Chapter 1

INTRODUCTION

1.1. Overview of Aradidae diversity and systematics

The Aradidae is a large cosmopolitan Heteropteran family, commonly known as flat bugs or bark bugs as they are usually found on or under the bark of dead trees. Most species are mycetophagous and they possess specially adapted and elongated mandibular and maxillary stylets which are usually coiled in the head (Lee & Pendergrast 1976), for sucking the juices of the fungi (Usinger & Matsuda 1959). Their flattened body-form and sombre colours are well adapted for life on or under bark.

The Aradidae occupies a rather isolated position within the Pentatomorpha (Leston, Pendergrast & Southwood 1954, Stys & Kerzhner 1975). They agree with the rest of the group in egg type, male genitalia and form of pseudarolia but differ by lacking trichobothria.

At present the family comprises more than 1 800 described species belonging to 214 genera. The Neotropical (472), Australian (including New Zealand) (466) and Oriental (436) regions are most species rich followed by the Afrotropical (201), Nearctic (115) and Palaearctic (105) regions. (Kormilev & Froeschner 1987 and data extracted from subsequent literature.) I am, however, aware of many undescribed species from the Afrotropical region and it is possible that this region will prove to be as species rich as the other regions of Gondwanian origin.

The Aradidae are subdivided into eight subfamilies of which the Chinamyersinae is confined to the Australian region while the Isoderminae and Prosympiestinae are also mainly Australian, each with a single species in the Neotropical region. The Aneurinae, Aradinae, Calisiinae and Mezirinae occur in all the major biogeographical regions while the Carventinae is absent only from the Palaearctic region. Gondwanaland seems to be the centre of diversification of all the subfamilies except the Aradinae, in which 158 of the 207 species occur in the Palaearctic and Nearctic regions. In all the other subfamilies by far the most species occur in regions of Gondwanian origin (refer to Table 1.1). From Table 1.1 it is also evident that the Mezirinae is by far the largest subfamilies (containing 1075 species) followed by the Carventinae (254), Aradinae (207), Aneurinae (139), Calisiinae (100), Prosympiestinae (13), Chinamyersinae (7) and Isoderminae (6).

Although more than 200 species of Aradidae have been described from the Afrotropical region, nearly all of them have been described by foreign entomologists working on museum collections or material collected by amateur entomologists from time to time. The most noteworthy of these entomologists are Kormilev from the USA, Hoberlandt from Czechoslovakia, Schouteden from Belgium and lately Heiss from Austria. Together they were responsible for the descriptions of about 70% of the Afrotropical region's species.

Relatively few species have been recorded from southern Africa. Hoberlandt (1958) listed only 11 species from this subregion. Subsequently 15 more species have been described or recorded from southern Africa (Hoberlandt 1959, Usinger & Matsuda 1959, Kormilev 1961, Kormilev & Heiss 1976, Jacobs 1986, Heiss & Jacobs 1989). For the past two decades I have collected extensively in South Africa and have accumulated more than 10 000 specimens belonging to an estimated 50 species, about half of these undescribed. The species belonging to the Carventinae are described in this work.

Table 1.1: The geographical distribution and number of species and genera of the Aradidae*

Subfamily	Total no. of genera & species	Neotropical	Nearctic	Palaearctic	Afro-tropical	Oriental	Australian and New Zealand
Aneurinae	7-139	4-46	2-11	3-8	4-13	2-36	4-25
Aradinae	4-207	2-14	2-81	2-77	1-10	2-19	1-6
Calisiinae	6-100	2-19	1-4	1-3	4-10	2-8	2-56
Carventinae	64-255	16-65	2-3	-	11-29	19-59	25-99
Chinamyersinae	4-7	-	-	-	-	-	4-7
Isoderminae	1-6	1-1	-	-	-	-	1-5
Mezirinae	124-1075	42-326	4-16	6-17	29-139	42-314	38-256
Prosympiestinae	4-13	1-1	-	-	-	-	3-12
Total	214-1802	68-472	11-115	12-105	49-201	67-436	78-464

* Modified from Kormilev & Froeschner 1987. (Excluding the taxa described in this work.)

1.2. Cytogenetic characteristics of the Heteroptera

The Heteroptera is one of the few groups which possesses holocentric chromosomes. The chromosomes do not have a localized centromere like in most eukaryotic groups but it is distributed along the length of each chromosome and it is often termed a diffuse centromere (Ueshima 1979). Buck (1967) reported that the kinetochore plate stretches along the total length of the chromosome in *Rhodnius prolixus* (Reduviidae) during mitosis while Ruthman and Permantier (1973) found that only about 4,2% of the metaphase plate is covered in *Dysdercus intermedius* (Pyrrhocoridae). Comings & Okada (1972) reported it covering up to 75% of the long axis of the chromosomes of *Oncopeltus fasciatus* (Lygaeidae).

Because of its holocentric nature the parts of a fragmented chromosome are not lost and may still move to the poles at anaphase (Hughes-Schrader & Schrader 1961, La Chance et al. 1970). This is not without exception as Seshachar et al. (1959) showed that acentric fragments and lagging chromosomes exist in *Eurybrachis apicalis* (Homoptera) after irradiation.

A kinetochore plate covering the largest part of chromosomes would interfere with chromosome segregation after interstitial crossing over and Comings & Okada (1972) showed that it is absent in Heteropteran chromosomes during meiosis. Various authors (Helenius 1952, Hughes-Schrader & Schrader 1961, Parshad 1958) have observed that the spindle attaches to one of the chromosome ends (telomeres) during meiosis. Nokkala (1985) recently showed that both telomeres of each chromosome have potential kinetic activity and that the telomere which is kinetically active during the first meiotic division is kinetically inactive during the second division. He and Nokkala & Nokkala (1984a, 1985) suggest that the chromosome type (monokinetic or holokinetic) is the result of relatively simple structural differences together with the different distribution of kinetic DNA sequences along the axial system of chromosomes.

There are also other peculiarities concerning Heteropteran chromosome behaviour which make them unique. In all but the family Tingidae and a few individuals of four other families (Belostomatidae, Coreidae, Notonectidae and Reduviidae) (Manna 1984) the sex chromosomes show a reverse segregation pattern (postreductional) from the autosomes (prereductional) during spermatogenesis (the males being the heterogametic sex). For example: In an individual with a XY sex chromosome system the X and Y chromosomes form univalents at metaphase I (MI) and undergo chromatid segregation at anaphase I (AI) so that each metaphase II (MII) cell contains the same chromosome complement. During MII the X and Y chromatids become associated for a short period before they segregate to opposite poles during anaphase II (AII) - the so-called "touch-and-go" pairing (Schrader 1940). In the females (the homogametic sex) meiosis is normal with the sex chromosomes forming bivalents and segregating normally.

The sex chromosomes are easy to identify at MII of spermatogenesis because of their unusual behaviour. Although they are monovalents at MI they are more difficult to identify because they look very much like ordinary bivalents.

The sex chromosome systems in male Heteropteran species could broadly be classified as X0, X_n0, XY and X_nY (Manna 1984). The Aradidae, with the exception of two species, all have XY or X_nY sex chromosome systems. The exception is a XY_n (XY_1Y_2) sex chromosome system which is recorded for the first time in this work.

The only feature of Heteropteran cytogenetics that is not also found outside of the suborder are the m-chromosomes. These chromosomes, which are usually much smaller than the autosomes and sex chromosomes, were first described as micro-chromosomes by Wilson (1905). When they are present there is always only a single pair. They are always unpaired during the meiotic prophase and no chiasmata are formed. During the first and second anaphase, they are negatively heteropicnotic. Generally the m-chromosomes orient themselves in the centre of the ring of autosomes at MI and usually at MII as well, and they are therefore described as median chromosomes by some authors. The

cytogenetic and genetic significance of the m-chromosomes is unknown. They apparently do not occur in the Aradidae.

Apart from the peculiarities mentioned above the course of meiosis is fairly conventional except for a diffuse stage (a term first used by Wilson (1912) directly after pachytene. In this stage the cell size increases and the chromosomes become partly despiralized, resulting in the nucleus returning to an interphase-like state. Immediately after the diffuse stage the chromosomes usually pass into a typical diakinesis. Each autosomal bivalent usually has one chiasma although larger chromosomes often have two chiasmata. More than two chiasmata per bivalent have not been recorded. The course of meiosis in the Aradidae is described in detail for *Adamanotus uncotibialis* in Chapter 4.

Many cytogeneticists believe that the trend in karyotype evolution in the Heteroptera would be towards a higher chromosome number (Ueshima 1979, Malipatel 1979, Newman & Cheng 1983, Mittal & Joseph 1984). They argue that chromosomes that have been fragmented can persist and easily get established because of their holokinetic nature (a process known as agmatoploidy). Thomas (1987) disputed this, he gave many examples of fusions and rightfully showed that in most of the supposed cases of agmatoploidy crucial evidence is lacking. He did, however, not dispute the fact that there seems to be a general increase in chromosome numbers, but pointed out that it is possible that lineages with a higher chromosome number are more successful and that there may be other processes by which the chromosome number can increase. There are several cases in the Heteroptera where the autosome number has been doubled between related species or genera without any evidence of a series of intermediate numbers. Although this suggests classical polyploidy, several authors (Hughes-Schrader & Schrader 1956, Akingbohungbe 1974, Ueshima 1979) pointed to weaknesses in this hypothesis. Aside from the traditional view that polyploidy should not be expected in sexually reproducing animals (Muller 1925, White 1946), the sex chromosomes have not doubled in most instances and the amount of chromatin in the species with the doubled autosome number is more or less equivalent to that in the ancestral karyotype, instead of the concomitant doubling that would be expected. To explain this situation Hughes-Schrader & Schrader (1956) and Schrader & Hughes-Schrader (1958) forwarded a hypothesis of chromatid autonomy whereby individual chromatids may have individuated to become neo-chromosomes. For autonomy to be possible, chromatids would at least have to be bineme. Because it is now widely accepted that chromosomes are unineme, White (1978) refers to the theory as "ancient". The only other possibilities are that a special process is responsible or that very strong orthoselection exists and that intermediates existed only temporarily. Neither of these hypotheses is particularly convincing and both are unsubstantiated (refer to discussion in 12.1.2)

Notwithstanding holokinetic chromosomes, chromosome numbers in the Heteroptera are quite stable. Most Heteropteran families can be characterized by a modal diploid complement, at least for the autosomes. For example, in the family Tingidae all but one of the fifteen cytogenetically known species have a chromosome number of 2n = 14XY (the exception has 12XY - Ueshima 1979). Likewise 25 of the 26 karyotypically known species of Corixidae have 2n = 24XY (the exception has 26XY). The

cytotaxonomy of various taxa in the Heteroptera has been studied and used as an aid in higher classification (Leston 1957, 1958, Manna 1958, Ueshima 1966, Ueshima & Ashlock 1980). The three Aradidae subfamilies (Aneurinae, Carventinae, Mezirinae) of which a significant number of species have been studied cytogenetically by myself shows an unprecedented variation in chromosome numbers. Many closely related species have vastly different chromosome numbers, and even within species there seems to be some variation.

Although the chromosome constitution of more than 1 200 Heteropteran species are known, Ueshima (1979) and Manna (1984) listed only three species belonging to the Aradidae. *Dysodius lunatus* ($2n=31X_1X_2Y$) and *Mezira pacifica* ($2n=27X_1X_2Y$) belong to the Mezirinae while *Isodermus gayi* ($2n=23X_1X_2Y$) belongs to the Isoderminae. Jacobs & Liebenberg (1980), Jacobs (1986), Heiss & Jacobs (1989) and Grozeva (1997) listed the chromosome numbers of several more species belonging to the Aneurinae, Aradinae, Calisiinae, Carventinae and Mezirinae. These and other unpublished data are presented in Table 11.1(p.258) and will be discussed in Chapter 11.

1.3. Scope of this study

Most taxonomy is traditionally done without taking cytogenetics into account. On the other hand very few cytogeneticists are taxonomists and they have to rely on identifications made by taxonomists (usually from museum specimens) who are often not even specialists on the particular taxa. Integrating these two disciplines provides the opportunity to study problem cases in more detail from both angles, often revealing possibilities not previously thought of. In this study I will use traditional taxonomic and cytogenetic information to show how they can complement each other, especially in taxonomic problem cases.

This study is mainly concerned with the Carventinae of South Africa. I have chosen the Carventinae for various reasons:

1) Preliminary studies have shown that there are many undescribed species. Until recently only four species in the genus *Dundocoris* were known from southern Africa (Hoberlandt 1959, Kormilev 1961). Recently Heiss & Jacobs (1989) created two more genera (*Pondocoris* and *Trichocarventus*) and described two more species. I have more than 20 undescribed taxa at hand.
2) All Carventinae species from southern Africa are apterous and have extremely low vagility. Furthermore they only occur in moist evergreen forests. These forests can roughly be divided into the coastal forests along the south and east coast, and the inland or montane forests which have a very patchy distribution on inland mountains, especially on the eastern escarpment of the Drakensberg. Their low vagility and the patchy occurrence of their habitat would mean that there are many isolated populations with interesting implications.
3) Many of these forests are relatively easily accessible for collecting enough specimens for both cytogenetic and taxonomic work.

Chapter 2

MATERIAL AND METHODS

2.1 Taxonomy

Specimens were collected and stored in 70% ethanol until they were mounted or prepared for examination by scanning electron microscope (SEM). The Carventinae are characterised by the presence of a resilient, insoluble incrustation that covers the greater part of the body and obscures the surface detail. It is difficult but necessary to remove this incrustation in order to examine and describe the sculpture. The incrustation was removed by submerging the whole specimen in a hot solution of 10% potassium hydroxide for 1-2 minutes to soften the incrustation while cleaning it in a Bransonic 321 ultrasonic cleanser. Parts were treated the same way or cleaned in the ultrasonic cleanser while still in 70% ethanol. They were glued to the SEM stubs with double-sided cellotape or with a special glue. In the case of whole specimens, a small amount of colloidal silver or graphite paste was applied below the neck, leg bases and pygophore (in a way that was not visible from above) to improve conductivity. They were then air dried and gold coated before examination and photography with a Hitachi Model S-450 SEM using an acceleration voltage of 15kV or 20kV.

When it was necessary to salvage specimens the gold coating was removed afterwards by submerging the specimen in a saturated solution of potassium cyanide in water until all the gold was dissolved. This process takes from a few minutes to a few hours.

The aedeagi were prepared from specimens that were collected in copulation. The ovipositor was carefully cut away and the aedeagus freed. The whole pygophore with the inflated aedeagus was dried by critical point drying and then prepared for, and examined under the SEM like the other specimens.

Measurements of specimens were obtained by projecting an image of the insect onto a digitizer tablet of a Kontron image analyser computer by means of a Zeiss SV8 stereo microscope fitted with a camera lucida. The measurements were then taken by using a cross-hair cursor. The correct scale was obtained by projecting the image of a stage micrometer (under the same magnification and focus setting used for the insects) onto the digitizer tablet and measuring a specific length. Special care was taken to ensure that the structure which was being measured lay on a horizontal plane in order to minimize errors of measuring three dimensional structures by means of two dimensional images. The diagnostic measurements that were used are as follows (see Fig. 1):

Total length: the distance from the tip of the head (usually the genae) to the tip of the pygophore (in males) or tergum 9 (in females). The genitalia of many of the mounted specimens in my collection are more or less extended as they become inflated during storage in 70% ethanol or Pampal's fluid. In these cases I compensated for the distance of extension while measuring.

Total width: the distance over the widest point of the abdomen (usually the posterior part of tergite 4).

Tergal disk length: the longitudinal length, at midline, of the abdominal tergal disk.

Tergal disk width: the distance over the widest point of the abdominal tergal disk (usually about one-third of the length of DELTg 4 from its posterior margin). In heavily incrusted specimens the incrustation was removed with a sharp needle to expose the margin.

Pronotal length: the distance, usually taken just off-centre from the midline, between the medioposterior angle of the pronotal disk and the anterior margin of the collar.

Pronotal width: the distance over the widest point of the pronotum (usually at the level of the posteriolateral angles).

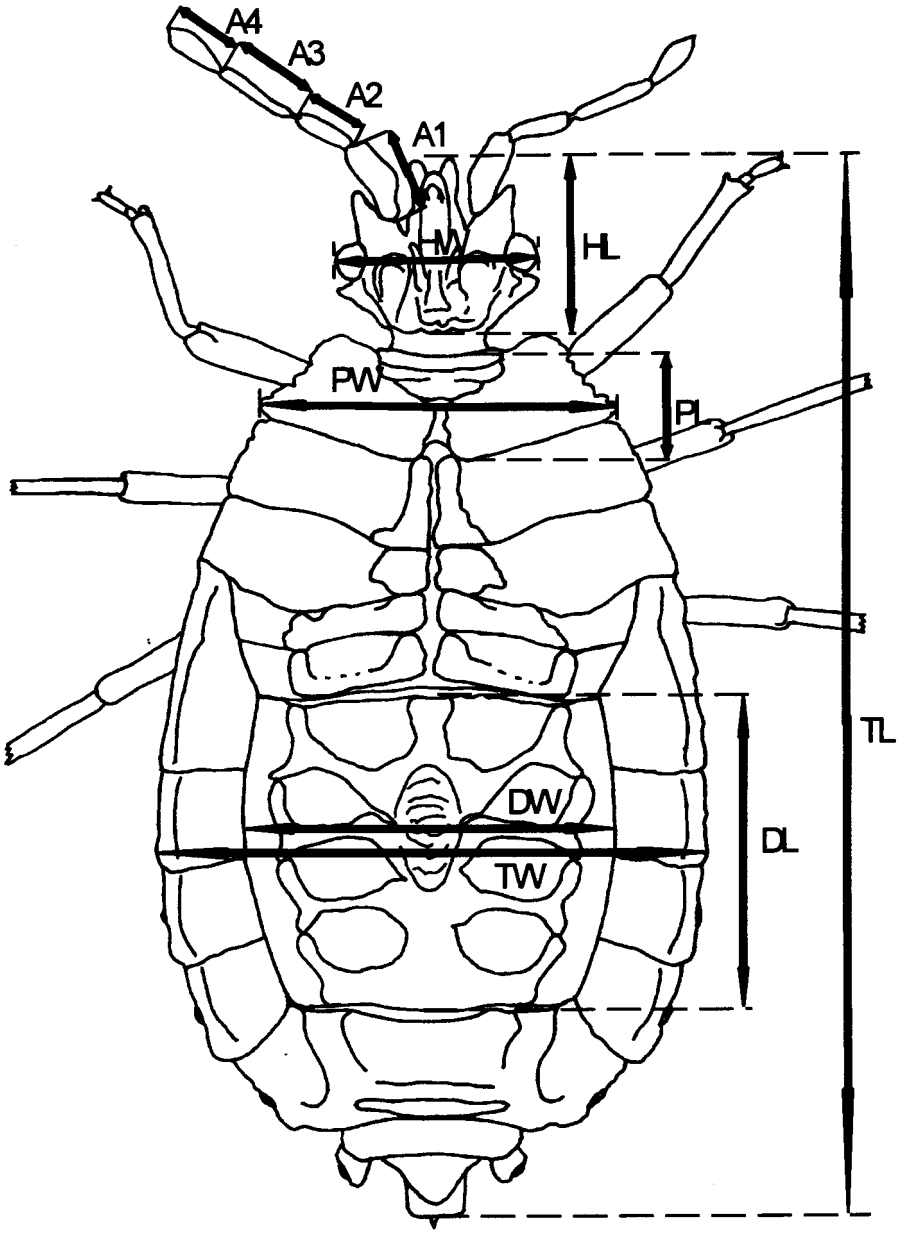
Head length: the distance from the anterior tip of rostrum (usually the genae but sometimes the clypeus) to the margin between the smooth neck area and the rough, elevated area of the head.

Head width: the distance between the outer margins of the eyes.

Antennal segments: length of the antennal segments, including the pedicel if pedicellate.

The material on which this study is based will be housed in the following institutions which are referred to in the text by the accompanying abbreviation.

AMGS- Albany Museum, Grahamstown, South Africa.
AMNH- American Museum of Natural History, New York, USA.
BMNH - British Museum (Natural History), London, England.
BMSA - National Museum, Bloemfontein, South Africa.
CASC - California Academy of Sciences. San Francisco, California, USA.
DHJS - D.H. Jacobs private collection, Pretoria, South Africa.
DMSA - Durban Museum and Art Gallery, Durban, South Africa.
EHIA - E. Heiss private collection, Josef Schraffl-strasse 2A, A- 6020 Innsbruck, Austria.
HNHM - Hungarian Natural History Museum, Budapest, Hungary.
ICCM - Carnegie Museum of Natural History, Pittsburg, Pennsylvania, USA.
ISNB - Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium.
MNHN - Museum National d'Histoire Naturelle, Paris, France.
MRAC - Museé Royal de l'Afrique Centrale, Tervuren, Belgium.
MZLU - Zoological Institute, Lund University, Lund, Sweden.
NHMV - Naturhistorisches Museum Wien, Vienna, Austria.
NHRS - Naturhistoriska Riksmuseet, Stockholm, Sweden.
NMBZ - National Museum of Zimbabwe, Bulawayo, Zimbabwe.
NMSA - Natal Museum, Pietermaritzburg, South Africa.
QBUM - Museum Nacional, Rio de Janeiro, Brazil.
QMBA - Queensland Museum, Brisbane, Australia.
SAMC - South African Museum, Cape Town, South Africa.
SANC - National Collection of Insects, Pretoria, South Africa.



A1-A4 - Length of antennal segments 1 to 4.
TL - Total length.
TW - Total width.
HL - Length of head.
HW - Width of head (across eyes).
PL - Length of pronotum.
PW - Width of pronotum.
DL - Length of abdominal tergal disk.
DW - Width of abdominal tergal disk.

Fig. 1. Measurements used in descriptions.

SEMC - Snow Entomological Museum, University of Kansas, Lawrence, Kansas.
SMWH - State Museum, Windhoek, Namibia.
TMSA - Transvaal Museum, Pretoria, South Africa.
USNM - Smithsonian Institution, National Museum of Natural History, Washington D.C., USA.
UZMD - Universitets Zoologish Museum, Copenhagen, Denmark.
UZMH - Zoological Museum, Helsinki, Finland.

The following morphological and cytogenetic terms and abbreviations are used in the text (refer to Jacobs 1986 for more detail of the morphological terms):

A1, 2, ...	-	autosome 1, 2, etc.
AI	-	anaphase I
AII	-	anaphase II
DELTg	-	dorsal external laterotergite (= connexivum)
LGI	-	lateral glabrous impression
MI	-	metaphase I
MII	-	metaphase II
MTg	-	mediotergite
VLTg	-	ventral laterotergite

2.2 Cytogenetics

Specimens were collected and kept alive in plastic vials (supplied with adequate footing) until they were fixed for cytogenetical studies in a freshly prepared solution of 2,5:1::methanol:propionic acid. Males were killed by dropping them into the fixative and immediately cutting them into two pieces through the thorax in order to assist the penetration of the fixative. (The small size of the insects renders it impractical to dissect the testes of unfixed individuals.) The fixed insects were stored in the fixative in a refrigerator (±4 °C) for a few days up to several years until preparations were made. The best results were obtained where specimens were stored in airtight glass vials for not longer than three months. Longer periods often resulted in poor staining and spreading of the chromosomes.

The preparations were made according to the following procedure:

1) Cover glasses (usually No 1, 22mm square) are covered with a thin layer of Mayer's albumin adhesive (Darlington & La Cour 1976) which is dried 3-5cm above an alcohol flame until is ceases smoking.
2) The testis (or a piece of testis) is dissected out and placed in a small drop of stain on a clear slide. The stain used was usually a 1% solution of carmine in 45% propionic acid.
3) A needle-point of ferric-acetate (a saturated solution in 45% acetic acid) is usually added to intensify the staining.

4) The testis is gently tapped with the flattened end of a piece of plastic knitting needle until the cells are well separated.
5) The cell suspension is covered with an albumized cover glass, taking care that no bubbles are trapped.
6) The slide is moderately heated (2-3 seconds directly above an alcohol flame while the slide is continuously moved to prevent local overheating) to soften the cells and to intensify the staining.
7) The slide is now quickly placed between a double layer of blotting paper and hard pressure (usually by pressing down with one's thumb) is applied on the cover glass to squash the cells and spread the chromosomes.
8) After ascertaining that the desired stages are present the cover glass is removed by inverting the slide in a petri- dish filled with 45% acetic acid with one end of the slide resting on a glass rod.
9) When the cover glass (to which the cells adhere) has separated from the slide it is dehydrated through a series of 60%, 80%, 96% and absolute ethanol, remaining in each for 1- 2 minutes. It is then mounted in Euparal on a clean slide and dried in an oven at 40°C for about a week.

The preparations were analysed with a Zeiss Lab 16 microscope and the photomicrographs taken under 512 times magnification on the negative (100x planapochromatic objective x 1,6 optovar x 3.2 magnification) with a Zeiss universal photomicroscope. The photomicrographs in the figures were not printed to the same magnification. Because of the squash method used in preparation of the slides, significant variation exists between slides and even between different areas on the same slide in the size of the chromosomes. It was therefore deemed more important that the figures should illustrate the morphology and arrangement of the chromosomes than the comparative sizes of the stadia and cells.

The idiograms were prepared as follows:
The areas of metaphase II chromosomes were used to compile the idiogram. Metaphase II was chosen because at this stage the chromatids of each chromosome are separate, all chromosomes are probably compacted to the same degree and, most important, the sex chromosomes are usually unambiguously identifiable. Only cells where the chromosomes were well spread and preferably seen in equatorial view were selected for measurements to minimize the chance that the two chromatids lie on top of each other. The chromosome areas were measured using a Quantimed 520 Image Analyser (Cambridge Instruments) with a CCD camera either directly connected to a Zeiss Lab 16 microscope when the cytogenetic preparations were used or connected to a macrolens when photomicrographs were used. More than one individual and usually about five cells per individual were measured whenever possible (refer to tables under each species), and three repetitions of each measurement were taken. The measurements were stored on computer disk and later transferred to the mainframe computer of the University of Pretoria where the data was processed using a SAS program developed by myself.

The SAS program compiled idiograms of the true and relative areas of the chromosomes. The relative areas were used for most comparisons as much variation in true areas occur because of differential squashing of cells. The relative area of each chromosome (including the sex chromosomes) was calculated as a percentage of the total of the area of all the autosomes. The sex chromosomes were explicitly excluded in calculating this total because it is a well known fact that in the Heteroptera the sex chromosomes are much more variable in size than the autosomes (Heizer 1950, Hughes- Schrader & Schrader 1961, Thomas 1987). I often observed relative size differences of sex chromosomes, even between conspecific individuals.

Comparison of true chromosome areas were mostly used to identify cases where chromosomes have the same relative sizes but their true sizes differ markedly between species, races or individuals as have been found in various taxa within the animal and plant kingdoms (Rees, Shaw & Wilkinson 1978, Riana & Rees 1983, Kenton 1984).

Various authors have shown that the DNA content of cells is positively and highly correlated with chromosomal volume (Rees et al. 1978, Fox 1969). I have used chromosome surface areas and not chromosome volume in all calculations for the following reasons:

1. Heteropteran chromosomes are relative fragile to squashing (Sands 1982). I have used only well squashed cells for measurements. In such cells the chromosomes are most probably in the form of flattened disks rather than cylindrical rods. Calculation of chromosome volumes (assuming they are cylindrical rods) from such flattened chromosomes would give inaccurate values. Furthermore, assuming the squashing does not lead to differential compacting of the chromosomes, the relative chromosome areas would be constant notwithstanding differential squashing of cells on the same preparation or of various preparations.
2. The shape of the chromosomes during meiosis, even if not squashed, does not lend itself to calculation of chromosome volume because it is not rod-like with a constant diameter. Mitotic metaphases were rare and the chromosomes were usually not well spread. Relative chromosome surface areas of flattened chromosomes should, however, be accurate parameters of the chromosome volumes and should also be highly correlated with DNA amount.

Various authors (e.g. Sands 1982, Satapathy & Patnaik 1988) have erroneously used F tests to compare the chromosomes of various species. They ignored the fact that, in compiling idiograms, reversal of the order of chromosomes often happens if the different chromosomes cannot be identified unambiguously (Essad, Amoux & Maia 1966, Matern & Simak 1968, Chetty, Upahaya & Kedharnath 1970). Reversal of chromosome order leads to the underestimation of statistical parameters like variance and standard deviation which in turn often leads to (false) significant statistical differences between chromosomes. Matern & Simak (1968) presented a method based on the folded normal distribution whereby these errors can be corrected when only two chromosomes are involved. This method, however, could not be applied where more than two chromosomes have similar sizes, and no statistical method exists to handle such cases. All the idiograms presented in this work, with their statistical parameters, are thus subject

to these errors. The only way such errors could be prevented is when every chromosome in every measured cell could be unambiguously identified. This is usually possible with G-banded chromosomes. However, G-band staining has thus far been ineffective in the Heteroptera. Muromoto (1975, 1978) has been able to obtain some G-bands in Heteroptera but their quality and structure render them impractical for general usage.

In spite of the inherent possibility of error in idiograms, I managed (in conjunction with the Department of Statistics at the University of Pretoria) to develop a statistical method to compare the idiograms of two species. This computer intensive method is based on the bootstrap method of Efron (1979a, 1979b), and is basically as follows:

1) Datasets, used to compile the idiograms of the two species, are combined.
2) Simulations of the two datasets are drawn with replacement from the combined dataset.
3) In each of the cells drawn the assumption is made that all the chromosomes, where there is a chance of reversal of order, are of the same size and they are also drawn with replacement. This is to correct for reversal of order and results in more conservative testing.
4) Idiograms are compiled from these simulated data sets and test statistics are calculated.
5) Points 2 - 4 are repeated a large number of times (more than 250 times) and the 95th and 99th percentiles are calculated for the empirical test sample distribution.
6) The test statistics are also calculated for the true datasets and compared with those of the empirical test sample distribution. If it differs significantly, the null-hypotheses that the two karyotypes are identical can be rejected.

The test statistics we used were $\{\bar{x}.(j)-\bar{y}.(j)\}^2$ for specific chromosomes and $\sum_j \{\bar{x}.(j)-\bar{y}.(j)\}^2$ for the karyotype as a whole. ($\bar{x}.(j)$ and $\bar{y}.(j)$ represent the mean chromosome areas for the two species respectively.)

I have used this procedure to test the hypotheses that two chromosomes of *Silvacoris heissi* (2n = 14XY) fused to form the large chromosome of *S. karkloofensis* (2n = 12XY) and the results are discussed under the genus concerned.

Chapter 3

KEYS TO GENERA AND SPECIES

3.1 Key to the genera of apterous Carventinae[1] of the Afrotropical Region:

1. Body very strongly gibbose, dorsal surface covered with large acinose granulations; less than 1,5 times as long as wide; pronotal collar absent; labium extending beyond posterior margin of the head . . . . . *Comorocoris* Heiss (Comores Islands)
Body not strongly gibbose, dorsal surface not acinose; more than 1,75x as long as wide; pronotal collar present; labium never extending beyond posterior margin of head. 2

2(1). Fused dorsal external laterotergites 1-3 (DELTg 1+2+3) extending anteriad to posterior margin of mesonotum and preventing metanotum from reaching lateral margin of body. 3
Metanotum reaching lateral margin of body. 4

3(2). Mesonotal median ridge diamond-shaped, extending posteriad to first abdominal tergite; postocular tubercles present; males with unciform outgrowth on hind tibia and a granulate outgrowth on hind femur . . . . . ***Adamanotus* gen. nov.** (South Africa)
Mesonotal median ridge not diamond-shaped, fused with metanotal ridge, widening posteriorly; postocular tubercles absent; males presumably without modified hind tibiae and femora. . . . . *Andobocoris* Hoberlandt (Madagascar)

4(2). Pro- and mesothorax with prominent lobulate extensions laterally; rostral atrium wide open. . . . . *Veroncaptera* Vasarhelyi (West Africa)
Pro- and mesothorax without lateral extensions; rostral atrium slit-like. 5

5(4). Whole body covered with conspicuous, erect, fairly long setae; eyes stylate. . . . . ***Trichocarventus*** Heiss & Jacobs (South Africa)
Body not covered with conspicuous setae; eyes sessile. 6

6(5). Abdominal tergites 1 and 2 (MTg 1+2) separated from metanotum by a suture; mesonotal median ridge basically a single elevation (although a median suture may be present). 7
Abdominal tergites 1 and 2 (MTg 1+2) not separated from metanotum by a suture; mesonotal median ridge always two longitudinal elevations separated by a median furrow. 8

[1] Those occurring in southern Africa in bold.

7(6). Abdominal tergite 2 with 2(1+1) deep pits laterally; mesonotal median ridge granulate and split anteriorly, well delimited from metanotal median ridge . . . . . ***Silvacoris*** **gen. nov.** (South Africa)
Abdominal tergite 2 without bilateral pits; mesonotal median ridge smooth, usually fused with metanotal median ridge and not split anteriorly . . . . ***Miteronotus*** **gen. nov.** (South Africa)

8(6). Elevations on median ridge of meso- and metanotum uninterrupted, extending from mesonotum to MTg 1; metanotum, MTg 1 and MTg 2 completely fused with no indications of sutures between them; head more than 1,05x as long as wide; males with 2(1+1) conspicuous protuberances on metasternum. . . . . ***Pondocoris*** Heiss & Jacobs (South Africa)
Elevations on median ridge of meso- and metanotum always separate; usually with some indications of sutures between metanotum, MTg 1 and MTg 2 laterally; head usually wider than long, if not, then less than 1,05x as long as wide; males without bilateral protuberances on metasternum. 9

9(8). Thorax with bar-like elevations medially, extending from posterior part of mesonotum to posterior margin of MTg 2; carinae on tergal disk reaching lateral margin; dorsal and ventral hems absent in females . . . . . ***Spiculanotus*** **gen. nov.** (South Africa)
Thorax without bar-like elevations; carinae on tergal disk Y-shaped, not reaching lateral margin; dorsal and ventral hems usually present in females. . . . . ***Dundocoris*** Hoberlandt (Southern & Central Africa)

3.2 Key to the species of *Silvacoris* gen. nov.

1. Dorsal visible part of paramere broadly triangular (Fig. 80); lateral margin of mesonotum straight; abdominal sternite 3 delimited from sternite 1+2 by a transverse suture . . . . . *pondolandensis* **spec. nov.**
Dorsal visible part of paramere triangularly elongate with a clubbed anterior apex (Fig. 72); lateral margin of mesonotum convexly rounded; abdominal sternite 3 not clearly delimited from sternite 1+2 by a suture (at most by sculpture anteriorly on sternite 3). 2

2(1). Males less than 4 mm long, females less than 4,9 mm long; mesonotal median ridge densely nodulate; chromosome number 2n(♂) = 14XY . . . . . *heissi* **spec. nov.**
Males longer than 4,4 mm, females longer than 5,2 mm; mesonotal median ridge sparsely nodulate; chromosome number 2n(♂) = 12XY . . . . . *karkloofensis* **spec. nov.**

3.3 Key to the species of *Miteronotus* gen. nov.

1. Antennal segment 1 longer than 2 and 3 combined; spiracles 3-7 lateral and visible from above . . . . . *knysnaensis* **spec. nov.**
Antennal segment 1 shorter than 2 and 3 combined; at least spiracles 3 and 4 sublateral and not visible from above. 2

2(1). Antennal segment 1 extending beyond apex of genae by just more than half its length; spiracles 5-7 lateral and visible from above . . . . . *labeosus* **spec. nov.**
Antennal segment 1 extending beyond apex of genae by less than half its length; spiracle 5 sublateral and not visible from above, 6-7 lateral and visible from above. 3

3(2). Lateral lobes of thoracic nota with prominent setiferous nodules bearing setae as long as height of nodules; rostral groove of males broadly oval and areolate; median notal ridge broad and strongly elevated; antennal segment 4 longer than 3. . . . . *bucculentus* **spec. nov.**
Setiferous nodules on lateral lobes of thoracic nota less prominent and setae very short, hardly recognizable; rostral groove of males elongate, not areolate; median notal ridge narrow and only moderately elevated; antennal segment 4 shorter than 3. . . . . *viginti* **spec. nov.**

3.4 Key to the species and subspecies of *Pondocoris* Heiss & Jacobs

1. Antennal segment 2 longer than 4, 1 longer than or subequal to 3; no wedge-like elevation present on MTg 2 and median furrow reaches back to posterior margin of MTg 2; body strongly explanate and less than 2,1x as long as wide in males and 2,05x in females; tubercles on metasternal protuberances of males small or obsolete, spiracle 5 of males usually not visible from above . . . . . *ampliatus* **spec. nov.**
Antennal segment 2 shorter than 4, 1 shorter than 3; usually with a wedge-like elevation on MTg 2 which prevents the median furrow of reaching the posterior margin of MTg 2 (if wedge-like elevation not present then males smaller than 5mm and a prominent median bar is present on MTg 1 and 2); body not strongly explanate and more than 2,2x as long as wide in males and 2,05x in females; tubercles on metasternal protuberances usually prominent in males (except in subspecies *decimus*), spiracle 5 of males visible from above . . . . . *latebrosus* Hoberlandt. . . .2

2(1). Tubercles on metasternal protuberances of males absent; wedge-like elevation absent from MTg 2; prominent median bar present on MTg 1 and 2; chromosome number 2n(♂) = 10XY . . . . . *latebrosus decimus* **subspec. nov.**
Tubercles on metasternal protuberances of males present and prominent; wedge-like elevation present on MTg 2 and median bar not present on MTg 1 and 2; chromosome number of males not 10XY. 3

3(2). Tergal disk wider than long; chromosome number 2n(♂) = 22XY. . . . . *latebrosus latebrosus* Hoberlandt.
Tergal disk slightly longer than wide or as long as wide, chromosome number of males 12XY or 14XY. 4

4(3). Chromosome number 2n(♂) = 14XY . . . . . *latebrosus quattuordecimus* **subspec. nov.**
Chromosome number 2n(♂) = 12XY . . . . . *latebrosus duodecimus* **subspec. nov.**

3.5 Key to the southern African species and subspecies of *Dundocoris* Hoberlandt.

1. Carinae on tergal disk not entire but nodulated. 2
Carinae on tergal disk entire. 7

2(1). Body elongate, about 2,2x as long as wide; DELTg 5-7 only very slightly protruding; tergal disk only slightly elevated along median line, less than 1,1x as wide as long in males and longer than wide in females . . . . . *begemanni* **spec. nov.**
Body less elongate, less than 2,14x as long as wide; DELTg 5-7 distinctly protruding; tergal disk distinctly elevated along median line, more than 1,15x as wide as long in males and wider than long in females. 3

3(2). Spiracle 4 more than a spiracle width from lateral margin; metanotum and MTg 1 completely fused with no indication of a suture; antennae more than 1,6x as long as width across eyes. . . . . *nodulicarinus* **spec. nov.** . . .4
Spiracle 4 less than a spiracle width from lateral margin; metanotum and MTG 1 laterally separated by a suture; antennae less than 1,55x as long as width across eyes. 6

4(3). Chromosome number 2n(♂) = 14XY . . . . . *nodulicarinus nodulicarinus* **subspec. nov.**
Chromosome number not as above. 5

5(4). Chromosome number 2n(♂) = $9XY_1Y_2$ . . . . . *nodulicarinus novenus* **subspec. nov.**
Chromosome number 2n(♂) = $7XY_1Y_2$ . . . . . *nodulicarinus septeni* **subspec. nov.**

6(3). Antennal segment 1 less than 1,6x as long as segment 2, evenly tapering towards apex; lateral margin of pronotum straight with anterolateral angle rounded; elevations of mesonotal median ridge not fused posteriorly, not wedging in between elevations of metanotal median ridge; males less than 3,7 mm long . . . . . *transvaalensis* **spec. nov.**
Antennal segment 1 more than 1,7x as long as segment 2, abruptly tapering towards apex just distal to curve in segment; lateral margin of pronotum concave with anterolateral angle angularly projected; elevations of mesonotal median ridge usually fused posteriorly, wedging in between elevations of metanotal median ridge; males longer than 3,7 mm. . . . . *marieps* **spec. nov.**

7(1). Spiracle 4 lateral and visible from above in males, in females usually similar but sometimes up to half a spiracle width from lateral margin and not visible from above. 8
Spiracle 4 not visible from above in both sexes. 13

8(7). Antennae more than 1,95x as long as width across eyes, first segment extending beyond apex of genae by about two-thirds of its length, segment 3 more than twice as long as segment 4. . . . . *stuckenbergi* Kormilev. . . 9
Antennae less than 1,9x as long as width across eyes, first segment extending beyond apex of genae by less than three-fifths of its length, segment 3 less than twice as long as segment 4. 10

9(8). Chromosome number 2n(♂) = 26XY . . . . . *stuckenbergi stuckenbergi* Kormilev
Chromosome number 2n(♂) = 28XY . . . . . *stuckenbergi ngomensis* **subspec. nov.**

10(8). Spiracle 3 lateral and visible from above; antennal segment 3 more than 1,3x as long as segment 1; MTG 1distinctly longer than MTG 2 . . . . . *schoemani* **spec. nov.** . .11
Spiracle 3 not lateral and usually not visible from above; antennal segment 3 less than 1,1x as long as segment 1; MTG 2 subequal to or slightly longer than MTG 1. 12

11(10). Karyotype with the largest autosome only slightly larger than the second largest autosome (Figs 267, 489-490) . . . . . *schoemani schoemani* **subspec. nov.**
Karyotype with the largest autosome distinctly larger than the second largest autosome (Figs 268, 492) . . . . . *schoemani dwesaensis* **subspec. nov.**

12(10). Elevations of metanotal median ridge often merging at posterior extreme where they wedge in between elevations of metanotal median ridge; spiracle 4 of females not lateral and visible from above; 2(1+1) prominent bulbous elevations present on VLTg 7 of males, these running anteromedially from below spiracle . . . . . *scholtzi* **spec. nov.**
Elevations of mesonotal median ridge parallel or slightly diverging posteriorly, never merging of wedging in between elevations of metanotal median ridge; spiracle 4 of females lateral and visible from above; elevations on VLTg 7 of males not prominent . . . . . *fuscus* **spec. nov.**

13(7). Large species, males longer than 4,2 mm and females longer than 5,2 mm; antennal segment 3 more than 2x as long as segment 2. 14
Small species, males shorter than 4,2 mm and females shorter than 5 mm; antennal segment 3 less than 1,85x as long as segment 2. 16

14(13). Abdomen with a longitudinal median yellow band on tergal disk, median protuberance without a black spot; antenna less than 1,7x as long as width across eyes, with segment 4 longer than 2 . . . . . *flavilineatus* **spec. nov.** . .15
Abdomen without a median yellow band on tergal disk but median protuberance blackish; antennae more than 1,9x as long as width across eyes, with segment 4 shorter than 2. . . . . . *nigromaculatus* Heiss & Jacobs

15(14). Chromosome number: 2n(♂) = 28XY . . . . . *flavilineatus flavilineatus* **subspec. nov.**
Chromosome number: 2n(♂) = $27X_1X_2Y$ . . . . . *flavilineatus ndabeniensis* **subspec. nov.**

16(13). Elevations of the mesonotal median ridge shorter than length of pronotum (excluding collar), usually diverging posteriorly, never merging at posterior extreme; without anterolateral tubercle on metasternum just behind mesocoxae (Fig. 406); antennae more than 1,6x as long as width across eyes; always with subapical tubercle on clypeus . . *natalensis* Kormilev.
Elevations of the mesonotal median ridge longer than length of pronotum behind collar, parallel or merging at posterior extreme and often wedging in between elevations of metanotal median ridge; with anterolateral tubercle on metasternum just behind mesocoxae (Fig. 407); antennae less than 1,6x as long as width across eyes; subapical tubercle on clypeus usually absent (except in subspecies *noduliclypeatus*) . . . . . *callani* Hoberlandt. . .17

17(16). Subapical tubercle on clypeus absent; antennae less than 1,5x as long as width across eyes; antennal segment 1 extending beyond apex of genae by two-fifths or less of its length; segment 4 more than 1,2x as long as 2; chromosome number: 2n(♂) = 28XY. . . . . *callani callani* Hoberlandt

Subapical tubercle on clypeus present; antennae more than 1,5x as long as width across eyes; antennal segment 1 extending beyond apex of genae by about half its length, segment 4 less than 1,1x as long as 2; chromosome number: 2n(♂) = 26XY. . . . . *callani noduliclypeatus* **subspec. nov.**

Chapter 4

GENUS *ADAMANOTUS* GEN. NOV.

4.1 *Adamanotus* gen. nov.

Type species: *Adamanotus uncotibialis* spec. nov.

Etymology: *Adamas* (L) = diamond, and *notum* (Gr) = dorsal thoracic plate, referring to the diamond-shaped median elevation of the mesonotum.

Apterous. Body oval, coated with a brownish incrustation.

Head: Slightly longer than wide. Genae produced beyond apex of clypeus. Subapical dorsal tubercle present on clypeus. Antenniferous lobes diverging anteriorly, apices acutely rounded. Eyes small, globular. Ocelli absent. Antennae about 1,5x as long as width of head, 4-segmented with first segment longest and thickest. Labium 3-segmented, only two segments visible externally, shorter than head, leaving head through a slit-like atrium. Labrum not discernible. Rostral groove well developed, closed posteriorly.

Thorax: Pronotum more than 2x as wide as long. Collar prominent with 2(1+1) large lateral tubercles and 2(1+1) smaller dorsolateral ones. Mesonotum with prominent diamond-shaped median ridge which extends posteriad to the first abdominal tergite (MTg 1) and splits the metanotum in two. Lateral parts of mesotergal disk separated from ridge by two deep furrows. Lateral lobes granular with straight, anteriorly converging margins. Metanotum divided into 2(1+1) parallelogram-shaped parts by mesonotal ridge; laterally prevented from reaching margin of body by fused dorsal external laterotergites 1-3 that extend anteriad to mesonotum. Metanotum, MTG 1 and MTG 2 fused. MTG 1 anteriomedially with 2(1+1) globose elevations, separated by a longitudinal lanceolate or semicordate sunken elevation. These elevations as high as elevation on abdominal disk. Lateral margins of MTg 1+2 straight, converging posteriorly.

Legs: Hind femur and tibia of male modified, hind femur with a granulate outgrowth posteriorly (Figs 13-14) and hind tibia with a unciform outgrowth (Fig. 19). Tarsi 2-segmented; distal segment longest, bearing two claws, each with associated curved pulvillus. Two bristle-like parempodia present.

Abdomen: **Dorsum**. Tergal disk (MTg 3-6) slightly wider than long, strongly elevated along median line, glabrous impressions separated by prominent, broad carinae. Submedian glabrous impressions surrounded by areolate surface. DELTg 1-3 fused, extending anteriad to posterolateral angle of mesonotum. Ventral laterotergites 5-7 with lateroposterior extensions visible from above. Paratergites 8 of male rounded, not reaching apex of pygophore.

Venter. Sternites 1-3 fused. Ventral laterotergites (VLTg) 3-7 well delimited by longitudinal sulci. Spiracles 2-4 sublateral; 5-7 lateral and visible from above; 8 subterminal.

Discussion: *Adamanotus* can easily be distinguished from all other African genera by the fused DELTg 1+2+3 which extends anteriad to the mesonotum and prevents the metanotum from reaching the

lateral margin of the body; the diamond-shaped median elevation on the thoracic notum and the sexually dimorphic, modified hind legs of the male.

4.1.1 *Adamanotus uncotibialis* spec. nov., Figs 4-23.

Diagnostic measurements are given in Table 4.1.

Apterous. Body coated with a brownish incrustation except the legs, antennae and labium. Body, especially legs, antennae and margins, covered with nodules bearing short, stiff setae (Figs 17-20). The following description is based on specimens with the incrustation removed.

Head: About 1,03x as long (neck region not included) as wide (across eyes). Genae straight or slightly diverging, produced beyond apex of clypeus; produced laterally at base to form a projection at level of antenniferous lobe; lateral margin concave. Jugae small. Vertex with three median longitudinal ridges, the lateral two well defined, the median one broader and irregularly nodose. Directly lateral of ridges are 2(1+1) oval interocular callosities, laterally bordered by two or three concentric ridges. Antenniferous lobes slightly declivous, diverging anteriorly, apices acutely rounded. Postocular lobes small, not reaching outer margins of eyes, lateral margins converging posteriorly. Antennae slender, 1,52x as long as width across eyes; first segment longest and thickest, slightly curved, tapering towards base; second segment subclavate, apex thickest; third segment thinnest, slightly thickening towards apex, pedicellate; fourth segment fusiform, with a short pedicel, conical apex pillose; relative lengths of segments 26:17:23:18,5. First segment of labium concealed in the head cavity, second segment flattened where it leaves the head through a slit-like atrium, third segment longest. Elevated rim of rostral groove coarsely granulated. Neck constricted just behind head, swollen posteriorly.

Thorax: **Dorsum**. Pronotum about 2,2x as wide as long. Pronotum constricted behind collar. Lateral lobes granulate, margin evenly convexly rounded, moderately elevated and slightly reflexed so that propleural margins visible from above. Disk smooth medially, with a deep longitudinal median furrow posteriorly that does not reach the collar, irregularly excavated laterally.

Mesonotum transverse, wider and shorter than pronotum. Lateral lobes granulate, margins straight, converging anteriorly. Disk separated into two parts by a prominent median diamond- shaped ridge which also splits the metanotum in two and reaches the first abdominal tergite (MTG 1). This ridge is strongly elevated posteriad (especially in females), and is separated by deep grooves from the rest of the mesonotum and by narrower and more shallow grooves from two triangular parts of the metanotum which is also strongly elevated postero-mediad. Mesonotum laterally separated from metanotum by a deep transverse sulcus at level of widest point of median ridge. Sulcus ends here in 2(1+1) deep pits.

Metanotum longer than mesonotum but prevented from reaching lateral margins of body by fused dorsal external laterotergites 1-3 (DELTg 1+2+3) that extend to mesonotum anteriorly. Metanotum divided into 2(1+1) parallelogram- shaped parts by mesonotal median ridge, each of which is divided into three distinct areas: a rising triangular part adjacent to the median ridge, a large subquadrate disk which is separated from the latter by a deep longitudinal groove that

Table 4.1 Measurements (in mm) of *Adamanotus uncotibialis* spec. nov.

	STRUCTURE		NGOME FOREST					HAWAAN FOREST				TOTAL[$]			
			HT[*]	N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD	Range
MALES	Total	length	5.42	10	5.21	0.135	5.06-5.45	10	4.85	0.168	4.56-5.12	30	5.05	0.303	4.23-5.59
		width	2.16	10	2.07	0.087	1.92-2.18	10	2.01	0.072	1.88-2.11	30	2.09	0.155	1.78-2.48
	Head	length	0.94	10	0.94	0.023	0.90-0.99	10	0.90	0.036	0.83-0.96	30	0.94	0.053	0.83-1.10
		width	0.92	10	0.93	0.025	0.87-0.97	10	0.89	0.026	0.84-0.94	30	0.92	0.039	0.84-1.03
	Pronotum	length	0.81	10	0.77	0.056	0.63-0.83	10	0.62	0.047	0.54-0.72	30	0.69	0.084	0.54-0.83
		width	1.52	10	1.47	0.051	1.37-1.53	10	1.43	0.039	1.37-1.49	30	1.46	0.073	1.30-1.65
	Tergal disk	length	1.29	10	1.26	0.050	1.19-1.36	10	1.14	0.034	1.10-1.23	30	1.24	0.111	1.02-1.49
		width	1.44	10	1.40	0.055	1.30-1.47	10	1.34	0.048	1.28-1.45	30	1.39	0.105	1.08-1.62
	Antennal segments	I	0.40	10	0.42	0.024	0.38-0.47	10	0.45	0.032	0.40-0.51	30	0.43	0.362	0.34-0.51
		II	0.30	10	0.29	0.016	0.25-0.32	10	0.28	0.024	0.24-0.32	30	0.28	0.023	0.23-0.32
		III	0.40	10	0.38	0.022	0.35-0.42	10	0.37	0.016	0.34-0.40	30	0.38	0.026	0.33-0.44
		IV	0.29	10	0.30	0.017	0.28-0.33	10	0.30	0.022	0.27-0.34	30	0.31	0.021	0.27-0.36
			AT[#]	N	Mean	SD	Range[$]	N	Mean	SD	Range[$]	N	Mean	SD	Range[@]
FEMALES	Total	length	6.10	10	6.19	0.234	5.81-6.58	10	5.75	0.146	5.54-6.00	30	5.91	0.426	4.79-6.61
		width	2.64	10	2.61	0.151	2.22-2.75	10	2.45	0.090	2.26-2.60	30	2.55	0.207	2.19-3.05
	Head	length	1.10	10	1.10	0.039	1.06-1.20	10	0.95	0.027	0.91-1.00	30	1.31	0.079	0.91-1.20
		width	1.03	10	1.03	0.025	1.00-1.09	10	0.95	0.028	0.90-1.00	30	1.00	0.053	0.90-1.10
	Pronotum	length	0.80	10	0.79	0.056	0.70-0.91	10	0.66	0.017	0.63-0.70	30	0.72	0.071	0.59-0.91
		width	1.63	10	1.56	0.082	1.40-1.68	10	1.58	0.060	1.47-1.68	30	1.59	0.093	1.40-1.80
	Tergal disk	length	1.62	10	1.67	0.109	1.43-1.82	10	1.50	0.060	1.40-1.62	30	1.59	0.152	1.34-1.96
		width	1.76	10	1.74	0.090	1.54-1.86	10	1.70	0.074	1.58-1.84	30	1.73	0.129	1.45-2.01
	Antennal segments	I	0.46	10	0.47	0.023	0.42-0.50	10	0.47	0.033	0.40-0.52	30	0.47	0.034	0.40-0.55
		II	0.30	10	0.33	0.030	0.29-0.41	10	0.28	0.027	0.23-0.32	30	0.31	0.038	0.23-0.41
		III	0.41	10	0.43	0.020	0.40-0.47	10	0.37	0.017	0.32-0.39	30	0.40	0.041	0.32-0.48
		IV	0.35	10	0.34	0.012	0.32-0.37	10	0.30	0.020	0.27-0.34	30	0.32	0.027	0.27-0.37

[*] HT = holotype. [#] AT = allotype.
[$] Including individuals from Ngome forest, Hawaan forest as well as 10 specimens from various other localities.

becomes more shallow posteriad, and a triangular granulate anterolateral part which is separated from the previous part by an irregular groove. Metanotum fused with MTG 1 but line of fusion discernable by the sculpture of the segments laterally (MTG 1 forms a smooth transverse elevation) and a groove medially.

MTG 1 and MTG 2 fused, medially with a lanceolate (males) or subcordate (females) longitudinal sunken ridge which is separated by a groove from 2(1+1) anterosubmedian globose elevations. From these elevations surface evenly declines laterally (forming previously mentioned smooth elevations) and posteriorly. Two (1+1) deep transverse indentations present posterolateral of these elevations, probably representing part of the intersegmental sulcus. Posterior margin undulate, lateral margins straight, converging posteriad.

Venter. Pro-, meso- and metasterna smooth. Pro- and mesosterna each with 2(1+1) nodules just mediad of the coxae. Meso- and metasterna each with a median oval finely rastrate area.

Legs: Slender, covered with setiferous tubercles. Trochanters clearly discernible. Femora slightly swollen, hind femur of male with a granulate tooth-like lobe posteriorly (Figs 13-14). Tibiae slender, protibial comb present, hind tibia of male with an unciform outgrowth bearing a pointed bunch of stiff setae apically, about 2/5 of its length from base (Figs 4, 19).

Abdomen: **Dorsum**. Tergal disk about 1,1x as wide as long, lateral margins convex, strongly elevated along median line with highest point at scent gland opening on posteriorly projecting margin of MTg 3; glabrous impressions separated by prominent broad carinae, area between submedian impressions and carinae irregularly areolate. Lateral margin of fused DELTg 1-3 slightly sinuate. Posterolateral angles of DELTg 5-7 with small rounded lobes, increasing in size on subsequent DELTg's, which are extensions of the ventral laterotergites. MTG 7 of males raised with a nodulate transverse ridge before posterior margin; paratergites 8 short, rounded, not reaching apex of pygophore. MTg 7 of females with a prominent transverse ridge before posterior margin; anterior to this ridge 2(1+1) large elevated areas, separated medially by a longitudinal, less elevated ridge, are present. Paratergites 8 produced posteriorly as 2(1+1) semi- acute lobes that nearly reach the level of the apex of tergite 9.

Venter (Fig. 6). Sternites 1-3 fused but 1+2 separated from 3 by foveate sculpture anteriorly on sternite 3. Oval finely rastrate areas medially present on sternites 1+2, 3-7. Intersegmental sutures 3/4, 4/5 and 5/6 well developed, reaching lateral margins of body. Intersegmental suture 6/7 in males bi- or trisinuate, in females produced anteriad medially to accommodate genitalia. Ventral laterotergites 3-7 (VLTg 3-7) well delimited by longitudinal sulci just laterad of longitudinal glabrous ridges. Spiracle 2 sublateral, far from lateral margin, placed on a prominent elevation; spiracles 3-4 sublateral but nearer to margin; 5-7 lateral and visible from above; 8 subterminal on paratergites.

Genitalia. Visible part of male pygophore (in caudal view) pyriform with rugose surface, dorsally with a split triangular median ridge which ends posteriorly just before a transverse ridge which is also split (Figs 15-16). In dorsal view of part usually obscured by MTg 7, 2(1+1) subquadrate 'pseudophallic styli' are present just posteriad of the dorsal visible parts of the parameres (Fig. 15). The lateral sensory areas, laterad of the proctiger, each bears a fringe of long hairs mesally and sparse short

setae laterally. The parameres (Figs 7-12) with a dorsomesal reflexed lobe, inner surface with long hairs, outer surface with a prominent ridge. Aedeagus as in Figs 17-18.

Female genitalia similar to those of most Carventinae.

Chromosome number. 2n(♂) = 16XY.

Habitat and distribution. Coastal and montane evergreen forests of the eastern parts of South Africa where they can be collected on moist fallen twigs and branches. The known distribution is shown in Fig. 2.

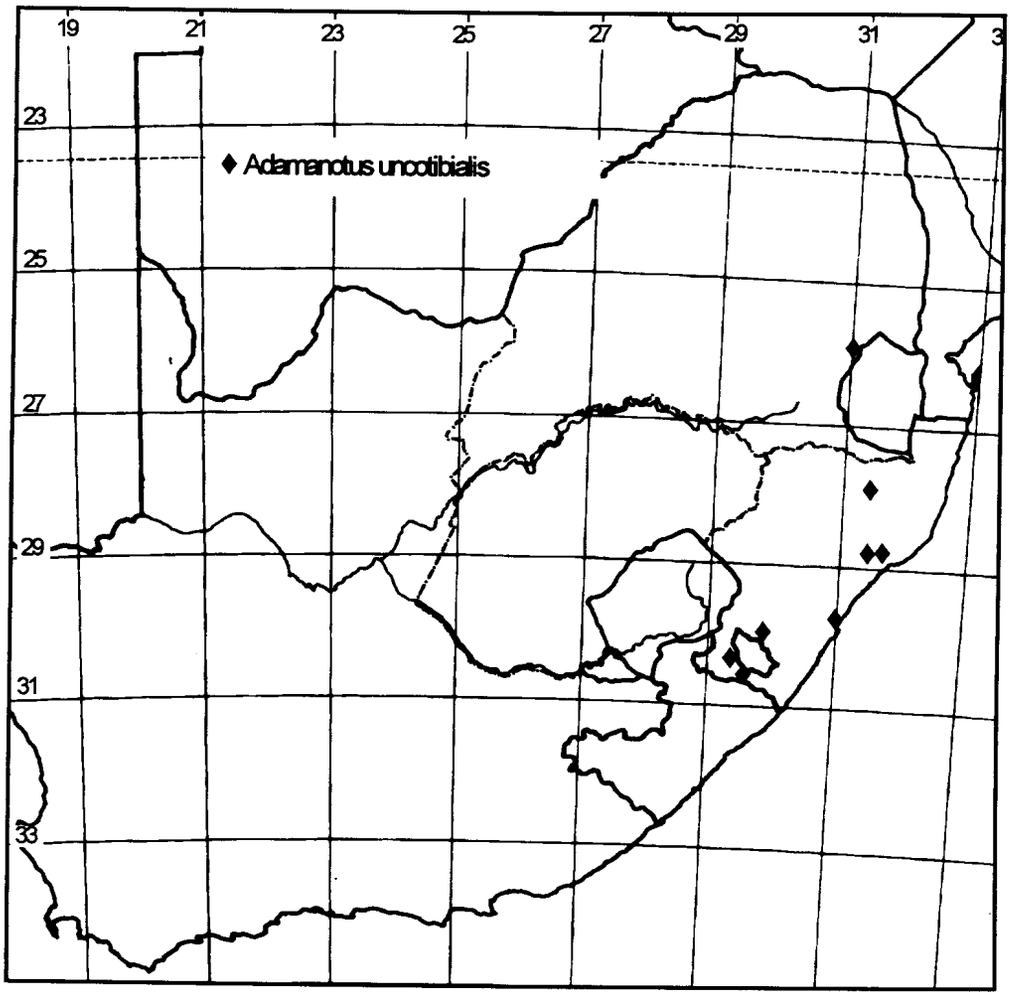


Figure 3. Distribution map of *Adamanotus uncotibialis* gen. et spec. nov.

Etymology. Uncus (L) = hook, and tibia (L) = tibia referring to the unciform protuberance of the hind tibia.

Discussion. This species is easily distinguished from all other described African species as discussed under the genus description. Small morphological differences exist between populations of different localities for example in the population from Hawaan Forest near Durban the individuals are significantly smaller than those from the type locality (Ngome forest). The relative lengths of the antennal segments are also slightly different between these populations.

MATERIAL EXAMINED: **SOUTH AFRICA**. ♂ Holotype: Ngome Forest, nr. Louwsburg, 27°49'S 31°25'E, 20-24.i.1983, D. H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 485 paratypes as follows: **Mpumalanga**. 2♂♂: nr. Barberton, 25°54'S 31°06'E, 30.vi.1979, D.H. Jacobs (DHJS). **Kwazulu-Natal**. 86♂♂♂ 76♀♀: Same data as holotype (2♂♂ 2♀♀ each AMGS, AMNH, BMNH, BMSA, CASC, DMSA, HNHM, ICCM, ISNB, MNHN, MRAC, MZLU, NHMV, NHRS, NMBZ, NMSA, QBUM, QMBA, SAMC, SANC, SEMC, SMWH, USNM, UZMD, UZMH, 20♂♂ 15♀♀ TMSA, 16♂♂ 11♀♀ DHJS); 16♂♂ 14♀♀: Ngoye Forest Reserve, nr Empangeni, 28°50'S 31°43'E, 11- 12.xii.1980, D.H. Jacobs (8♂♂ 8♀♀ DHJS, 8♂♂ 6♀♀ TMSA); 5♂♂ 6♀♀: ditto, 22.viii.1985 (2♂♂ 3♀♀ BMNH, 3♂♂ 3♀♀ MRAC); 12♂♂ 7♀♀: ditto, E. Heiss (EHIA); 13♂♂ 9♀♀: Dhlinza Forest, Eshowe, 28°54'S 31°27'E, 12.iv.1980, D.H. Jacobs (3♂♂ 3♀♀ CASC, 3♂♂ 2♀♀ USNM, 7♂♂ 4♀♀ DHJS); 6♂♂ 4♀♀: ditto, 21.viii.1985 (3♂♂ 2♀♀ DHJS, 3♂♂ 2♀♀ TMSA); 42♂♂ 15♀♀: ditto, E. Heiss (EHIA); 1♂: Z.A.33, Dhlinza Forest, Eshowe Dist., x.1960, Humus, no collector given (TMSA); 28♂♂ 33♀♀: Hawaan Forest, nr. Umhlanga Rocks, 29°42'S 31°05'E, 26.i.1983, D.H. Jacobs (2♂♂ 2♀♀ each AMNH, BMNH, BMSA, CASC, MRAC, NMSA, SANC, SEMC, SMWH, USNM, 3♂♂ 5♀♀ TMSA, 5♂♂ 8♀♀ DHJS); 15♂♂ 8♀♀: Nxumeni Forest, nr. Donnybrook, 29°56'S 29°51'E, 1.xii.1981, D.H. Jacobs (9♂♂ 6♀♀ DHJS, 6♂♂ 2♀♀ TMSA); 21♂♂ 17♀♀: Ngele Forest, nr. Kokstad, 30°32'S 29°41'E, 28.xi.1981, D.H. Jacobs (11♂♂ 9♀♀ DHJS, 10♂♂ 8♀♀ TMSA); 31♂♂ 13♀♀: Lesser Stinkwood Forest, nr. Kokstad, 30°33'S 29°43'E, 29.xi.1981, D.H. Jacobs (11♂♂ 5♀♀ DHJS, 20♂♂ 8♀♀ TMSA). **Eastern Cape**. 1♂ 4♀♀: Sneezewood Forest, nr. Umzimkulu, 30°15'S 29°37'E, 1.xii.1981, D.H. Jacobs (DHJS).

4.2 Cytogenetics of the genus *Adamanotus*

The chromosome number of *A. uncotibialis* is 2n=16XY. The idiogram for this species is presented in Fig. 3 and tables 4.2 and 4.3 contain data regarding chromosome measurements of specific individuals and populations used in compiling the idiogram.

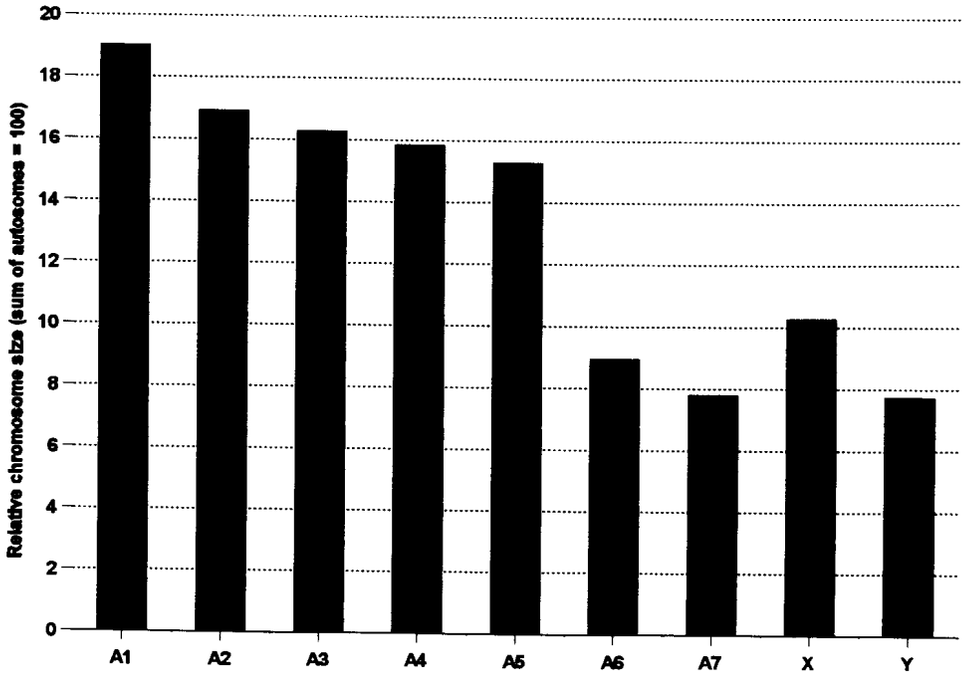


Figure 3. Idiogram of *Adamanotus uncotibialis*.

The meiosis of *A. uncotibialis* is regular and of the typical Heteropteran type where the sex chromosomes are prereductional while the autosomes are postreductional. In the early pre-pachytene meiocytes (Figs 24 & 25) the autosomes are an entangled mass of heteropicnotic clumps and threads. The sex chromosomes can often be recognised as densely compacted heteropicnotic bodies which are usually associated.

At pachytene (Figs 26 & 27) the autosomes form long linear bivalents which still appear entangled in most of the cells (Fig. 27). In less squashed cells, viewed from the appropriate angle, they can be seen to be in a bouquet formation where all the bivalent ends are associated in a limited area, presumably connected to the nuclear membrane (Fig. 26). The sex chromosomes are positively heteropicnotic and almost always associated but usually individually recognisable. A single nucleolus is present, visible as a negatively heteropicnotic body, which is invariably associated with one of the sex chromosomes.

After pachytene the meiocyte enlarges markedly, the bivalents become fuzzy and the cell enters the diffuse/diplotene stage (Figs 28-31) which replaces a true diplotene stage. At this stage there is a marked difference in autosomal behaviour between the Hawaan forest population and the rest of the studied populations of *A. uncotibialis*. In most populations the autosomes become partly decompacted, forming heteropicnotic chromomere-like nodules of variable size, connected by threadlike or granular less intensely stained chromatin. Some bivalents may still be recognizable but the individual chromosomes and chromatids are usually not discernable (Figs 28 & 29). This is a long stage as indicated by the abundance of cells in this stage on most preparations. After this stage the cells rapidly enter diakinesis. In the Hawaan forest population the autosomes do not despiralize to the same extent and the bivalents, individual chromosomes and chromatids are usually clearly discernable at all times during the diffuse/diplotene stage (Figs 30 & 31). The two chromosomes of a bivalent with a terminal chiasma are often some distance apart, connected by two thin chromonemata. A true diffuse stage is absent in this population and replaced by a diplotene stage. Cells in the diplotene stage are as numerous as the diffuse stage cells in other populations indicating that it is also a long stage and suggesting a correspondence between the two stages. The behaviour of the sex chromosomes are the same in both cases: they unite to form a single smooth circular heteropicnotic body which is still associated with a negative heteropicnotic nucleolus of subequal size. The individual sex chromosomes are usually not discernable, except in a low percentage of cases where they form separate bodies.

At diakinesis (Figs 32 & 33) the bivalents become well defined and the chiasmata are conspicuous. Most of the bivalents have one or two terminal chiasmata (1/1 or 2/2) but 1/0, 2/1 and even 2/0 bivalents do also occur. Table 4.4 contains the results of a chiasma analysis done on seven individuals from three populations. The X and Y chromosomes can be distinguished but stay associated until late diakinesis or early metaphase I. The nucleolus becomes progressively smaller until it disappears during late diakinesis. As the autosomes become more compacted they stain darker and during late diakinesis they are isopicnotic with the sex chromosomes.

Table 4.2. True and relative chromosome areas for *A. uncotibialis.*

Locality	No. of individuals studied	Cells*	True chromosome areas (μm²) and standard deviation.										
			A1	A2	A3	A4	A5	A6	A7	X	Y	Autosomes	All chromosomes
Ngome Forest	8	40	2.91(±0.51)	2.55(±0.45)	2.46(±0.43)	2.38(±0.41)	2.30(±0.38)	1.32(±0.21)	1.15(±0.18)	1.47(±0.22)	1.10(±0,23)	15.06(±2.51)	17.62(±2.86)
Ngoye Forest	3	15	2.64(±0.48)	2.45(±0.42)	2.34(±0.38)	2.27(±0.40)	2.20(±0.41)	1.40(±0.20)	1.22(±0.20)	1.56(±0.20)	1.05(±0.15)	14.53(±2.44)	17.14(±2.63)
Hawaan Forest	6	24	2.71(±0.54)	2.37(±0.45)	2.32(±0.45)	2.26(±0.45)	2.17(±0.44)	1.27(±0.25)	1.08(±0.20)	1.51(±0.24)	1.26(±0.22)	14.18(±2.77)	16.95(±3.18)
Sneezewood Forest	1	5	3.35(±0.26)	3.02(±0.27)	2.92(±0.32)	2.83(±0.30)	2.72(±0.27)	1.49(±0.20)	1.37(±0.24)	1.82(±0.10)	0.96(±0.11)	17.69(±1.75)	20.47(±1.87)
Nxumeni Forest	2	10	2.72(±0.36)	2.48(±0.29)	2.35(±0.32)	2.31(±0.30)	2.24(±0.28)	1.26(±0.19)	1.14(±0.16)	1.47(±0.15)	1.17(±0.22)	14.48(±1.82)	17.13(±2.11)
TOTAL	20	94	2.82(±0.51)	2.51(±0.44)	2.42(±0.43)	2.35(±0.42)	2.27(±0.40)	1.32(±0.22)	1.15(±0.20)	1.51(±0.22)	1.13(±0.23)	14.83(±2.55)	17.47(±2.86)
			Relative chromosome areas (% of total area of autosomes) and standard deviation.										
Ngome Forest	8	40	19.29(±0.78)	16.94(±0.52)	16.28(±0.33)	15.81(±0.28)	15.27(±0.42)	8.77(±0.58)	7.65(±0.50)	9.78(±0.79)	7.31(±1.16)		
Ngoye Forest	3	15	18.17(±0.68)	16.85(±0.45)	16.14(±0.37)	15.64(±0.33)	15.10(±0.40)	9.68(±0.45)	8.41(±0.48)	10.83(±1.33)	7.35(±1.25)		
Hawaan Forest	6	24	19.14(±0.81)	16.71(±0.40)	16.34(±0.37)	15.90(±0.35)	15.32(±0.30)	8.97(±0.43)	7.62(±0.32)	10.73(±0.92)	9.00(±0.96)		
Sneezewood Forest	1	5	18.97(±1.11)	17.06(±0.25)	16.47(±0.37)	16.01(±0.49)	15.36(±0.42)	8.41(±0.36)	7.72(±0.68)	10.30(±0.50)	5.46(±0.67)		
Nxumeni Forest	2	10	18.76(±0.86)	17.13(±0.41)	16.19(±0.57)	15.94(±0.48)	15.44(±0.44)	8.68(±0.61)	7.85(±0.45)	10.19(±0.64)	8.09(±1.07)		
TOTAL	20	94	19.00(±0.88)	16.90(±0.47)	16.27(±0.38)	15.83(±0.35)	15.28(±0.39)	8.94(±0.62)	7.79(±0.53)	10.26(±1.00)	7.73(±1.40)		

* A maximum of five cells (with three repeats each) per individual were measured. The average of the three repeats for each cell were used to calculate the statistics.

Table 4.3. Variation in true and relative chromosome areas between individuals of the same population. (Five cells of each individual of the Ngome forest population were measured)

Individual	True chromosome areas (μm^2) and standard deviation.										
	A1	A2	A3	A4	A5	A6	A7	X	Y	Autosomes	All chromosomes
1	2.91(±0.41)	2.61(±0.36)	2.51(±0.32)	2.41(±0.34)	2.33(±0.35)	1.34(±0.17)	1.14(±0.08)	1.44(±0.14)	0.89(±0.11)	15.26(±1.96)	17.59(±2.17)
2	2.68(±0.37)	2.24(±0.28)	2.19(±0.25)	2.16(±0.26)	2.09(±0.28)	1.20(±0.13)	1.07(±0.13)	1.33(±0.15)	0.93(±0.14)	13.66(±1.67)	15.92(±1.93)
3	2.93(±0.48)	2.53(±0.43)	2.44(±0.43)	2.29(±0.31)	2.21(±0.28)	1.27(±0.19)	1.08(±0.17)	1.42(±0.22)	0.92(±0.13)	14.76(±2.24)	17.10(±2.45)
4	3.25(±0.59)	2.78(±0.44)	2.60(±0.44)	2.56(±0.43)	2.49(±0.40)	1.28(±0.16)	1.16(±0.17)	1.50(±0.23)	1.05(±0.20)	16.11(±2.58)	18.67(±2.97)
5	3.48(±0.61)	3.07(±0.60)	2.99(±0.55)	2.90(±0.54)	2.73(±0.47)	1.62(±0.23)	1.41(±0.24)	1.70(±0.29)	1.46(±0.24)	18.19(±3.17)	21.35(±3.66)
6	2.42(±0.17)	2.20(±0.27)	2.12(±0.22)	2.06(±0.19)	2.01(±0.20)	1.15(±0.12)	1.05(±0.13)	1.32(±0.18)	1.06(±0.16)	13.01(±1.26)	15.39(±1.56)
7	2.81(±0.22)	2.51(±0.29)	2.41(±0.28)	2.35(±0.26)	2.27(±0.27)	1.36(±0.15)	1.16(±0.17)	1.60(±0.19)	1.28(±0.15)	14.86(±1.60)	17.74(±1.82)
8	2.76(±0.34)	2.49(±0.29)	2.39(±0.35)	2.32(±0.32)	2.25(±0.30)	1.32(±0.26)	1.10(±0.10)	1.41(±0.18)	1.18(±0.14)	14.64(±1.90)	17.24(±2.16)
Total	2.91(±0.51)	2.55(±0.45)	2.46(±0.43)	2.38(±0.41)	2.30(±0.38)	1.32(±0.21)	1.15(±0.18)	1.47(±0.22)	1.10(±0.23)	15.06(±2.51)	17.62(±2.86)
	Relative chromosome areas (% of total area of autosomes) and standard deviation.										
1	19.04(±0.87)	17.12(±0.72)	16.47(±0.20)	15.78(±0.28)	15.22(±0.49)	8.83(±0.53)	7.54(±0.65)	9.49(±0.75)	5.84(±0.45)		
2	19.62(±0.53)	16.43(±0.16)	16.08(±0.22)	15.84(±0.36)	15.31(±0.27)	8.84(±0.40)	7.87(±0.33)	9.79(±0.46)	6.81(±0.47)		
3	19.86(±0.47)	17.13(±0.46)	16.45(±0.54)	15.56(±0.48)	15.06(±0.57)	8.58(±0.33)	7.35(±0.35)	9.67(±1.16)	6.33(±0.93)		
4	20.10(±0.60)	17.27(±0.30)	16.10(±0.36)	15.87(±0.24)	15.45(±0.49)	7.99(±0.64)	7.22(±0.49)	9.34(±0.35)	6.54(±0.73)		
5	19.15(±0.55)	16.82(±0.50)	16.40(±0.44)	15.90(±0.34)	15.03(±0.32)	8.96(±0.59)	7.74(±0.41)	9.37(±0.70)	8.03(±0.43)		
6	18.68(±0.70)	16.85(±0.57)	16.26(±0.24)	15.87(±0.16)	15.44(±0.35)	8.82(±0.42)	8.08(±0.31)	10.12(±0.74)	8.15(±0.62)		
7	18.98(±0.78)	16.87(±0.39)	16.20(±0.23)	15.80(±0.21)	15.25(±0.42)	9.14(±0.33)	7.76(±0.52)	10.74(±0.42)	8.66(±1.14)		
8	18.87(±0.63)	17.06(±0.57)	16.26(±0.42)	15.84(±0.26)	15.38(±0.38)	8.99(±0.70)	7.59(±0.56)	9.69(±0.88)	8.11(±0.51)		
Total	19.29(±0.78)	16.94(±0.52)	16.28(±0.33)	15.81(±0.28)	15.27(±0.42)	8.77(±0.58)	7.65(±0.50)	9.78(±0.79)	7.31(±1.16)		

Table 4.4. Summary of chiasma analysis of seven individuals of *Adamanotus uncotibialis*.

Population	Number of individuals investigated*	Average number of bivalent types per cell					Average number of chiasmata per cell	Average number of terminalised chiasmata per cell
		2/2	2/1	2/0	1/1	1/0		
Sneezewood forest	1	3.50	0.13	0	3.1	0.26	10.63	10.23
Ngome forest	3	0.92**	0	0	5.74**	0.33	7.92**	7.58**
Hawaan forest	3	0.41**	0	0	6.50**	0.08	7.41**	7.32*
Total	7	1.07##	0.02##	0	5.69##	0.22##	8.09##	7.85##

* 30 cells per individual analysed.
* Significant or ** highly significant differences between individuals of a population.
# Significant or ## highly significant differences between the populations.

At metaphase I (MI) (Figs 34 & 35) the autosomal bivalents form a ring on the periphery of the spindle. The sex chromosome univalents lie inside the autosomal ring, usually not in the centre but halfway to the periphery (Fig. 35).

Anaphase I (AI) (Figs 36 & 37) is a very short stage which is seldom encountered on the preparations. The microtubuli attach to one of the telomeres of each autosome, thus behaving like telocentric chromosomes. (It is uncertain where the spindle attaches to bivalents with two terminal chiasmata.) When the autosomes separate the two chromatids of each become clearly visible (Fig. 36). In the sex chromosomes the spindle attaches to one end of each chromatid and a chromatid of each sex chromosome segregates to opposite poles, so that AI is reductional for the autosomes but equational for the sex chromosomes. At the poles the autosomes form a ring with the X and Y chromosomes (consisting of a single chromatid each) lying inside the ring, usually associated with each other (Fig. 37).

The cells enter the metaphase II stage (Fig. 38) directly, without a true interkinesis. The autosomes form a peripheral ring with the sex chromosomes, which exhibit the so-called "touch-and-go" pairing, in the centre of it. The X-Y structure is usually easily recognized as it is heteromorphic, with the X presumably the larger chromosome (Fig. 38).

At anaphase II (AII) (Fig. 39) the spindle again attaches to the telomeres and the two chromatids of each autosome segregate (equational) while the X and Y chromosomes segregate to opposite poles (reductional).

At telophase II (Fig. 40) the sex chromosome (X or Y) again lies in the centre of a ring of autosomes. The centrioli, which are also sometimes visible at MI, MII, AI, AII and telophase I (e.g. Figs 34 & 42), are usually distinguishable at this stage resembling a small extra chromosome (Fig. 40).

Spermatogonial metaphase plates (Fig. 41) were encountered on most preparations, but the cells are small and the chromosomes are usually not well-spread, as they are interconnected.

A low percentage of cells with meiotic abnormalities were encountered in most individuals. These include MI with misaligned autosomes (Fig. 43) or sex chromosomes, AI with laggards or late segregating chromosomes (Figs 42 & 44), MII with misaligned autosomes or sex chromosomes (Fig.

45), MII with unequally distributed sex chromosomes (Fig. 46), tetraploid MII cells (Fig. 47) and AII cells with laggards and/or bridges (Figs 48-50).

4.2.1 Discussion.

Very little information is available on the cytogenetics of the Aradidae. Ueshima (1979) list the chromosome numbers of only three species, two belonging to the Mezirinae and one to the Isoderminae. They all possess X_1X_2Y sex chromosome systems. Jacobs (1986) and Heiss & Jacobs (1989) reported the chromosome numbers of ten more taxa belonging to the Aneurinae and Carventinae. I also have at hand unpublished cytogenetic data on many more taxa of the Carventinae, Mezirinae and Calisiinae. Different genera, and species within a genus, often have markedly different chromosome numbers, e.g. ranging between 16XY and $43X_1X_2X_3Y$ in eight South African aneurid taxa (Jacobs 1986), in *Brachyrhynchus* between 14XY and 48XY (unpublished data) and in the Carventinae between $7XY_1Y_2$ and 32XY (unpublished data). Because of the large variation in chromosome number it is risky to speculate on the ancestral chromosome number of the Aradidae. 2n=14XY, however, has been encountered in three of the six subfamilies so far studied (Calisiinae, Carventinae and Mezirinae) and also in several genera including *Calisius*, *Brachyrhynchus*, *Dundocoris*, *Pondocoris* and *Silvacoris*. 14XY has been proposed as the modal number of the Protoheteroptera (Manna 1984) and the Pentatomorpha. The Aradoidea represent a very early offshoot of the latter (Kumar 1967). It is thus probable that 14XY is the ancestral chromosome number of the Aradidae and I shall proceed from this assumption in the cytogenetic discussions throughout this work (for a discussion on the ancestral chromosome number of the Aradidae refer to 12.1.1).

In *A. uncotibialis* (2n=16XY) fragmentation could account for the two extra chromosomes. The fact that two chromosome pairs are markedly smaller than the rest supports this hypothesis.

From Table 4.3 it is evident that large variation in actual chromosome areas exists between individuals. This is probably due to differential squashing and not to real differences in chromosomal areas. The relative chromosome areas stay fairly constant between individuals (Table 4.3) as well as between the populations (Table 4.2).

In general the course of meiosis in *A. uncotibialis* follows the general pattern of the Heteroptera. The dissimilarity in the diffuse/diplotene stage between the Hawaan forest population and the rest of the populations is peculiar. The presence of a true diplotene stage and absence of the diffuse stage in the former and the reverse situation in the latter, indicates a correspondence between these stages and that they probably serve the same function. The reason for the difference and what it actually signifies, remains unknown.

Chiasma analysis on some of the individuals showed that significant differences in the number of chiasmata exist between populations and also between individuals of the same population (Table 4.4), e.g. the individual from Sneezewood forest has a very high percentage of bivalents with two terminalised chiasmata (= ring bivalents) - on average more than three of the five large bivalents and often all five (e.g. Fig. 32) - while the individuals of Hawaan forest have on average less than one of these bivalents per two meiocytes. In the Ngome forest population they are common in one individual (nearly two per

meiocyte) but rare in the other two. The reasons for and significance of these differences are not known at this stage.

Although abnormal meiocytes were observed in most individuals, they seem to occur in individuals of the Hawaan forest population at a higher frequency than in the others (which is, however, difficult to prove because of their low frequency). Whether this is related to the aberrant diffuse/diplotene stage in this population is unknown. Aberrant meiocytes were frequently observed in other Carventid species as well and it is not an uncommon phenomenon in the Heteroptera and in some cases it occurs regularly, for example in the harlequin lobe of some Pentatomidae (Schrader 1960, Ueshima 1979).

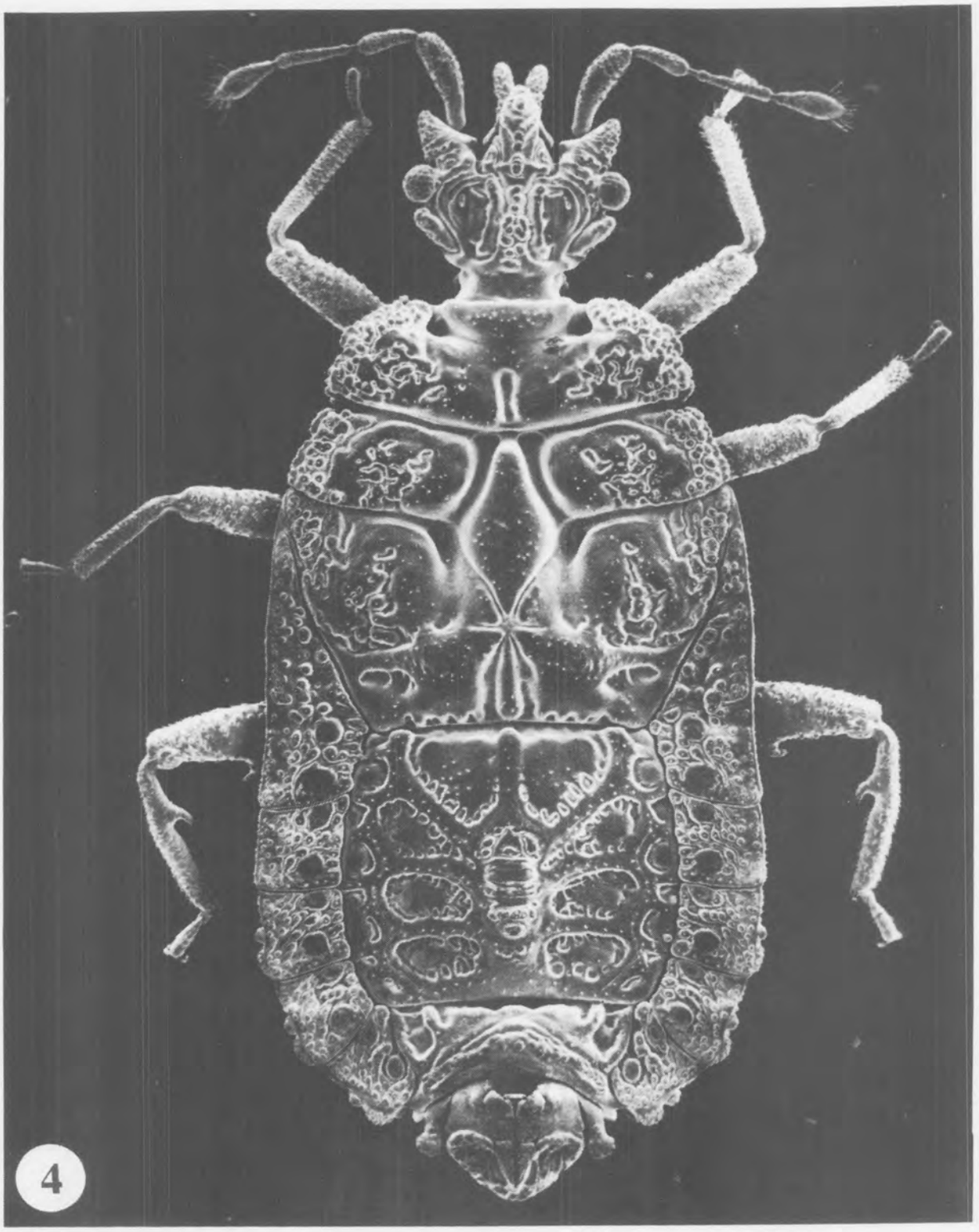
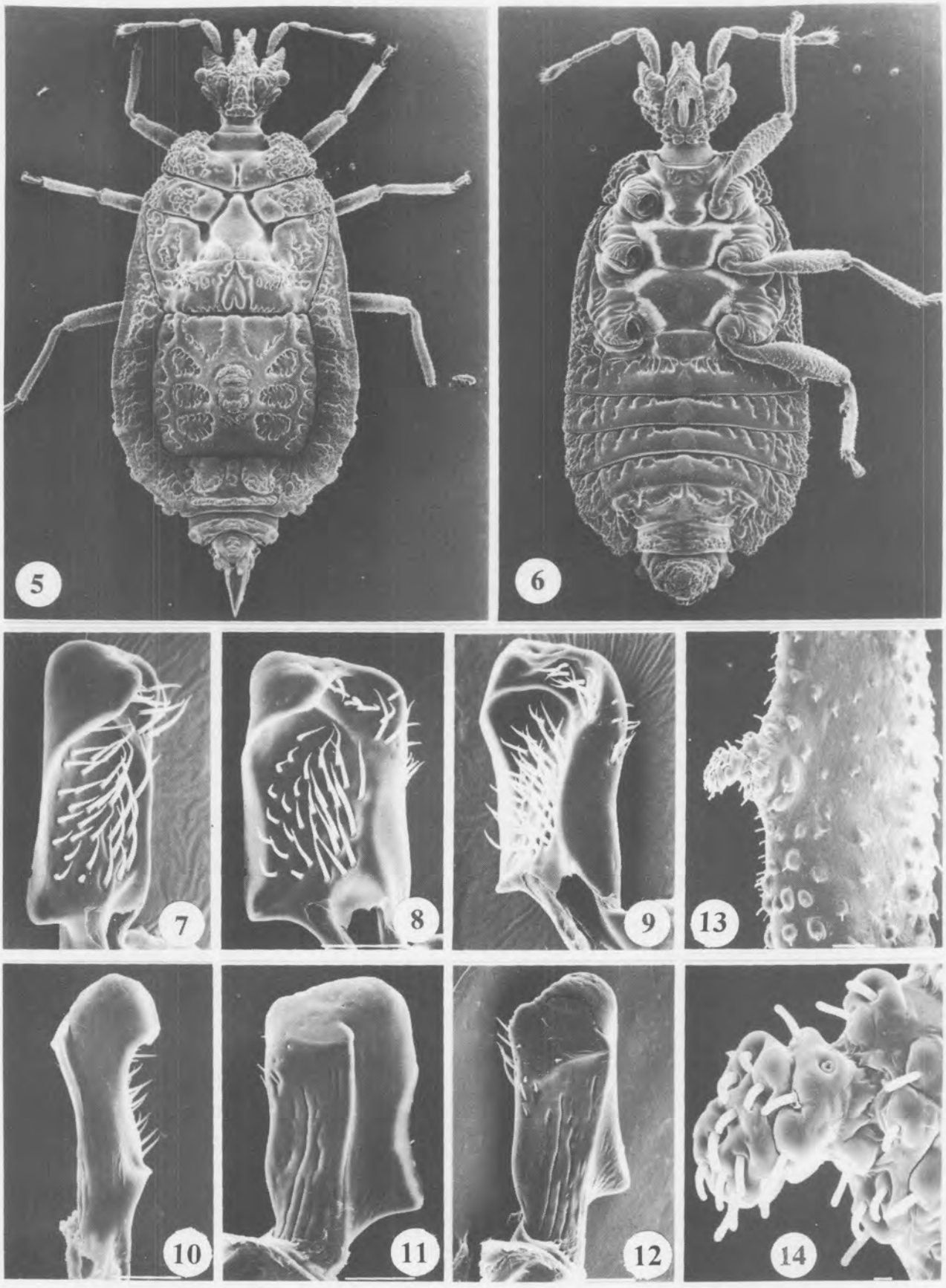
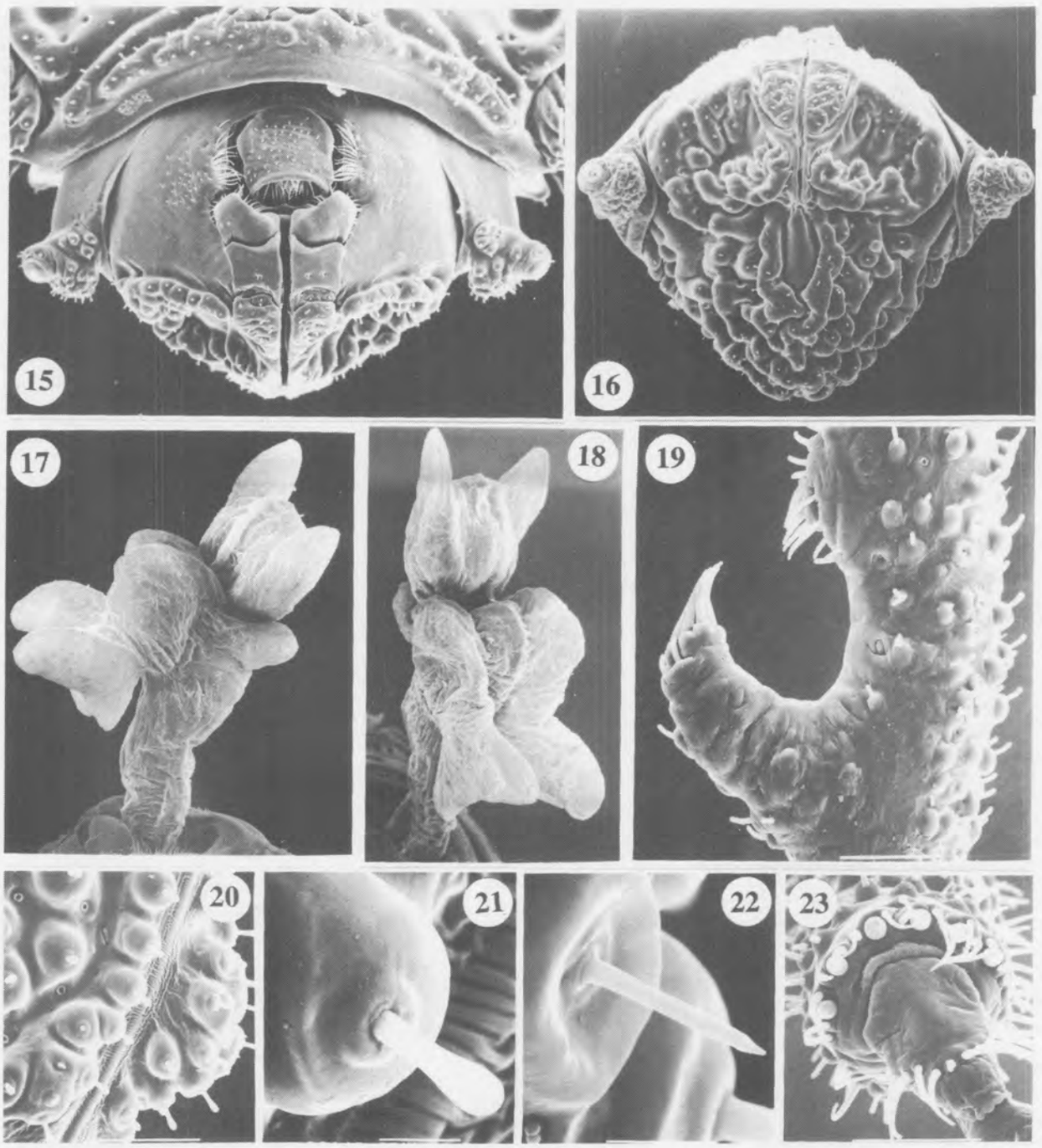


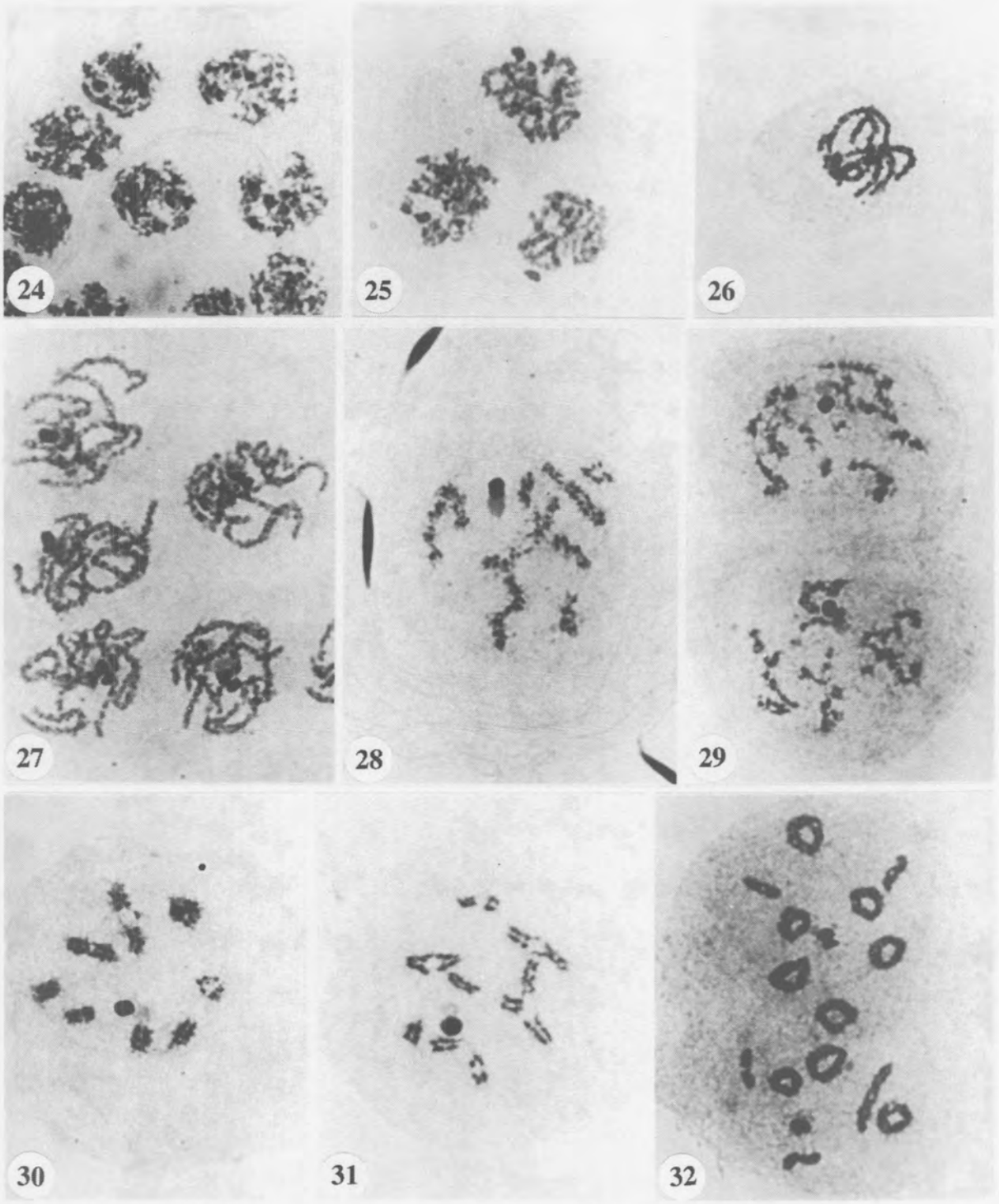
Fig. 4. Scanning electron photomicrograph of *Adamanotus uncotibialis* **gen. et spec. nov.**, dorsal aspect of male paratype.



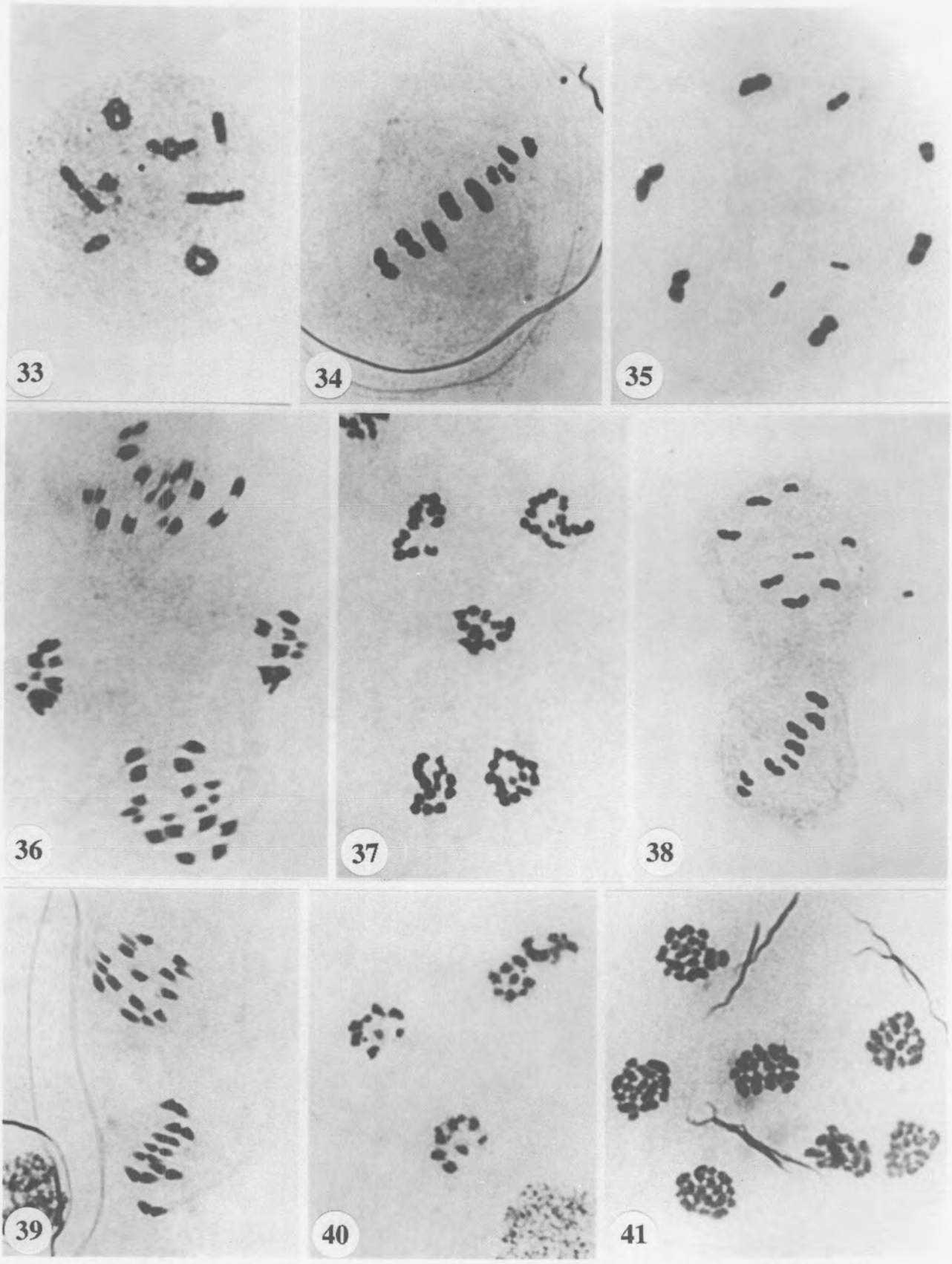
Figs 5-14. Scanning electron photomicrographs of *Adamanotus uncotibialis* **gen. et spec. nov.** 5. Female paratype, dorsal aspect. 6. Male paratype, ventral aspect. 7-12. Different aspects of the left paramere (scale bar = 50 μm). 13. Hind femur of male with protuberance (scale bar = 50 μm). 14. Close-up view of protuberance (scale bar = 5 μm).



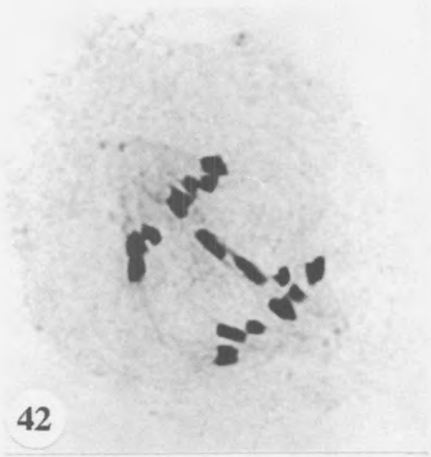
Figs 15-23. Scanning electron photomicrographs of *Adamanotus uncotibialis* **gen. et spec. nov.** 15-16. Pygophore. 15. Dorsal aspect (scale bar = 50 μm). 16. Caudal aspect (scale bar = 50 μm). 17-18. Inflated aedeagus. 17. Lateroposterior aspect. 18. Dorsoposterior aspect. 19. Unciform outgrowth of hind tibia of male (scale bar = 50 μm). 20. Lateral extension of ventral laterotergite 5 at posterolateral angle of DELTg 5, dorsal view, showing the sculpture and different types of setae (scale bar = 50 μm). 21. Short stiff clavate seta (scale bar = 5 μm). 22. Short thin acute seta (scale bar = 5 μm). 23. Apex of tibia showing pointed curved setae and prominent conical setae (scale bar = 50 μm).

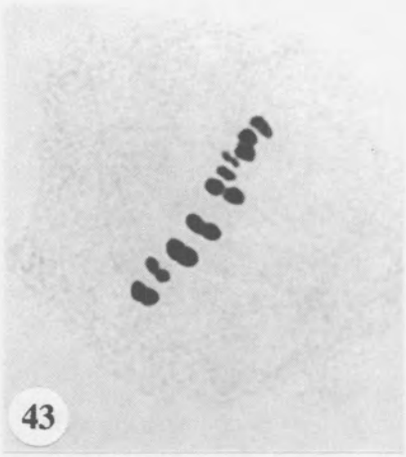


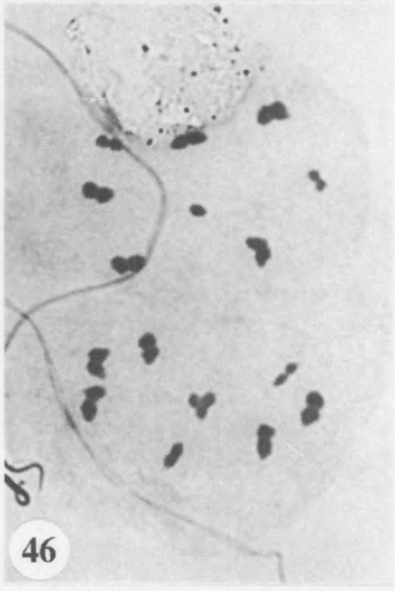
Figs 24-32. Meiotic stages in *A. uncotibialis*. 24-25. Pre-pachytene stages. 26. Pachytene displaying the typical bouquet formation. 27. Pachytene as appearing in well-spread cells. 28. Early diplotene/diffuse stage. 29. Diplotene/diffuse stage. 30. Early diplotene/diffuse stage in the Hawaan forest population. 31. Diplotene/diffuse stage in the Hawaan forest population. 32. Diakinesis (showing five ring bivalents in one cell).

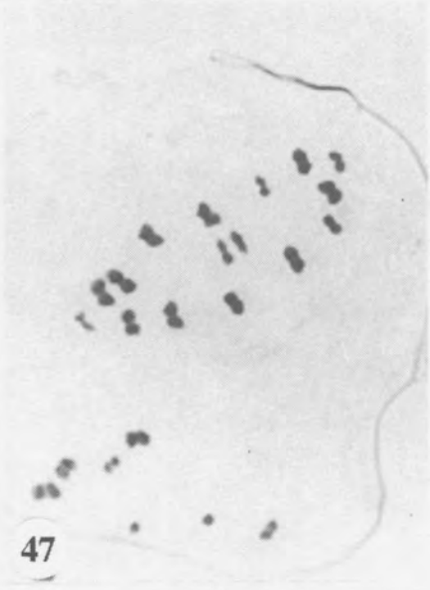


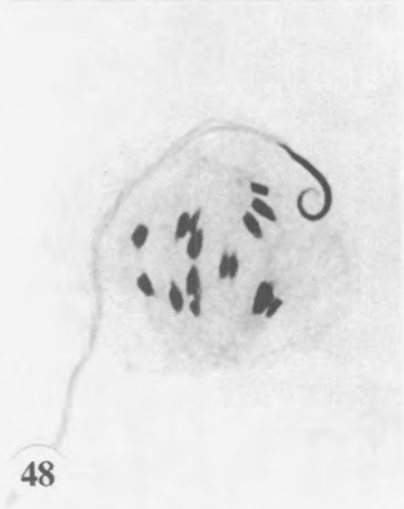
Figs 33-41. Meiotic stages in *A. uncotibialis*. 33. Diakinesis. 34-35. Metaphase I. 34. Equatorial view. 35. Polar view. 36. Anaphase I. 37. Late anaphase/telophase I. 38. Metaphase II. 39. Anaphase II. 40. Late anaphase/telophase II. 41. Spermatogonial metaphases.

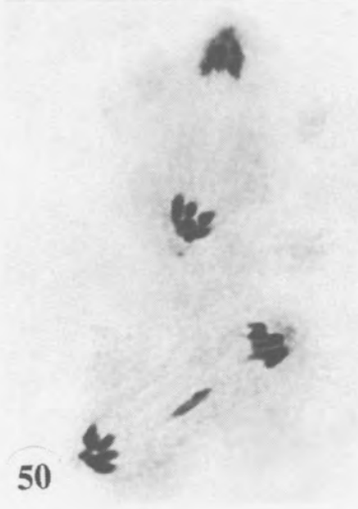












Figs 42-50. Examples of abnormal meiocytes observed in *A. uncotibialis*. 42. Anaphase I with late segregating autosome. 43. Metaphase I with malorientated bivalent. 44. Anaphase I with dicentrically attached lagging sex chromosome. 45. Metaphase II with malorientated sex chromosomes. 46. Unbalanced metaphase II cells. The lower cell with three sex chromosomes (chromatids) and the upper cell with one. 47. Tetraploid metaphase II cell. 48. Anaphase II with dicentrically attached lagging sex chromosomes. 49. Anaphase II with chromatid bridges and lagging chromosomes. 50. Anaphase II with lagging chromosome.

Chapter 5

GENUS *SILVACORIS* GEN. NOV.

5.1 Silvacoris gen. nov.

Type species: *Silvacoris heissi* spec. nov.

Etymology: *Silva* (L) = forest, referring to the fact that they only occur in indigenous forests.

Apterous. Body broadly oval, incrustate, shining and granular beneath incrustation. The following description is based on individuals with the incrustation removed, unless otherwise indicated.

Head: Wider (across eyes) than length excluding neck area. Genae produced beyond apex of clypeus. Subapical dorsal tubercle present on clypeus. Antenniferous lobes well developed, diverging anteriorly, apices acute but extreme tips rounded. Eyes small, globular. Ocelli absent. Postocular tubercles present but not prominent. Antennae about 1,5x as long as width of head, 4-segmented, first segment thickest, extending beyond apex of genae, second segment shortest and more slender, third longest, slightly and evenly widening towards apex, fourth segment fusiform, second shortest. Labium 3-segmented, only two segments visible externally, shorter than head, leaving head through a slit-like atrium. Labrum not discernable. Rostral groove well developed and closed posteriorly.

Thorax: Dorsum. Pronotum about 3x as wide as long. Collar prominent, with 2(1+1) large lateral tubercles and 2(1+1) smaller dorsolateral ones. Pronotum constricted behind collar. Lateral lobes densely granulate, moderately elevated and slightly reflexed so that propleural margins are visible from above. Disk formed by 2(1+1) smooth plates, separated medially by a deep longitudinal furrow; between the medial furrow and the collar a transverse elevation is present which is separated from both the collar and the disk by moderate depressions. Posterior margin of each side straight but directed slightly anteriorly from midpoint, separated from mesonotum by a deep sulcus.

Mesonotum transverse, wider and shorter than pronotum, comprising 2(1+1) subrectangular plates laterally, separated from metanotum by a deep sulcus and a arrow-shaped median ridge which is strongly elevated and variously granulate. Lateral lobes densely granulate, slightly reflexed so that mesopleural margins are visible from above. Disk irregularly excavated except for glabrous area adjacent to median ridge.

Metanotum longer and slightly wider than mesonotum, consisting of 2(1+1) transverse lateral plates which are separated by a median bar. This bar is continuous with the mesonotal ridge as well as to a rim forming the posterior margin of the metanotum. The part directly adjacent to this bar is elevated and granular, followed by a smooth anterolaterad sloping part, the irregularly excavated main part of the disk and the granulate lateral lobe. Metapleural margin visible from above. For about lateral half laterally the metanotum is separated from MTg 1 by a narrow but clear sulcus and medially by an abrupt elevation of MTg 1. The intersegmental suture is visible as a light coloured, less sclerotized line for the total distance.

MTg 1 and 2 together form a transverse trapeziform plate. For about the lateral third MTg 1 is clearly delimited from MTg 2 by a prominent concave sulcus. It forms a narrow bar which widen

slightly laterally before arching latero-anteriad to where it ends near the lateral margin in an acute point. For the mesal three-fifths the line of demarcation is not clear but MTg 1 can be distinguished as the anterior, strongly elevated, usually more granular part while MTg 2 is the posterior, more depressed and smoother part. MTg 1 is medially divided by a longitudinal bar that may reach the posterior margin of the metanotum and also divide MTg 2. MTg 2 is laterally depressed (behind the lateral bar of MTg 1), forming a smooth subrectangular or subtriangular area with a characteristic and prominent pit.

Venter. Prosternum with semi-tuberculate median part. Meso- and metasterna smooth, each with a median oval finely depressed area.

Legs: Slender, covered with setiferous tubercles. Trochanters discernable. Femora and tibiae unmodified. Protibial comb present. Tarsi 2-segmented, distal segment longest, bearing two claws, each with associated curved pulvillus. Two bristle-like parempodia present.

Abdomen: Dorsum. Tergal disk (MTg 3-6) wider than long, strongly elevated along median line which is highest on MTg 4-5; lateral and anterior margins convex; glabrous impressions separated by prominent carinae. DELTg 1-3 fused but remnants of the sulcus between DELTg 2 and 3 may be discernable; position of DELTg 1 is indicated by the prominent protruding part of reflexed ventral laterotergite 1 (VLTg 1); posteroexterior angle of DELTg 2-7 with small but increasing in size expansions formed by the reflexed ventral laterotergites; all DELTg's densely tuberculate except for prominent LGI's. MTg 7 of males strongly raised medially for the reception of the pygophore. MTg 7 of females with a prominent nodulate transverse ridge and just anterior to this ridge, a large transverse, subrectangular elevated area is present; paratergites 8 produced posteriorly as 2(1+1) semi-acute lobes that nearly reach to the level of the apex of tergite 9.

Venter. Sternites 1-3 fused. Oval, slightly depressed, finely rastrate areas medially present on sternites 1+2, 3-7. Intersegmental sutures 3/4, 4/5, 5/6 and 6/7 well developed, reaching lateral margins of body; 6/7 in females medially produced anteriad to accommodate genitalia. VLTg 3-6 well delimited by longitudinal sulci. Spiracle 2 sublateral, situated about half the width of the VLTg from lateral margin; placed on a prominent elevation; spiracles 3-4 sublateral but nearer to margin; 5-7 lateral and visible from above; 8 subterminal on paratergites.

Genitalia: Visible part of pygophore pyriform with a rugose surface, dorsally with 2(1+1) longitudinal triangular ridges separated by a cleft which ends about at level of paratergites 8; ventral of this a narrow pit, formed by prominent carinate ridges, is present. In dorsal view of the part usually obscured by MTg 7, 2(1+1) subquadrate "pseudophallic styli" are present just posteriad of the dorsal visible parts of the parameres. Lateral sensory areas each bears a fringe of long hairs mesally and sparse short setae laterally. Female genitalia similar to those of most Carventinae.

Discussion: *Silvacoris* is characterized by a stout, broadly oval body and the unique appearance of the thoracical and abdominal terga, especially the deep pits laterally on second abdominal tergum (MTg 2). It is related to *Miteronotus* from which it can be distinguished by the above characters as well as the granulate mesonotal median ridge which is usually split anteriorly and well delimited from the metanotum and abdominal terga; the abdominal tergal disk which is more than 1,1 times as wide as long; and the dorsal laterotergites which are about as long as wide, while they are distinctly longer than wide in *Miteronotus*.

Three species of Silvacoris are known, all very similar in appearance and occurring in the evergreen coastal and montane forests of Kwazulu-Natal and Transkei.

5.1.1 *Silvacoris heissi* spec. nov., Figs 57-64

Diagnostic measurements are given in Table 5.1. Apterous. Body coated with a whitish incrustation, especially the thoracical disk and the anterior part of DELTg 1+2+3; the latter visible as two lateral white spots which contrast strongly with the less coated darker adjacent parts. The following description is based on specimens with the incrustation removed.

Table 5.1 Measurements (in mm) of *Silvacoris heissi* spec. nov. from Dhlinza forest.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range	AT#	N	Mean	SD	Range
Total	length	3.67	10	3.72	0.120	3.48-3.86	4.61	10	4.56	0.083	4.41-4.72
	width	1.87	10	1.94	0.057	1.85-2.03	2.49	10	2.40	0.104	2.14-2.50
Head	length	0.63	10	0.64	0.022	0.61-0.68	0.73	10	0.71	0.020	0.69-0.75
	width	0.81	10	0.81	0.026	0.77-0.87	0.89	10	0.88	0.018	0.84-0.91
Pronotum	length	0.46	10	0.48	0.026	0.43-0.52	0.58	10	0.56	0.023	0.51-0.59
	width	1.35	10	1.36	0.037	1.29-1.41	1.57	10	1.54	0.049	1.44-1.63
Tergal disk	length	1.12	10	1.14	0.046	1.10-1.27	1.36	10	1.40	0.042	1.35-1.49
	width	1.24	10	1.30	0.046	1.23-1.38	1.58	10	1.57	0.068	1.46-1.71
Antennal segments	I	0.33	10	0.31	0.013	0.28-0.34	0.33	10	0.33	0.026	0.28-0.38
	II	0.25	10	0.24	0.014	0.22-0.28	0.26	10	0.27	0.022	0.24-0.32
	III	0.39	10	0.36	0.026	0.31-0.40	0.39	10	0.39	0.032	0.32-0.44
	IV	0.29	10	0.28	0.016	0.25-0.30	0.30	10	0.31	0.032	0.24-0.37

* HT = holotype. # AT = allotype.

Head: About 1,25x as wide (across eyes) as long (neck region not included). Genae straight, produced beyond apex of clypeus, produced laterad at base at level of antenniferous lobe. Jugae small. Vertex with three irregularly nodose, median ridges, lateral two ending on the jugae while the median one extends on the clypeus to the subapical tubercle. Directly lateral of the ridges are 2(1+1) oval interocular callosities. Antennae slender, 1,48x as long as width across eyes; first segment thickest, second longest, slightly curved and tapering towards base; second segment shortest, slender but gradually thickened towards apex; third segment longest and very slender, slightly and evenly thickening towards apex, pedicellate; fourth segment fusiform, with a short pedicel, conical apex pilose; relative lengths of segments 13:10:15:11,5. First segment of labium concealed in head cavity, second segment flattened where it leaves the head through a slit-like atrium, third segment subequal in length to second segment (including concealed part). Elevated rim of broadly oval rostral groove coarsely granulate. Neck slightly constricted just behind head.

Thorax: Dorsum. Pronotum about 2,8x as wide as long. Posterior margin slightly sinuate. Lateral lobes granulate, lateral margins converging anteriad, straight posteriorly but evenly convexly rounded anteriorly, produced anteriorly to form a anteromesally directed projection at level of collar. Disk smooth medially but with an uneven surface.

Mesonotum very short, about 5,6 times as wide as long (measured at level of lateral lobes). Lateral lobes granulate, with lateral margins convexly rounded anteriorly resulting in a prominent lateral cleft between the pro- and mesonotum. Disk smooth but uneven adjacent to median ridge, followed by a coarsely granulate area and a smooth sinuate strip adjacent to lateral lobes. Elevated median ridge with granulations on its whole surface, bisected with a median longitudinal fossula, anterior apex bifid. It extends posteromedially as a narrow median bar that divides the metanotum and is continuous with a transverse rim which separates the metanotum and MTg 1. Mesonotum laterally separated from metanotum by a deep, transverse, slightly sinuate sulcus which ends adjacent to median ridge in 2(1+1) deep pits; posteriorly on the median ridge it is separated only by a shallow groove that turns posteriad along the median bar.

Metanotum mesally shorter but laterally much longer than mesonotum. Lateral lobes granulate, slightly raised. Dorsal margin of metapleura prominent from above. Disk with elevated oval granular part adjacent to median bar, followed laterally by a smooth glabrous part sloping sharply laterad to level of the deep pits, a longitudinal rectangular rugose area, a sublateral sinuate glabrous strip and a rugose strip adjacent to the lateral lobes. The metanotum is medially delimited from MTg 1 by the postnotal rim, submedially by the rim and MTg 1 that is abruptly raised at this point and laterally by a thin sulcus.

MTg 1 consists of a lateral smooth bar and a median raised, transverse, rugose area that is medially divided by a longitudinal bar that also transects MTg 2. MTg 2 consists of a smooth depressed lateral subrectangular area with the characteristic pit and a raised submesal, fairly smooth part that is steeply sloping posteriad; posteromesally 2(1+1) prominent tubercles are present.

Venter and Legs: As for genus.

Abdomen: Dorsum. Tergal disk about 1,13x as wide as long. Carinae separating glabrous impressions somewhat granular, prominent, except for the posterior carina on MTg 6 which is very weakly developed or indistinguishable. Surface between carinae and impressions sparsely punctate. Posterior angles of DELTg 2-4 very slightly produced, those of DELTg 5-7 increasingly more produced.

Venter: (Fig. 58) Sternites 1-3 fused, but 1+2 elevated and separated from 3 by foveate sculpture anteriorly on sternite 3. Longitudinal sulci delimiting VLTg 3-6 very slightly sinuate except at extremities where it bend mesad anteriorly and laterad posteriorly. Anterior LGI not prominent especially on VLTg 4-7. Spiracle 2 sublateral, situated about half the width of VLTg from lateral margin, placed on a prominent tubercle; spiracles 3-4 sublateral, placed about a spiracle width from lateral margin, not visible from above; spiracles 5-7 lateral, visible from above, 5 directed laterally, 6 and 7 placed on reflexed protuberances of VLTg and directed slightly dorsally.

Genitalia: Visible part of pygophore (in caudal view) as for genus (Fig. 63). In dorsal view (Fig 64) visible part of parameres broad posteriorly, narrowing anteriad and clubbed at apex, most of dorsal

surface set with short stiff setae. Dorsal part of removed parameres angularly bifid, inner surface covered with long setae, base with a prominent finger-like extension (Figs 59-62).

Chromosome number: 2n(♂) = 14XY.

Habitat and distribution: Coastal and montane evergreen forests of Kwazulu-Natal and Zululand, where they occur on moist fallen twigs and branches. In these forests they seem to be local and prefer the moister parts. Their known distribution is shown in Fig. 51.

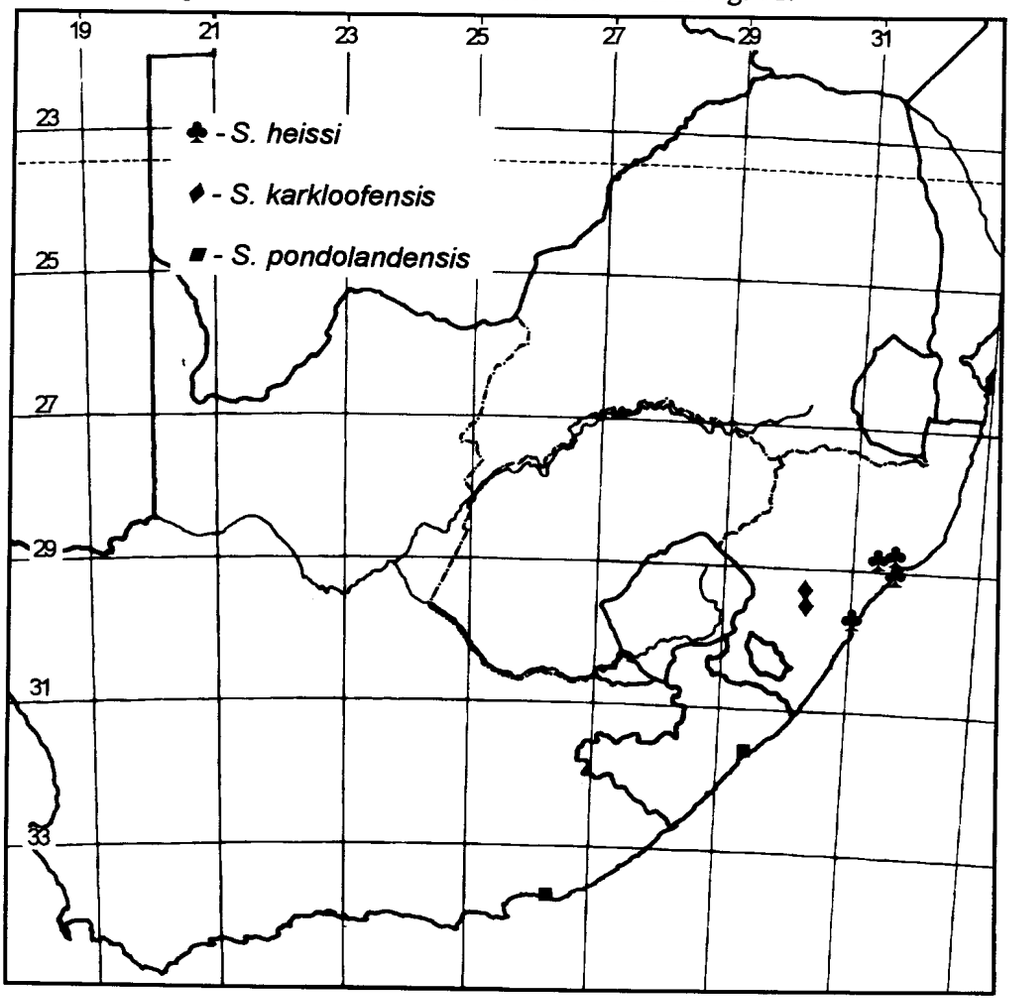


Fig. 51. Distribution map of the ***Silvacoris*** **species.**

Etymology: It is a pleasure to dedicate this species to my friend Dipl-Ing Ernst Heiss who has contributed much to our knowledge of the Aradidae.

Discussion: This species is closely related and very similar to *Silvacoris karkloofensis*, and differences are discussed under the latter.

MATERIAL EXAMINED: **SOUTH AFRICA, Kwazulu-Natal**. ♂ Holotype: Dhlinza forest, Eshowe, 28°54′S, 31°27′E, 12.iv.1980, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 137 paratypes as follows: Kwazulu-Natal. 5♂♂ 9♀♀: Umgoye Forest Reserve, nr. Empangeni, 28°50′S, 31°43′E, 11-12.xii. 1980, D.H. Jacobs (DHJS); 68♂♂ 49♀♀: Same data as holotype (DHJS EHIA) 2♀♀: Umlalazi Nature Reserve, nr. Mtunzini, 28°58′S 31°46′E, 21-23.viii.1985, D.H. Jacobs (DHJS); 2♂♂

2♀♀: Umhlanga Rocks Nature Reserve, nr. Durban, 29°42'S 31°06'E, 10-11.ix.1991, D.H. Jacobs (DHJS).

5.1.2 *Silvacoris karkloofensis* spec nov. Figs 65-72.

This species is in general facies very similar to *Silvacoris heissi* and only differences and specific proportions are covered in the following description. For aspects not mentioned; the description of the genus and *Silvacoris heissi* applies equally well to this species.

Diagnostic measurements are given in Table 5.2. Incrustation greyish resulting that the incrustation on DELTg 1+2+3 does not contrast as clearly with adjacent areas.

Table 5.2. Measurements (in mm) of *Silvacoris karkloofensis* spec. nov.

STRUCTURE		MALES [All(5) from Townbush, HT from Karkloof]					FEMALES (9 from Karkloof, 1 from Townbush)				
		HT*	N	Mean	SD	Range	AT#	N	Mean	SD	Range
Total	length	4.89	5	4.82	0.231	4.57-5.10	5.48	10	5.51	0.100	5.38-5.73
	width	2.30	5	2.28	0.080	2.16-2.36	2.89	10	2.85	0.074	2.74-2.97
Head	length	0.89	5	0.89	0.027	0.84-0.92	0.95	10	0.96	0.013	0.93-0.98
	width	0.99	5	0.97	0.029	0.93-1.01	1.07	10	1.05	0.026	1.01-1.08
Pronotum	length	0.56	5	0.57	0.038	0.50-0.61	0.67	10	0.63	0.027	0.59-0.68
	width	1.61	5	1.60	0.072	1.48-1.66	1.83	10	1.78	0.046	1.71-1.85
Tergal disk	length	1.44	5	1.42	0.073	1.30-1.49	1.72	10	1.74	0.062	1.65-1.86
	width	1.49	5	1.50	0.080	1.39-1.61	1.77	10	1.81	0.055	1.74-1.92
Antennal segments	I	0.37	5	0.38	0.015	0.35-0.40	0.40	10	0.41	0.015	0.37-0.43
	II	0.30	5	0.28	0.007	0.27-0.30	0.29	10	0.30	0.009	0.28-0.32
	III	0.36	5	0.36	0.022	0.33-0.40	0.40	10	0.41	0.013	0.38-0.43
	IV	0.28	5	0.28	0.012	0.25-0.28	0.30	10	0.29	0.008	0.28-0.31

* HT = holotype. # AT = allotype.

Head: About 1,1x as wide (across eyes) as long (neck region not included). Genae longer and produced further beyond apex of clypeus than in *Silvacoris heissi*. Antennae 1,34x as long as width of head, relatively more stout than that of Silvacoris heissi, relative lengths of segments: 19:14:18:14. Antenniferous lobes prominent, when viewed from below anterior margin obtusely bent resulting in the apices being longer and more anteriorly directed than in Silvacoris heissi.

Thorax: Dorsum. Pronotum about 2,8x as wide as long. Lateral margins straight or slightly concave. Mesonotum with median ridge much less granulate than in *Silvacoris heissi*, almost smooth in most individuals, median longitudinal fossula absent or only very weakly developed, anterior apex usually not as prominent bifid and pointing as in *Silvacoris heissi*. Metathoracical disk with sublateral

glabrous strip usually absent or only recognizable on posterior half. Submesal tubercles on MTg 2 less prominent than in *Silvacoris heissi* and absent in a few individuals.

Venter. A deep median pit is present at the anterior end of the median oval rastrate area of sternum 2.

Abdomen: Dorsum. Tergal disk about 1,05x as wide as long. Carinae separating glabrous impressions usually relatively thicker than in *Silvacoris heissi* and posterior carina on MTg 6 better developed, usually distinguishable. Posteroexterior angles of DELTg 2-4 clearly produced, those of DELTg 5-7 forming lateral lobes.

Venter (Fig. 66). Sternites 1+2 not as sharply elevated and not well delimited from 3. Longitudinal sulci delimiting VLTg 3-6 clearly sinuate in males, less so in females. Anterior LGI's prominent on all segments, especially so in males.

Genitalia: Pygophore and parameres very similar to that of *Silvacoris heissi* but parameres lacking the fingerlike extension at base, in its place a much shorter tooth-like extension is present (Figs 67-70).

Chromosome number: 2n(♂) = 12XY.

Habitat and distribution: Thus far only collected in the montane evergreen forest in the Pietermaritzburg vicinity (Fig. 51).

Etymology: Named after Karkloof, the type locality.

Discussion: *Silvacoris karkloofensis* is very closely related to *Silvacoris heissi* and if it was not for the large and constant size difference and different chromosome number its specific status could be questioned. It can be distinguished from the latter species by being larger, more elongate oval in general facies, having the postero-exterior angles of the laterotergites more produced, the antenniferous lobes longer and more anteriorly directed and the elevated median mesonotal ridge much less nodose.

MATERIAL EXAMINED: **SOUTH AFRICA. Natal**. ♂ holotype: Shaws Wood farm, Karkloof, 29°19′S 30°18′E, 1.ii.1983, D.H. Jacobs. (TMSA); ♀ allotype: ditto (TMSA); 26 paratypes as follows: 1♂ 16♀♀: Same data as holotype (DHJS); 5♂♂ 4♀♀: Town bush, Pietermaritzburg, 29°33′S 30°20′E, 31.i.1983, D.H. Jacobs (DHJS, TMSA).

5.1.3 *Silvacoris pondolandensis* spec. nov. Figs 73-80.

Although this species is much larger than *Silvacoris heissi* it is also very similar to it in general facies and only differences and specific proportions are covered by the following description.

Diagnostic measurements are given in Table 5.3.

Table 5.3 Measurements (in mm) of *Silvacoris pondolandensis* spec. nov.

STRUCTURE		MALE PT#	FEMALES				
			HT*	N	Mean	SD	Range
Total	length	-	5.71	3	5.65	0.077	5.56-5.71
	width	2.37	2.97	3	2.92	0.180	2.72-3.07
Head	length	0.87	0.94	3	0.95	0.017	0.93-0.97
	width	0.96	1.13	3	1.09	0.045	1.04-1.13
Pronotum	length	0.64	0.69	3	0.67	0.050	0.61-0.70
	width	1.72	1.94	3	1.93	0.065	1.86-1.99
Tergal disk	length	1.46	1.79	3	1.80	0.067	1.74-1.87
	width	1.61	1.91	3	1.93	0.051	1.89-2.00
Antennal segments	I	0.36	0.40	3	0.40	0.014	0.38-0.41
	II	0.29	0.31	3	0.32	0.012	0.30-0.33
	III	0.39	0.41	3	0.41	0.026	0.38-0.43
	IV	0.31	0.29	3	0.29	0.006	0.28-0.30

* HT = holotype. # PT = paratype.

Head: About 1,1x as wide (across eyes) as long (neck region not included). Antenna 1,3x as long as width of head, relative lengths of segments: 12,5:10:13:9. Anterior margins of antenniferous lobes straight as viewed from below.

Thorax: Dorsum. Pronotum about 2,8x as wide as long, lateral margins slightly concave. Mesonotum with median ridge granulated and median longitudinal fossula well developed. Lateral margins straight, converging anteriad. Metathoracical disk with sublateral glabrous strip only present on posterior half. MTg 2 with characteristic pits very prominent and deep; medially a semicircular depression occurs that is bisected by the median longitudinal bar. Adjacent to the bar 2(1+1) tubercles are present posteriorly. These tubercles are distinct in all the specimens at hand but not so prominent as in *Silvacoris heissi*.

Venter. A large median pit is present at the anterior end of the median oval rastrate area of sternum 2.

Abdomen: Dorsum. Tergal disk about 1,1x as wide as long. Posterior carina on MTg 6 clearly discernable in all specimens at hand.

Venter. Sternites 1+2 elevated and separated from 3 by a thin suture. Longitudinal sulci delimiting VLTg 3-6 sinuate in male, straight in females. Anterior LGI's clearly distinguishable on all segments.

Genitalia: Visible dorsal part of parameres (Fig. 80) broadly triangular, very different from the previous two species.

Chromosome number: 2n(♂) = 14XY.

Habitat and distribution: Coastal evergreen forests in the Eastern Cape (Fig. 51).

Etymology: Derived from Pondoland, an old name for the region in which it was collected.

Discussion: *Silvacoris pondolandensis* is larger than the other two species of the genus and the males can immediately be distinguished by the different shape of the parameres. It seems to have a combination of characteristics of the other two species. It agrees with *Silvacoris heissi* in the shape of the antenniferous lobes, the nodose mesonotal ridge with longitudinal fossula, weakly produced posteroexterior angles of laterotergites 2-4 and its chromosome number. It agrees with *Silvacoris karkloofensis* in large size, the presence of a pit or sternum 2, the prominent anterior lateral glabrous impressions (LGI) and sinuate sulci delimiting ventral laterogites (VLTg) in males. It differs from both in the male genitalia, the straight lateral margin of the mesonotum, the sculpture of mediotergite 2 (MTg 2) and sternite 1+2 of the abdomen being delimited from 3 by a transverse suture along its total width.

MATERIAL EXAMINED: **SOUTH AFRICA** . **Eastern Cape**. ♀ holotype: Port St. Johns, 31°37′S 29°32′E, 3.xii.1981, D.H. Jacobs (TMSA). 3 paratypes as follows: **Eastern Cape**. 1♂ 1♀: Same data as holotype. (The male is not designate as allotype as it was cut into several pieces to dissect its testis for cytogenetical studies); 1♀: SE. Cape Prov., Alexandra Forest Station, 33°43′S 26°23′E, 5.xii.1987, E-Y 2553, groundtraps, 2 days, leg. Endrödy-Younga (TMSA).

5.2 Cytogenetics of the genus Silvacoris

The locality and number of individuals of *Silvacoris* species that were cytogenetically studied are presented in table 5.4. The course of meiosis is similar to *Adamanotus uncotibialis*. The sex chromosome univalents usually lie inside the ring of autosomal bivalents at MI but often not in the centre. At MII, however, they occupy (with few exceptions) the centre of the peripheral ring of autosomes. A true diffuse stage is present in all the populations studied.

5.2.1 *Silvacoris heissi* (Figs 52, 81-82).

The chromosome number of *S. heissi* is 2n = 14XY. The true and relative chromosome areas for *S. heissi* are presented in table 5.5 and an idiogram, based on chromosome areas at MII, in Fig. 52. The six autosomes are about of similar size, forming a gradual series with relative areas ranging from about 14-19 persent of the total area of the autosomes. The larger sex chromosome (presumably the X) is of similar size to the fourth largest autosome while the smaller sex chromosome (presumably the Y) is somewhat smaller than the smallest autosome. [At MI (Fig 81) the sex chromosomes appear much smaller than the autosomes. This is because they are univalents while the autosomes are bivalents. At MII (Fig 82) the X-Y "touch and go pairing" structure is of about similar size than the autosomes, but the X and Y themselves are much smaller than the autosomes because they consist of single chromatids

Table 5.4. Locality and numbers of individuals of *Silvacoris* species cytogenetically studied.

Locality	Co-ordinates	Date collected	No. of individuals cytogenetically studied
Silvacoris heissi			
Ngoye forest, nr. Empangeni	28°50'S 31°43'E	11-12/xii/1980	3
Dhlinza forest, Eshowe	24°54'S 31°27'E	12/iv/1980	5
Silvacoris karkloofensis			
Shaws Wood farm, Karkloof, nr. Pietermaritzburg	29°19'S 30°18'E	1/ii/1983	2
Town Bush, Pietermaritzburg	29°33'S 30°20'E	31/i/1983	4
Silvacoris pondolandensis			
Port St. Johns, Eastern Cape	31°37'S 29°32'E	3/xii/1981	1

at this stage while the autosomes consist of two chromatids. To get a comparable picture the sex chromosomes must be compared with only one chromatid i.e. half of a autosome at this stage. The reader should keep this in mind throughout this study as the attention will not be drawn to it again.]

5.2.2 *Silvacoris karkloofensis* (Figs 53, 83-84).

The chromosome number of *S. karkloofensis* is 2n = 12XY. The true and relative chromosome areas for *S. karkloofensis* are presented in Table 5.6 and an idiogram in Fig. 53. One of the autosomes is much larger, about of double size, than the other four which are of about similar size, forming a more or less gradual series with relative areas between 13,5 and 18,5 persent of the total area of the autosomes. The larger sex chromosome (presumably the X) is a little larger than the second largest autosome while the smaller sex chromosome (presumable the Y) is somewhat smaller than the second smallest autosome.

5.2.3 *Silvacoris pondolandensis* (Figs 54, 85-86).

The chromosome number of *S. pondolandensis* is 2n = 14XY. The true and relative chromosome areas are presented in Table 5.7 and an idiogram in Fig. 5.4. The karyotype of *S. pondolandensis* is very similar to that of *S. heissi* and the only observable difference seem to be that the smaller sex chromosome (presumably the Y) is somewhat larger, being about the same size as the second smallest autosome and only slightly smaller than the X-chromosome.

Table 5.5: True and relative chromosome areas of *S. heissi*.

True chromosome areas (µm²) and standard deviation.				Relative chromosome areas (% of total area of autosomes) and standard deviation.		
Chromosome	Dhlinsa forest	Ngoye forest	TOTAL	Dhlinsa forest	Ngoye forest	TOTAL
Individuals	1	2	3	1	2	3
Cells	5	9	14	5	9	14
A1	2.96(±0.25)	3.47(±0.71)	3.29(±0.63)	18.73(±0.91)	19,24(±0.61)	19.06(±0.74)
A2	2.87(±0.23)	3.33(±0.66)	3.12(±0.57)	18.12(±0.25)	18.08(±0.56)	18.10(±0.46)
A3	2.73(±0.30)	3.11(±0.59)	2.97(±0.53)	17.22(±0.39)	17.28(±0.45)	17.26(±0.42)
A4	2.58(±0.20)	2.99(±0.50)	2.84(±0.45)	16.33(±0.53)	16.63(±0.60)	16.52(±0.58)
A5	2.42(±0.26)	2.73(±0.47)	2.62(±0.42)	15.27(±0.32)	15.23(±0.81)	15.25(±0.66)
A6	2.27(±0.20)	2.42(±0.40)	2.37(±0.35)	14.33(±0.53)	13.52(±0.73)	13.82(±0.76)
X	2.57(±0.40)	2.98(±0.44)	2.83(±0.46)	16.21(±1.97)	16.73(±2.01)	16,54(±1.93)
Y	1.96(±0.25)	2.22(±0.45)	2.13(±0.40)	12.41(±1.42)	12.50(±2.40)	12.47(±2.04)
Autosomes	15.84(±1.36)	17.98(±3.28)	17.22(±2.89)			
All chromosomes	20.30(±1.80)	23.19(±3.93)	22.18(±3.53)			

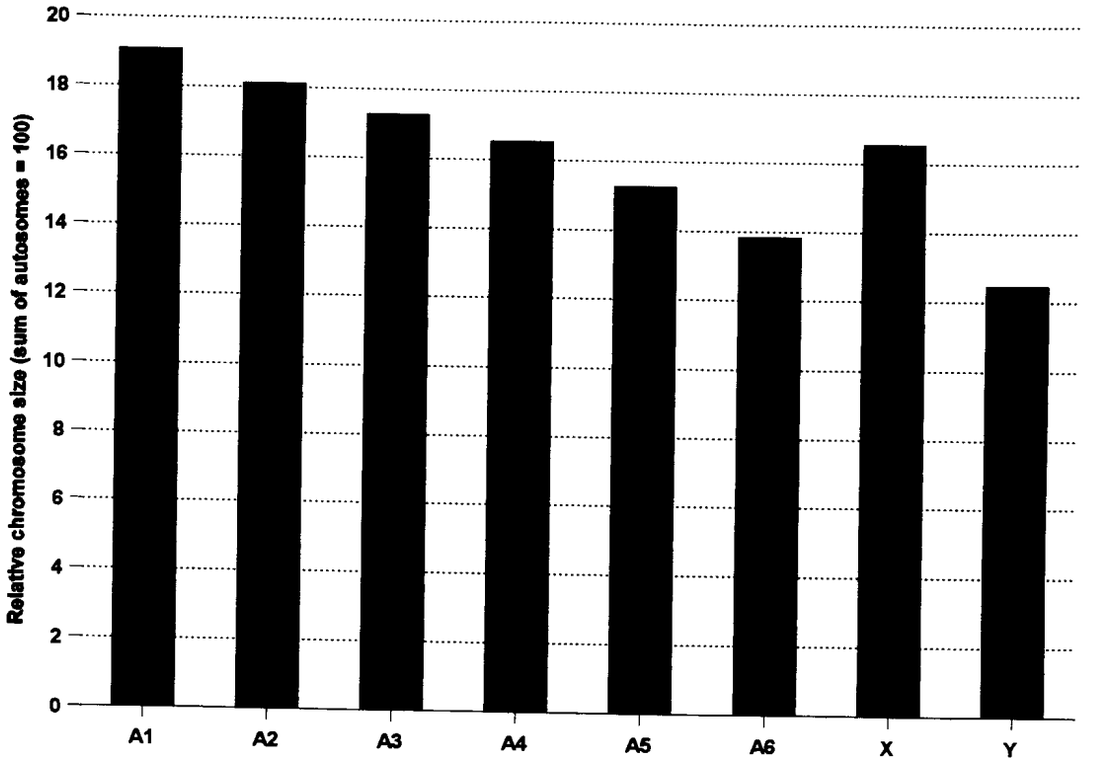


Figure 52. Idiogram of *Silvacoris heissi*.

Table 5.6: True and relative chromosome areas of *S. karkloofensis*.

True chromosome areas (μm²) and standard deviation.				Relative chromosome areas (% of total area of autosomes) and standard deviation.		
Chromosome	Town Bush	Karkloof	TOTAL	Town Bush	Karkloof	TOTAL
Individuals	3	1	4	3	1	4
Cells	15	3	18	15	3	18
A1	5.50(±0.85)	6.25(±0.09)	5.62(±0.82)	34.41(±1.80)	35.47(±1.56)	34.59(±1.77)
A2	2.95(±0.48)	3.21(±0.34)	3.00(±0.46)	18.45(±0.84)	18.16(±1.04)	18.40(±0.85)
A3	2.78(±0.43)	3.00(±0.17)	2.92(±0.41)	17.39(±0.66)	16.70(±0.39)	17.32(±0.64)
A4	2.61(±0.41)	2.76(±0.25)	2.64(±0.38)	16.34(±0.84)	15.70(±1.01)	16.23(±0.87)
A5	2.14(±0.29)	2.41(±0.14)	2.18(±0.29)	13.42(±0.89)	13.66(±0.15)	13.46(±0.81)
X	3.10(±0.42)	3.18(±0.06)	3.11(±0.38)	19,49(±2.15)	18.06(±1.26)	19.25(±2.07)
Y	2.45(±0.36)	2.27(±0.08)	2.43(±0.34)	15.46(±1.38)	12,88(±0.24)	15.03(±1.60)
Autosomes	15.98(±2.32)	17.66(±0.85)	16.26(±2.22)			
All chromosomes	21.54(±2,94)	23.11(±0.86)	21.80(±2.75)			

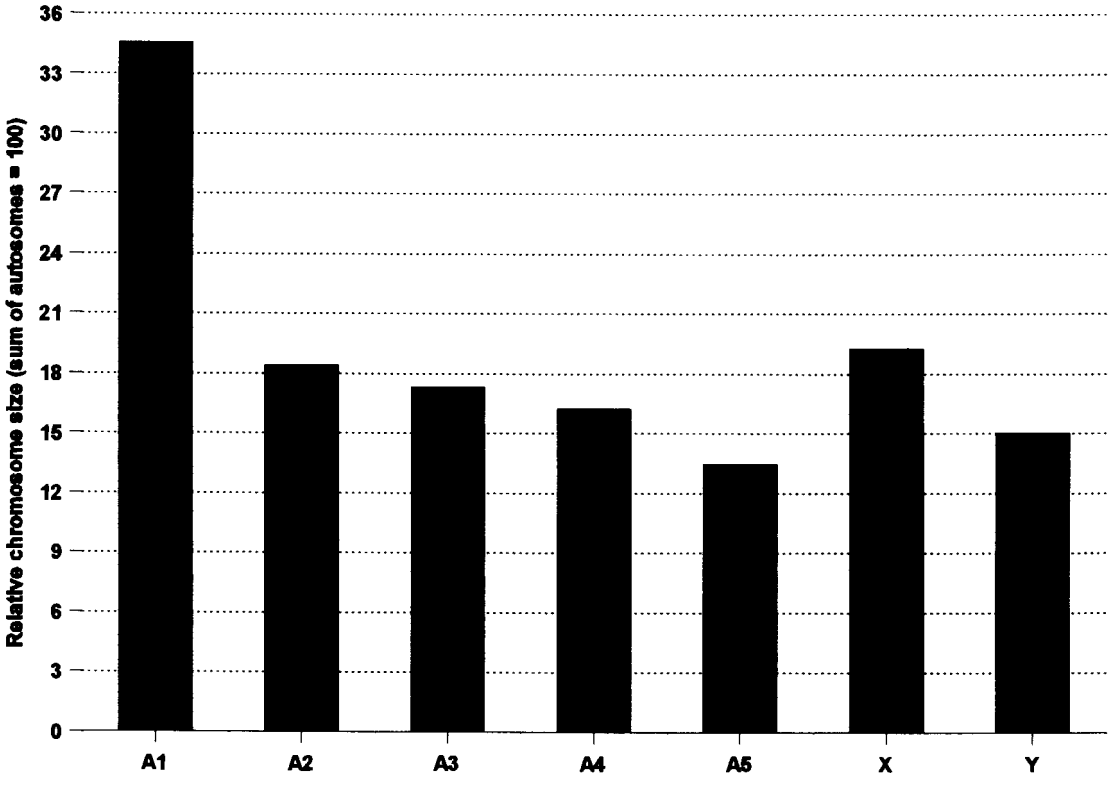


Figure 53. Idiogram of *Silvacoris karkloofensis*.

Table 5.7: True and relative chromosome areas of *S. pondolandensis*.

True chromosome areas (µm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Port St. Johns	Port St. Johns
Individuals	1	1
Cells	6	6
A1	3.04(±0.40)	19.13(±0.54)
A2	2.84(±0.47)	17.87(±0.48)
A3	2.75(±0.37)	17.33(±0.18)
A4	2.67(±0.38)	16.79(±0.37)
A5	2.44(±0.33)	15.36(±0.89)
A6	2.14(±0.27)	13.52(±0.67)
X	2.66(±0.45)	16.74(±1.13)
Y	2.45(±0.33)	15.43(±0.24)
Autosomes	15.88(±2.16)	
All chromosomes	20.99(±2.91)	

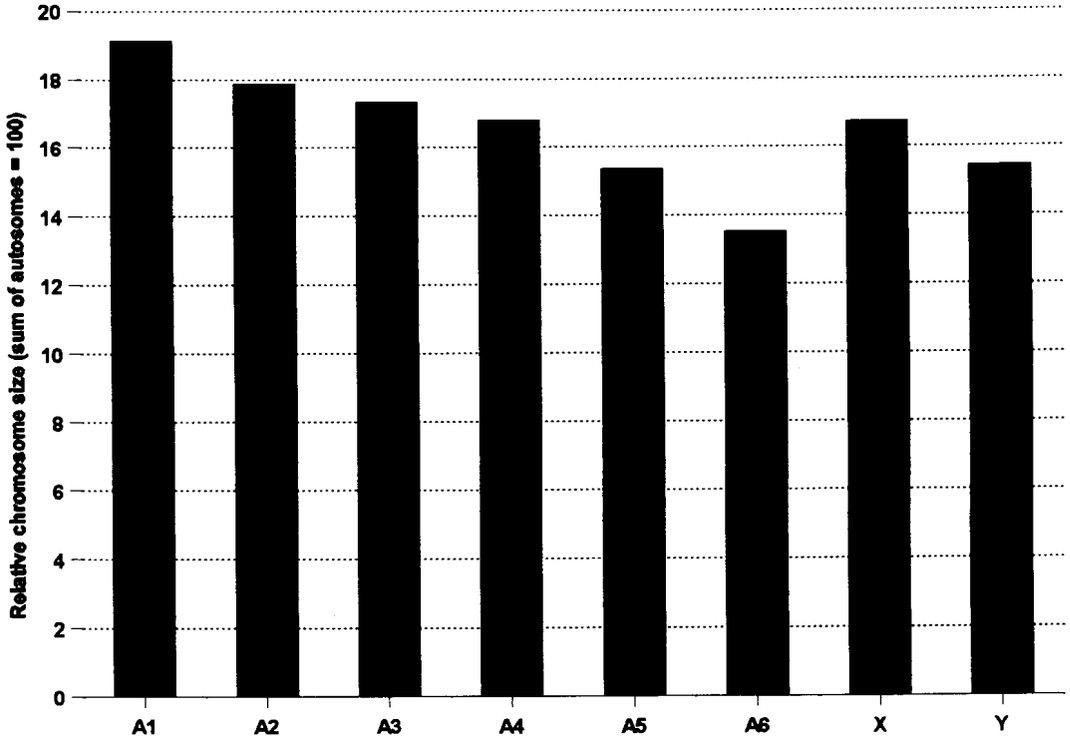


Figure 54. Idiogram of *Silvacoris pondolandensis*.

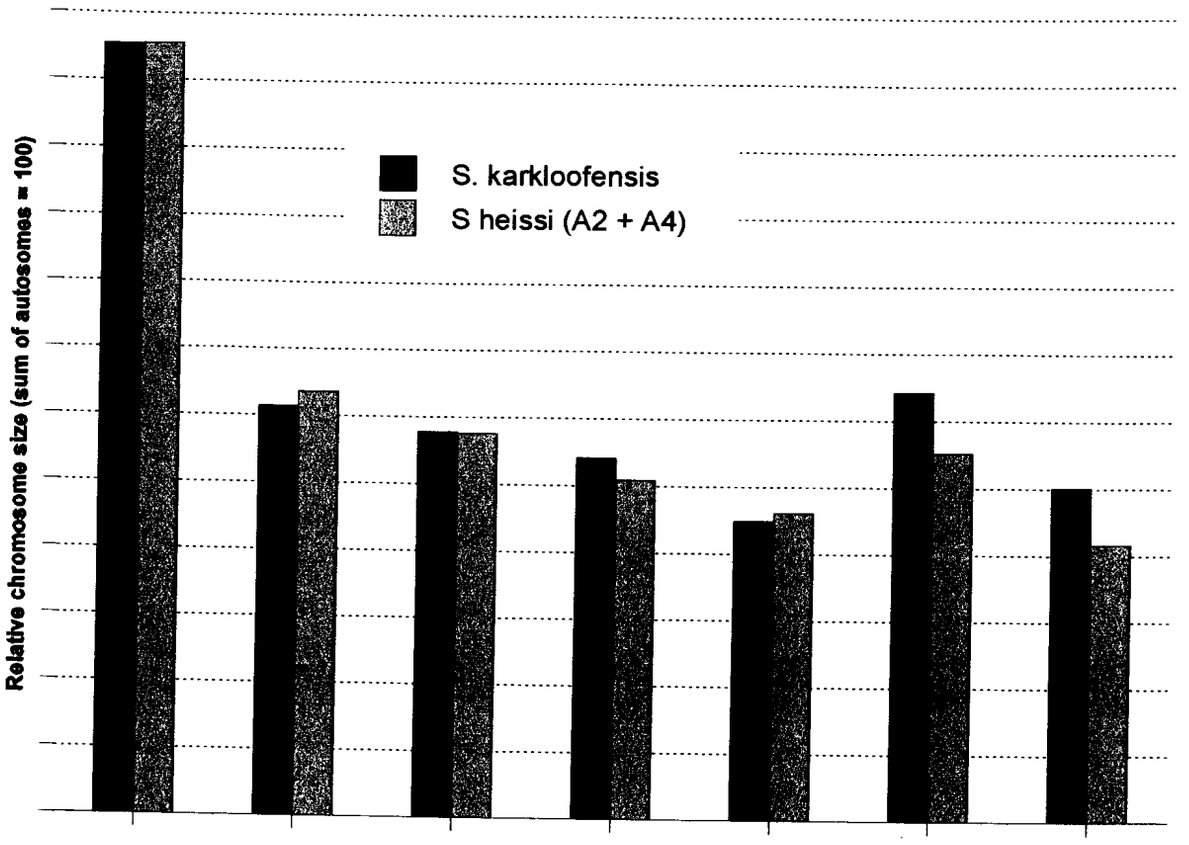


Figure 55. Comparison of the idiograms of *S. heissi* and *S. karkloofensis* with autosomes A2 and A4 of *S. heissi* added.

5.2.4 Discussion:

It is evident from both their morphology and karyotypes that the three *Silvacoris* species are closely related. Both *S. heissi* and *S. pondolandensis* have a chromosome number of 2n = 14XY which, as will be discussed in 12.1.1, is probably the ancestral number for the Aradoidea as well as the Pentatomorpha. There is little doubt that the larger autosome of *S. karkloofensis* originated from the fusion of two chromosomes, probably from *S. heissi* or a common ancestor.

I have tested this hypothesis with the means of the bootstrap method described in 'Material and Methods' above. From visual comparison it seems that the large autosome could have originated from either the fusion of autosomes A2 and A4 (Fig. 55) or A1 and A5 (Fig. 56) of *S. heissi*. Both these possibilities were tested. When the values of autosomes A2 and A4 of *S. heissi* were added to get the large autosome of *S. karkloofensis* the test statistics showed significant differences for autosomes A2 and A4 (Table 5.8) in the case of relative chromosome sizes. When the values autosomes A1 and A5 of *S. heissi* were added to get the large autosome of *S. karkloofensis* no significant differences for any of the autosomes were detected (Table 5.9).

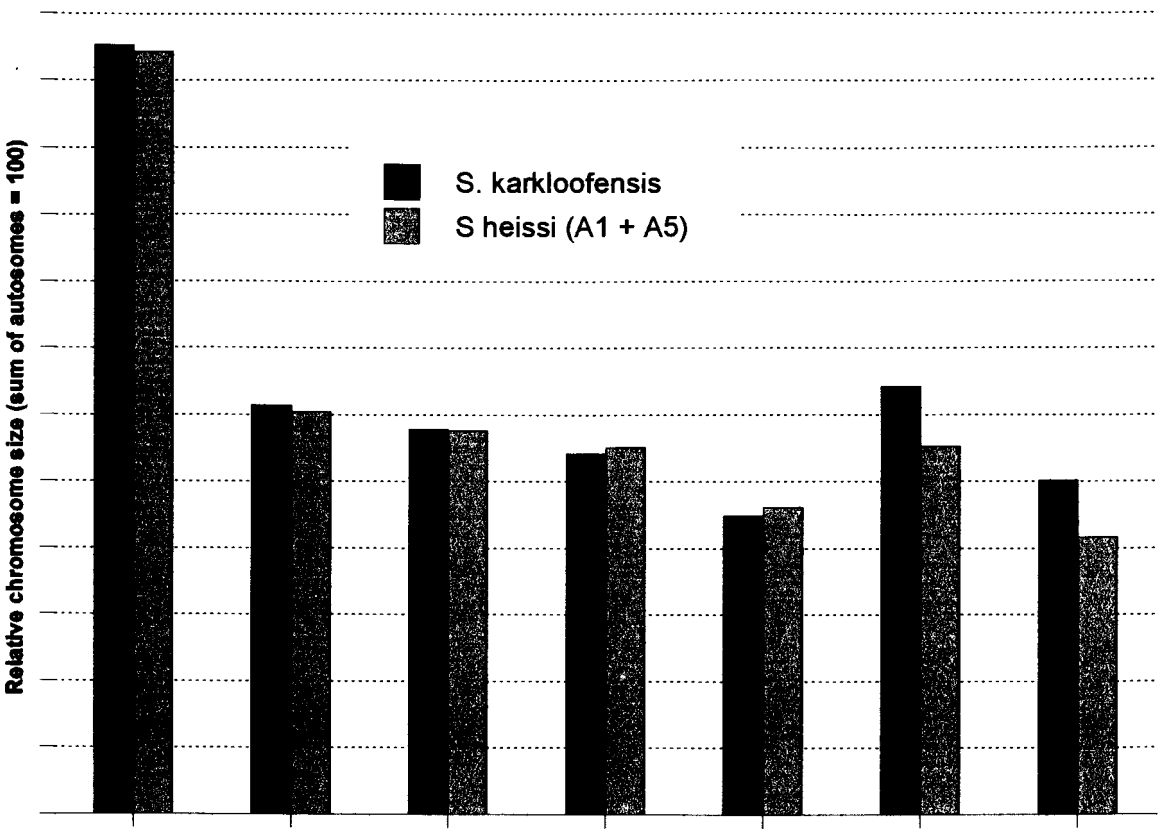


Figure 56. Comparison of the idiograms of *S. heissi* and *S. karkloofensis* with autosomes A1 and A5 of *S. heissi* added.

In both cases there were no significant differences when the true chromosome areas were used. This can be explained (and it was even expected) by the fact that differential squashing of the cells resulted in large variation in these values.

It is thus highly likely that autosomes A1 and A5 of *S. heissi* (or a common ancestor with similar karyotype) fused during the speciation process to from the large autosome of *S. karkloofensis*.

From the combined morphological and cytogenetical data the phylogeny of the three *Silvacoris* species is clear: *S. pondolandensis* is the most primitive species, exhibiting the plesiomorphic karyotype and parameres. *S. heissi* and *S. karkloofensis* both show the apomorphic parameres while the latter also show a derived karyotype.

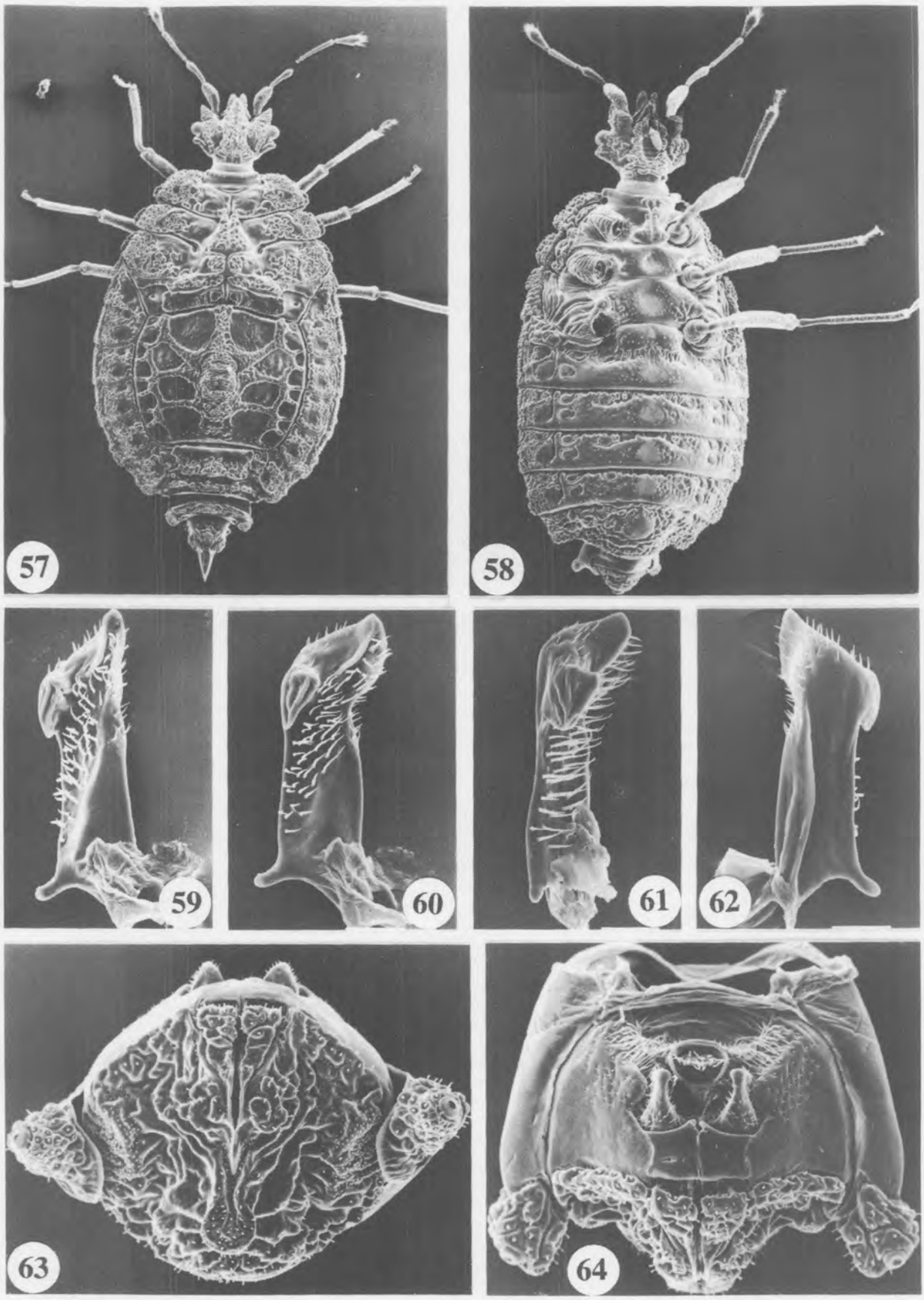
Table 5.8: Test statistics for testing the hypothesis that chromosomes A2 and A4 of *S. heissi* fused to form chromosome A1 of *S. karkloofensis*.

Relative chromosome areas (% of total area of autosomes).			
Chromosome	**95th percentile**	**99th percentile**	**Test statistics**
A1	1.0655	2.0145	0.0022
A2	0.3119	0.4263	0.4604 **
A3	0.3776	0.5845	0.0018
A4	0.5177	0.9254	0.9040 *
A5	0.4199	0.9716	0.0717
Sum of autosomes	2.7987	3.0322	1.4402
True chromosome areas.			
A1	0.3292	0.5187	0.0409
A2	0.1086	0.2219	0.0471
A3	0.0953	0.1892	0.0081
A4	0.0748	0.1822	0.0052
A5	0.0672	0.1639	0.0137
Sum of autosomes	0.5994	1.1399	0.1151

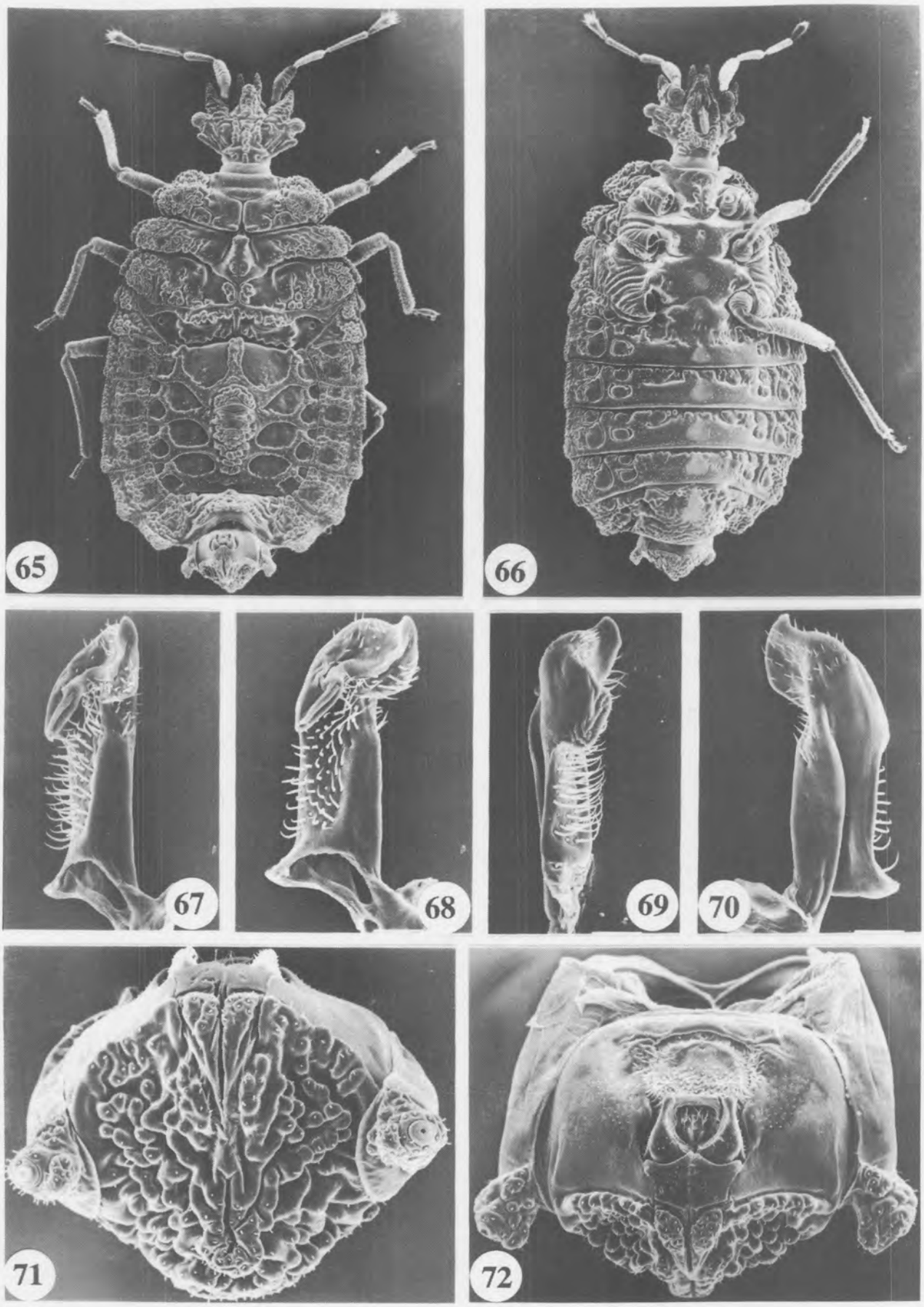
* Significant and ** highly significant values.

Table 5.9: Test statistics for testing the hypothesis that chromosomes A1 and A5 of *S. heissi* fused to form chromosome A1 of *S. karkloofensis*.

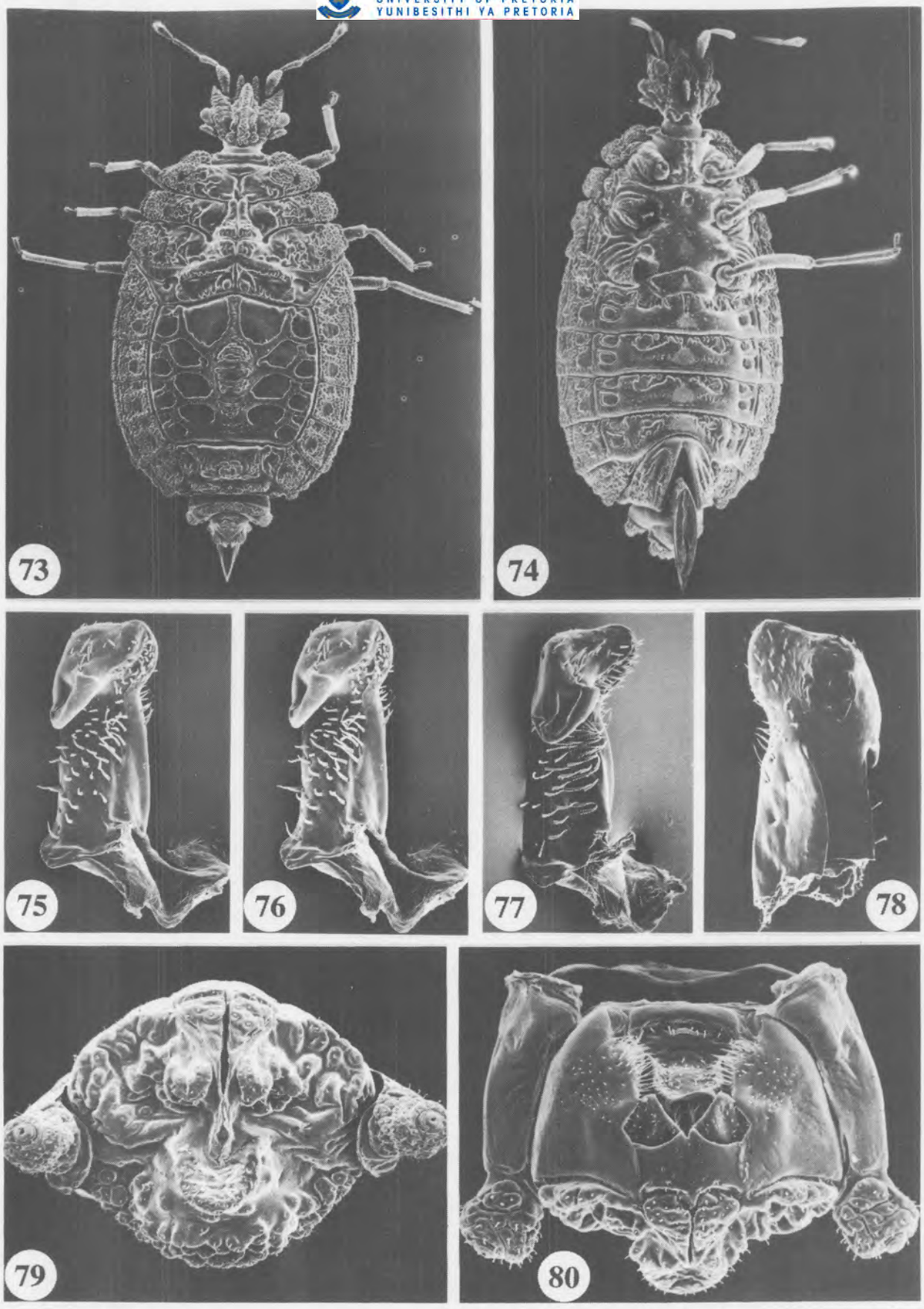
Relative chromosome areas (% of total area of autosomes).			
Chromosome	**95th percentile**	**99th percentile**	**Test statistics**
A1	1.1827	2.0140	0.0498
A2	0.3205	0.5741	0.1402
A3	0.3211	0.5354	0.0018
A4	0.5223	0.7590	0.1389
A5	0.5416	1.4318	0.0717
Sum of autosomes	2.1786	3.0507	0.4025
True chromosome areas.			
A1	0.3265	0.6602	0.0242
A2	0.1103	0.1830	0.0017
A3	0.1004	0.1643	0.0081
A4	0.0940	0.2213	0.0223
A5	0.0700	0.1095	0.0137



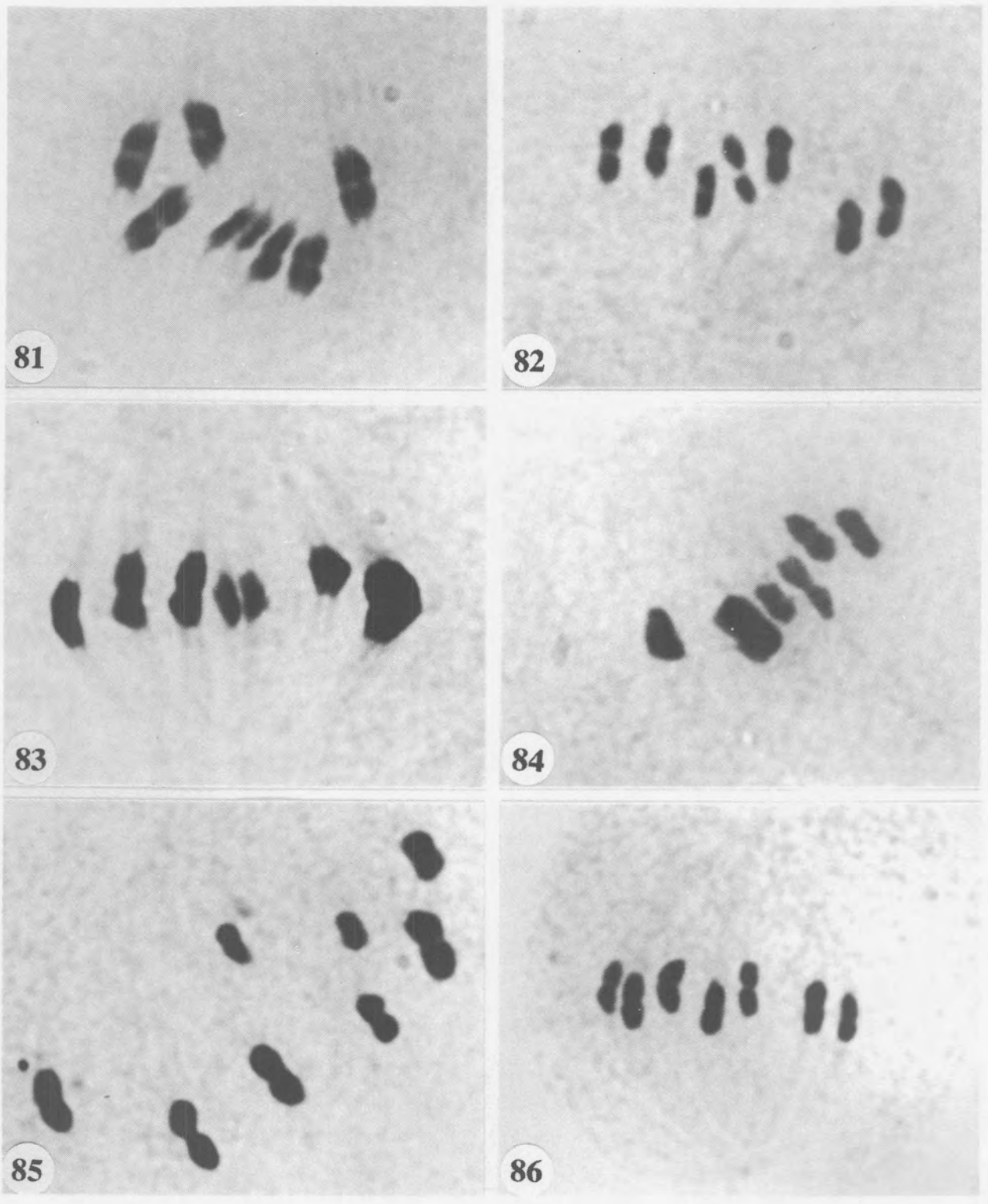
Figs 57-64. Scanning electron photomicrographs of *Silvacoris heissi* **gen. et spec. nov.** 57. Female paratype, dorsal aspect. 58. Male paratype, ventral aspect. 59-62. Different aspects of the left paramere (scale bar = 50 μm). 63-64. Pygophore. 63. Caudal aspect. 64. Dorsal aspect.



Figs 65-72. Scanning electron photomicrographs of *Silvacoris karkloofensis* **gen. et spec. nov.** 65. Male paratype, dorsal aspect. 66. Male paratype, ventral aspect. 67-70. Different aspects of the left paramere (scale bar = 50 μm). 71-72. Pygophore. 71. Caudal aspect. 72. Dorsal aspect.



Figs 73-80. Scanning electron photomicrographs of *Silvacoris pondolandensis* **gen. et spec. nov.** 73-74. Female paratype. 73. Dorsal aspect. 74. Ventral aspect. 75-78. Different aspects of the left paramere. 75-76. Stereo pair of mesal aspect. 77. Medioposterior view. 78. Lateral aspect of dorsal part. 79-80. Pygophore. 79. Caudal aspect. 80. Dorsal aspect.



Figs 81-86. Meiotic stages in *Silvacoris* species. 81-82. *S. heissi* 81. Metaphase I. 82. Metaphase II. 83-84. *S. karkloofensis*. 83. Metaphase I. 84. Metaphase II. 85-86. *S. pondolandensis*. 85. Metaphase I. 86. Metaphase II.