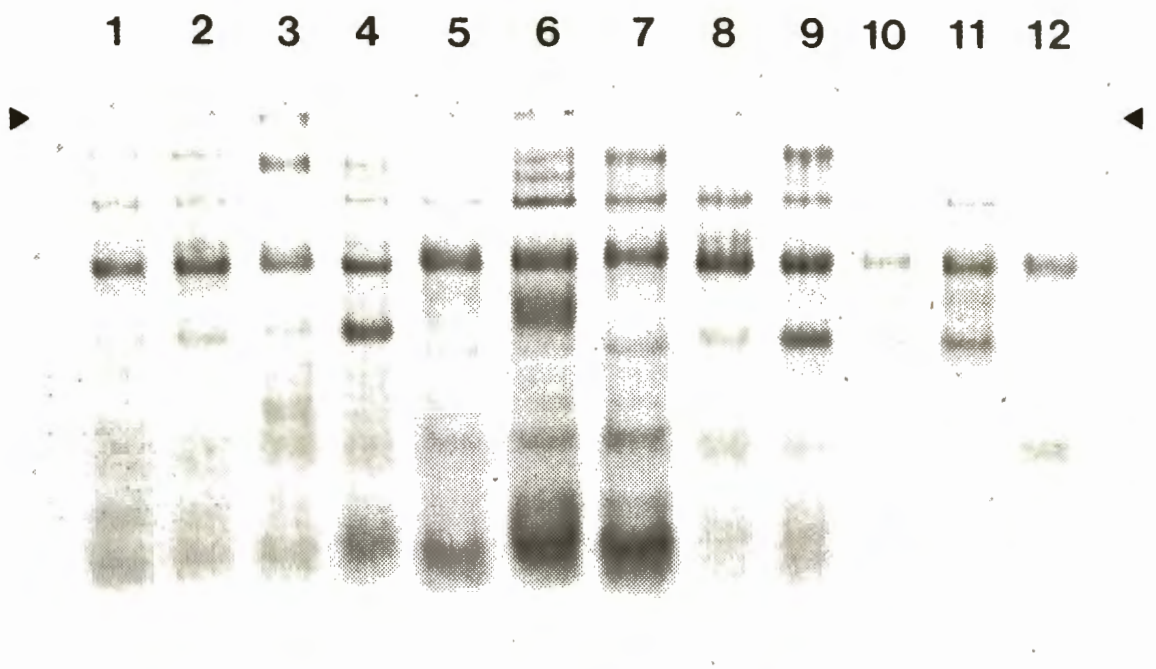


Fig. 110. Electrophoretogram showing the relationship between *Hadogenes troglodytes* (Peters) from the Zoutpansberg (samples 1-2), *H. gracilis* Hewitt from Brits (samples 3-4) and *H. phyllodes* (Thorell) from the following localities: Samples 5-6 from Keimoes, 7 from Zeekoebaard Nek, 8 from Leerkranz, 9-10 from Limewell and 11-12 from Bergenaarspad.

differ considerably with regard to the electrophoretic profiles (fig. 111). The fact that the banding patterns of *H. phyllodes* and *H. gracilis* differ so markedly supports the decision reached in the taxonomic section (see 5.2.13) whereby the accepted subspecies of *H. gracilis* viz *H. gracilis namaquensis* and *H. gracilis fluvialis* were placed in synonymy with *H. phyllodes*. A study of electrophoretic profiles of specimens collected at several localities in the north western Cape shows that while they differ with geographic locality, they are more markedly different from *H. gracilis* (figs 110-111). These electrophoretic results suggest that a more detailed study of the north western Cape species is

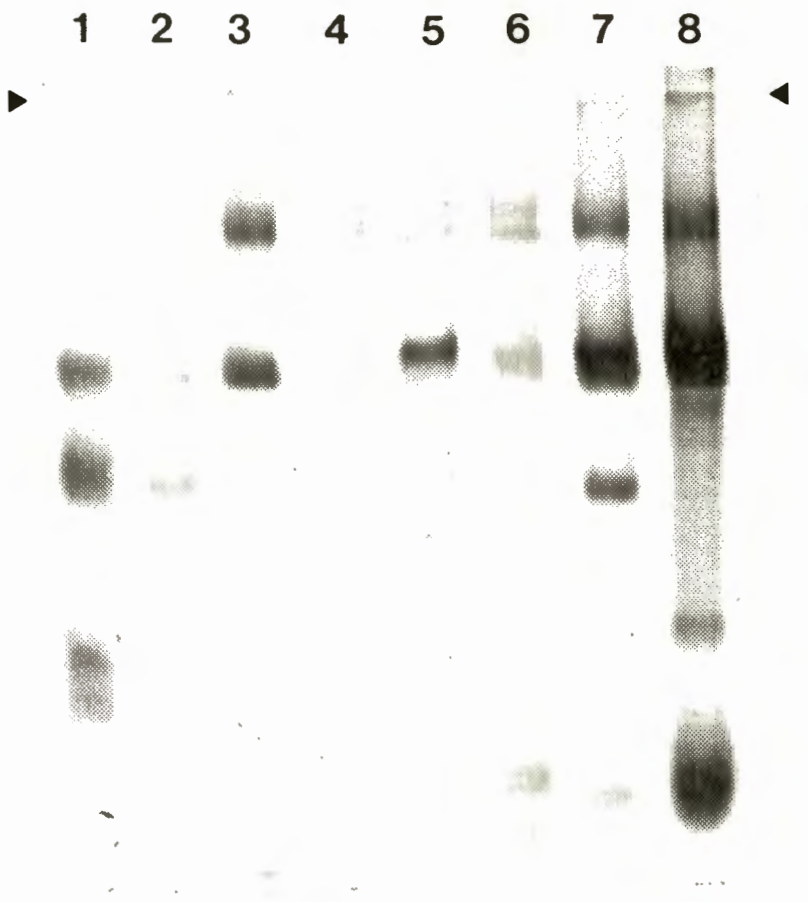


Fig. 111. Electrophoretogram showing profile differences between the following species: 1. *Hadogenes phyllodes* (Thorell) from Louisvale, 2. *H. tityrus* (Simon) from Helskloof, 3-4. *H. phyllodes* from Steinkopf, 5. *H. zumpti* spec. nov. from Tatasberg, 6-7. *H. phyllodes* from Horingsgat and 8. *H. granulatus* Purcell from Shamva.

needed and the conclusions reached in the taxonomic section are tentative. The new species described in this account, *H. zumpti* differs very distinctly from other species of the *H. troglodytes* group (fig. 111), which, once again supports the morphological findings.

7.0 CONCLUSION

Some of the taxonomic decisions reached in this thesis are tentative such as the synonymy of *H. gracilis fluvialis* and *H. gracilis namaquensis* with *H. phyllodes* and five of the described subspecies of *H. trichiurus* with the typical form. The reason for these decisions being tentative is that the types could not be obtained for examination as they were lost or the museums housing them either failed to respond or refused to loan the material. This type of problem could be overcome if taxonomists describing new species would divide the type material amongst two or more museums, at least one of which should be a local institution.

The electrophoretic studies conducted proved that acrylamide gel electrophoresis can be a tremendous aid to the taxonomist provided slab gel methods are employed. Differences in the banding patterns are frequently very subtle and it would thus not be possible to assess minor differences when using disc-gel methods. In general, the electrophoresis results confirmed the morphological findings.

Great care had to be taken in assessing the chromosome counts because of the high frequency of polyploidy in scorpions. Ideally, chromosomes from tissue other than gonads should be assessed as both meiotic and mitotic divisions occur in the gonads. The vast differences in chromosome number amongst many of the species make it clear that chromosomes are a valuable taxonomic aid which has been totally ignored in the past. Possibly this is because cytogenetical methods are very costly operations which can only be afforded by large academic institutions. Differences in chromosome number observed were in keeping with the decisions reached on purely morphological considerations in all cases where chromosome studies were possible.

Two important findings made as a result of the morphological examination were that in species of *Hadogenes*, the trichobothria are not constant for a given species and that the less prominent a taxonomic character is the more it is prone to individual variation. For this reason, only very pronounced species characteristics were exploited in the key. Vachon (1973) has categorically stated that the number and position of the trichobothria is constant for a given species. Examination of species belonging to all southern African scorpion genera except *Hadogenes* has confirmed Vachons' statement. However, in species of *Hadogenes*, the number and position of trichobothria is not constant and invariably differs on the left and right pedipalps of a given individual. In spite of this individual variation, it was possible in a few cases to exploit trichobothrial counts to identify species.

In some scorpion genera such as *Buthotus*, species can be identified by the general morphology of the male paraxial organ. Unfortunately, in species of *Hadogenes* individual variation of the paraxial organs examined appeared to exceed the species differences. Accordingly, the use of these organs as a taxonomic aid was abandoned in all cases except for the description of the new species, *H. zumpti*.

The morphological terminology used in this thesis is based upon the comparative anatomical studies of Snodgrass (1952) and the amendments proposed by Stahnke (1970). As this system of nomenclature is far more rational than that used by French workers such as Vachon, new commers to the field should be encouraged to follow the system outlined here.

An important contribution to the study of *Hadogenes* species is the inclusion of accurate distribution maps for each species. This information together with the photographs of each species and the key to the species will enable the non-specialist to identify any given specimen with a high degree of accuracy.

No taxonomic work can ever be the last word on the subject and while this study has made a contribution to the knowledge of the genus *Hadogenes*, it has not been able to solve all the problems. Indeed it has exposed many of the problem areas for the first time and it is hoped that some of these problems such as the *H. tityrus*, *H. trichiurus* and *H. phyllodes* species complexes will form the subject of a future, more detailed study.

8.0 APPENDICES

8.1 Appendix 1. Abbreviations

AM Albany Museum, Grahamstown
BIS N,N^1 - Methylene-bisacrylamide
BM British Museum (Natural History), London
CBBR-250 Coomasie Brilliant Blue R-250 (ICI)
F1 First filial generation
GM Goteborg Museum, Goteborg
HPC Harington Private Collection, Johannesburg
MNHN Museum National d'Histoire Naturelle, Paris
NA Numerical aperture
NM Natal Museum, Pietermaritzburg
NMS Naturhistorische Museum, Senckenbergia, Senckenberg
p. page
PHA Phytohaemagglutin
SAIMR South African Institute for Medical Research, Johannesburg
SAM South African Museum, Cape Town
SDS Sodium dodecylsulphate
SEM Scanning electron microscope
SMN State Museum, Windhoek
SMRS Specific Mate Recognition system
spec. nov. New species *(species nova)*
Syn. nov. New synonym
TEMED N,N,N^1,N^1-tetramethylethylenediamine
TM Transvaal Museum, Pretoria
2n diploid chromosome number

8.2 Appendix 2. Origins of the species names

Hadogenes: The bearded deamon, probably so named because the species of this genus are generally exceptionally large and the pedipalps are embellished with a dense covering of setae and trichobothria.

H. bicolor: Two coloured. The legs of this species are much lighter in colour than the body and pedipalps.

H. gracilis: Gracile - elegant. Males of this species are very long and slender.

H. granulatus: Granular. The vesicle of the male is very coarsely granular in this species.

H. gunningi: Named after Dr J.W.B. Gunning who was the director of the Staats Museum in Pretoria. The Staats Museum later became the Transvaal Museum.

H. lawrencei: Named in honour of the distinguished South African arachnologist, Dr R.F. Lawrence.

H. minor: Small. This species in one of the smaller species in the genus.

H. paucidens: Few teeth. The origin of this name is not apparent but it does have relatively few pectinal teeth and the ventral surface of the last metasomal segment is sparsely covered with tooth-like granules.

H. phyllodes: Leaf shaped. The body of this scorpion could be regarded as leaf-shaped.

H. taeniurus: Banded. The posterior portion of the tergites of this species are often lighter in colour than the anterior region which imparts a transverse banded pattern to the animal.

H. trichiurus: Hairy tail. This was the first species of the genus to be described. All species of the genus have numerous long setae covering the metasomal segments.

H. tityrus: A fictitious monster said to be bred between a sheep and a goat. The reason for choosing this name is not clear.

H. troglodytes: A cave dweller, and possibly named thus because these scorpions are found in the cracks and crevices of rocks.

H. zuluanus: From Zululand.

H. zumpti: Named in honour of Prof. F.K.E. Zumpt who was the head of the department of Medical Entomology at the South African Institute for Medical Research.

9.0 ACKNOWLEDGEMENTS

I am deeply indebted to the following people and institutions: The South African Institute for Medical Research through its director, J. Metz, for the facilities needed to undertake this study. My colleagues, J.A. Ledger, F.K.E. Zumpt, C.B. Martindale, B. Friedman, J. Segerman, A.C. Cantrell and S.D. Berson for advice and technical assistance. C.A. Green and R. Hunt for advice on chromosome preparation. L. Losacco for all the typing involved with the project. M. Anderson and her staff for advice and the drawings for figs 18-19. The British Council for helping to make it possible for me to visit the British Museum in London for three months. K. Hyatt and F. Wanless of the British Museum, V. Whitehead and E.B. Eastwood of the South African Museum, S. Louw and C.G. Coetzee of the State Museum (Windhoek), W.D. Haacke of the Transvaal Museum, the Director, Naturhistorische Museum, Senckenbergia, M. Vachon of the Museum National d'Histoire Naturelle and B. Lamoral of the Natal Museum for the loan of Museum specimens. For collecting specimens, E. van der Merwe, J.A. van Rooyen, H. Biggs, B.P.W. Fratscher, M. Crees, F. Matthews, I. Davidson and A. Harington. For the SEM photographs, the Director and J. Harris, N.P.R.L., Council for Scientific and Industrial Research. D. Addis for loaning equipment and donating all the photographic materials needed to prepare the illustrations and photographs for duplication. G. Thompson for duplication and my late father for locating the co-ordinates of many obscure place names encountered in the literature and museum records. My supervisor, P.D. Theron for commenting on the manuscript and my wife, Santa, for encouragement.

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