Cytotaxonomy, classification and phylogeny of African Carventinae (Heteroptera: Aradidae)

by

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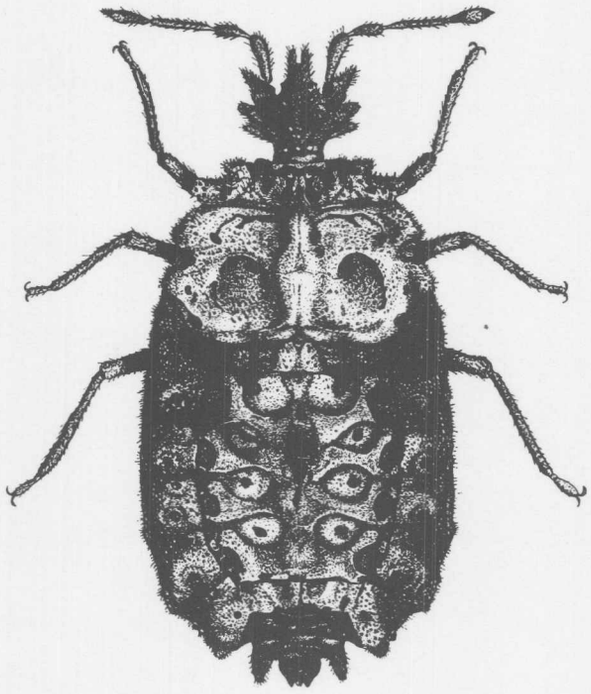

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Abstract

The southern African species of the Aradidae subfamily Carventinae are revised, resulting in the recognition of 7 genera, 24 species and 10 subspecies (excluding the nominal ones). Of these, 4 genera, 18 species and 10 subspecies are described as new. A neotype is designated for *Dundocoris natalensis*. Keys to the genera and species are given. Scanning electron photomicrographs of the dorsal and ventral aspects and external genitalia are provided for all the species.

The cytogenetics of the group are discussed and idiograms, based on chromosome area measurements, and photomicrographs of meiotic stadia (mostly metaphase I and metaphase II) are presented for all but one species. The chromosome numbers of the species vary between 2n = $7XY_1Y_2$ and 2n = 32XY and XY, X_1X_2Y and XY_1Y_2 sex chromosome systems occur. Multiple sex chromosome systems that originated from autosome-sex chromosome fusions are described for the first time in the Heteroptera. A unique case where two homologous autosomes have fused with the X- and Y-chromosomes respectively, is reported. Karyotype evolution and the origin of the different chromosome numbers are discussed and hypotheses presented. Pseudoploidy, fusions and to a lesser extent fragmentation, have played the major role in the karyotype evolution of the Carventinae. The cytogenetics of the other subfamilies of the Aradidae are briefly discussed and illustrated. It is argued that the ancestral chromosome number for the Carventinae and Aradidae (and therefore also the Pentatomorpha) is 2n = 14XY.

The morphological and cytogenetic data are integrated in the classification of the Carventinae and several of the subspecies are based on chromosome number differences. The homeostatic genetic species concept is proposed and its application to the Carventinae is discussed. Phylogenies for the genera and species are proposed.

The text is accompanied by more than 540 figures and more than 60 tables.

Samevatting

Die Suidelike Afrikaanse species van die Aradidae subfamilie Carventinae word hersien en dit het tot gevolg dat 7 genera, 24 species en 10 subspecies (met uitsluiting van die nominale subspecies), erken word. Van hierdie word 4 genera, 18 species en 10 subspecies as nuut beskryf. 'n Neotipe vir *Dundocoris natalensis* word aangewys. Identifikasiesleutels tot die genera en species word voorsien. Skandeerelektronmikroskoop foto's van die dorsale en ventrale aansigte word vir al die species ingesluit.

Die sitogenetika van die groep word bespreek en idiogramme, gebaseer op chromosoomoppervlakte metings, asook fotomikrogramme van die meiotiese stadia (hoofsaaklik meteafase I en metafase II) word vir al die species, uitgesonderd een, voorsien. Die chromosoomgetalle van die species wissel tussen $2n = 7XY_1Y_2$ en $2n = 32XY$, en XY, X_1X_2Y en XY_1Y_2 geslagschromosoomsisteme kom voor. Veelvuldige geslagschromosoomsisteme wat ontstaan het as gevolg van outosoom-geslagschromosoom samesmeltings word vir die eerste keer in die Heteroptera beskryf.. 'n Unieke geval waar twee homoloë autosome met die X- en Y-chromosome onderskeidelik saamgesmelt het, word rapporteer. Kariotiepevolusie en die oorsprong van die verskillende chromosoomgetalle word bespreek en hipoteses om dit te verklaar word aangebied. Pseudoploidie, samesmeltings en fragmentasie tot 'n mindere mate het die hoofrolle gespeel in die kariotiepevolusie van die Carventinae. Die sitogenetika van die ander subfamilies van die Aradidae word kortliks bespreek en geïllustreer. Dit word argumenteer dat die voorvaderlike chromosoomgetal van die Carventinae en Aradidae (en daarom ook van die Pentatomorpha) $2n = 14XY$ is.

Die morfologiese en sitogenetiese data word integreer in die klassifikasie van die Carventinae en verskeie van die subspecies is gebaseer op chromosoomgetal verskille. Die homeostatiese genetiese specieskonsep word voorgestel en die toepassing daarvan op die Carventinae word bespreek. 'n Filogenie word voorgestel vir die genera en species.

Die teks word aangevul deur meer as 540 illustrasies en meer as 60 tabelle.

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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).

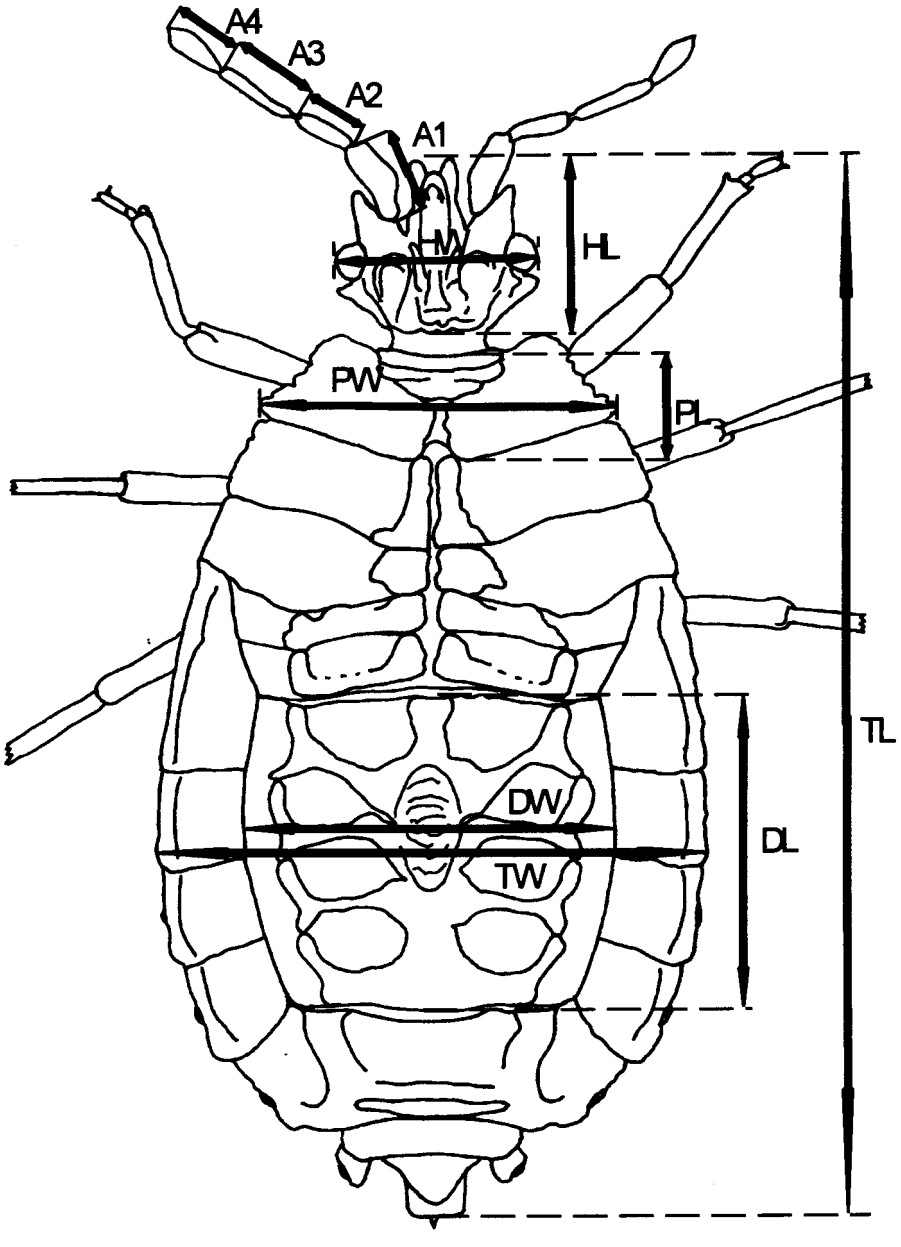
Head length: the distance from the anterior tip of rostrum (usually the genae but sometimes the clypeus) to the margin between the smooth neck area and the rough, elevated area of the head.

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.

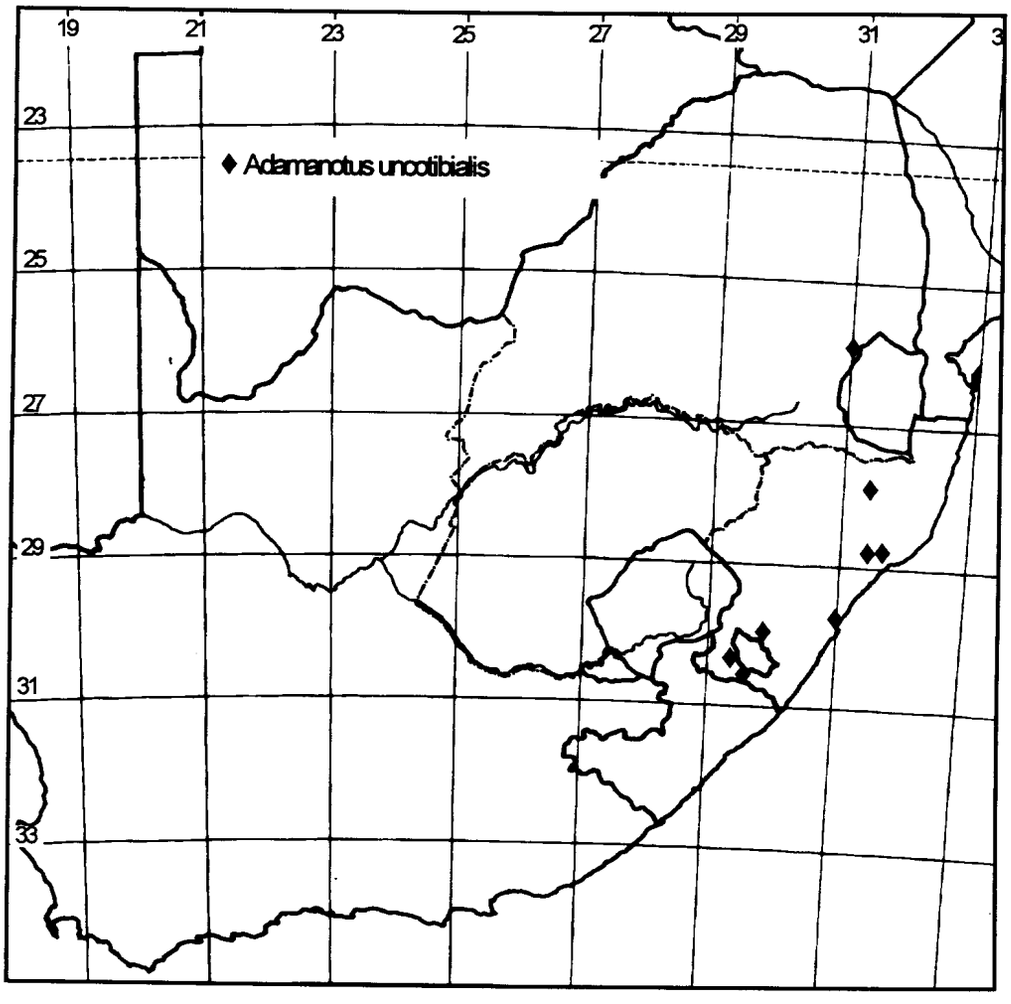


Figure 3. Distribution map of *Adamanotus uncotibialis* gen. et spec. nov.

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.

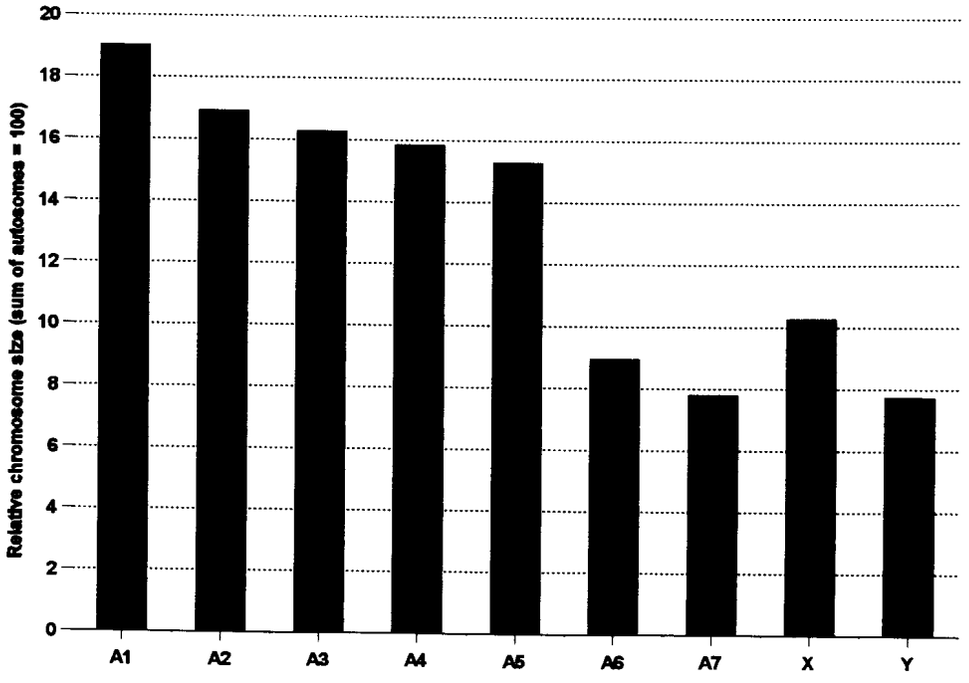


Figure 3. Idiogram of *Adamanotus uncotibialis*.

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).

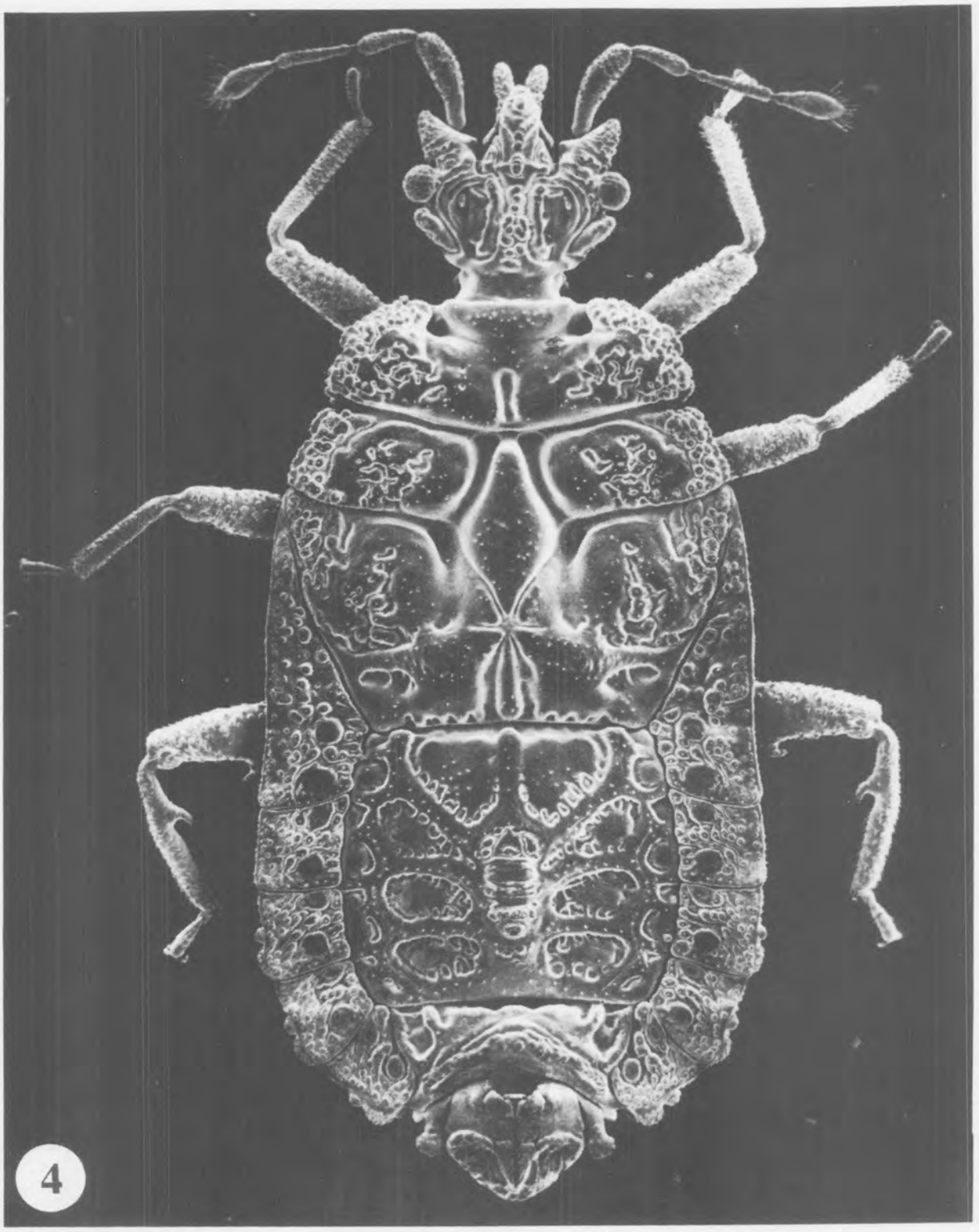
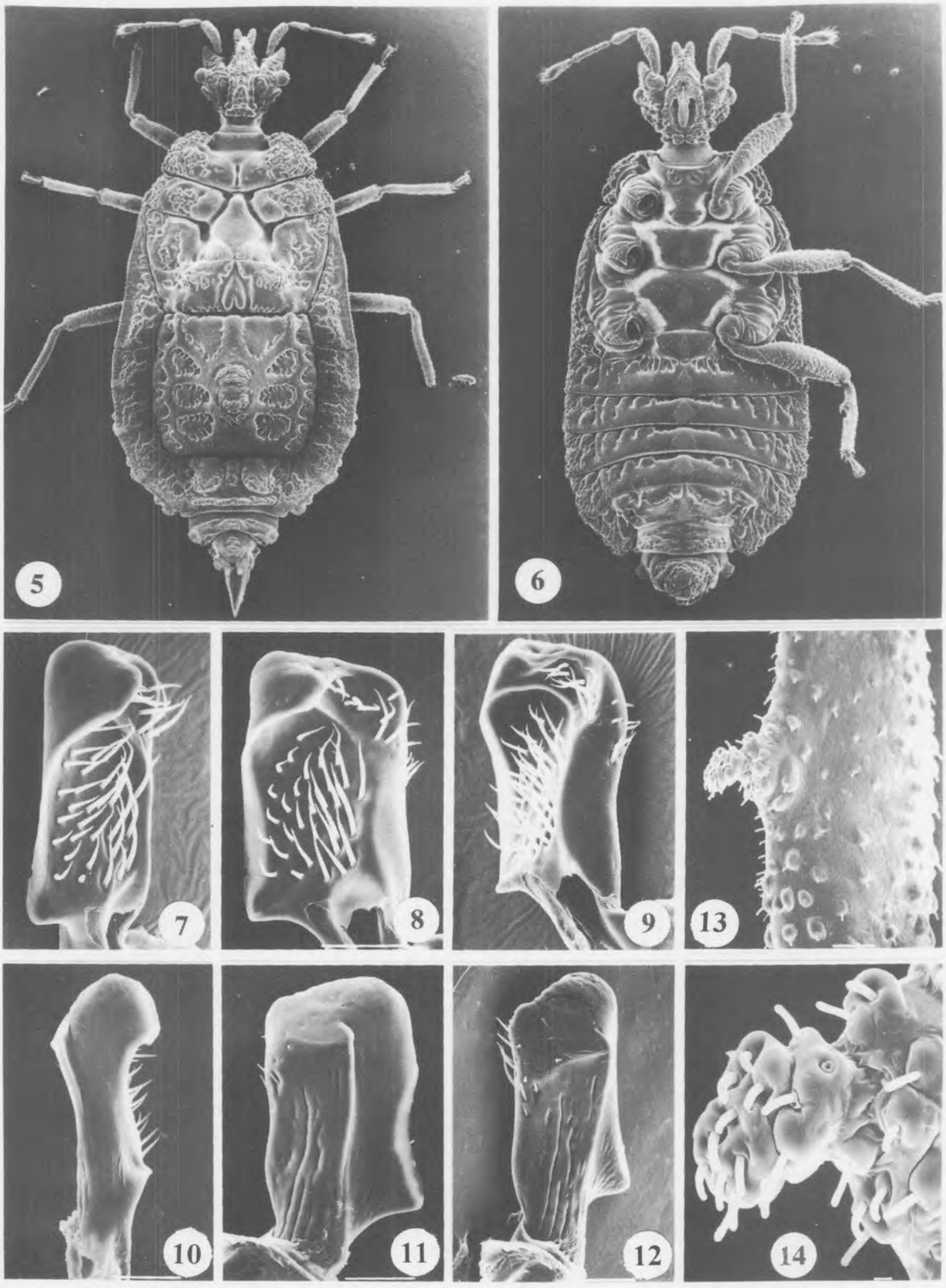
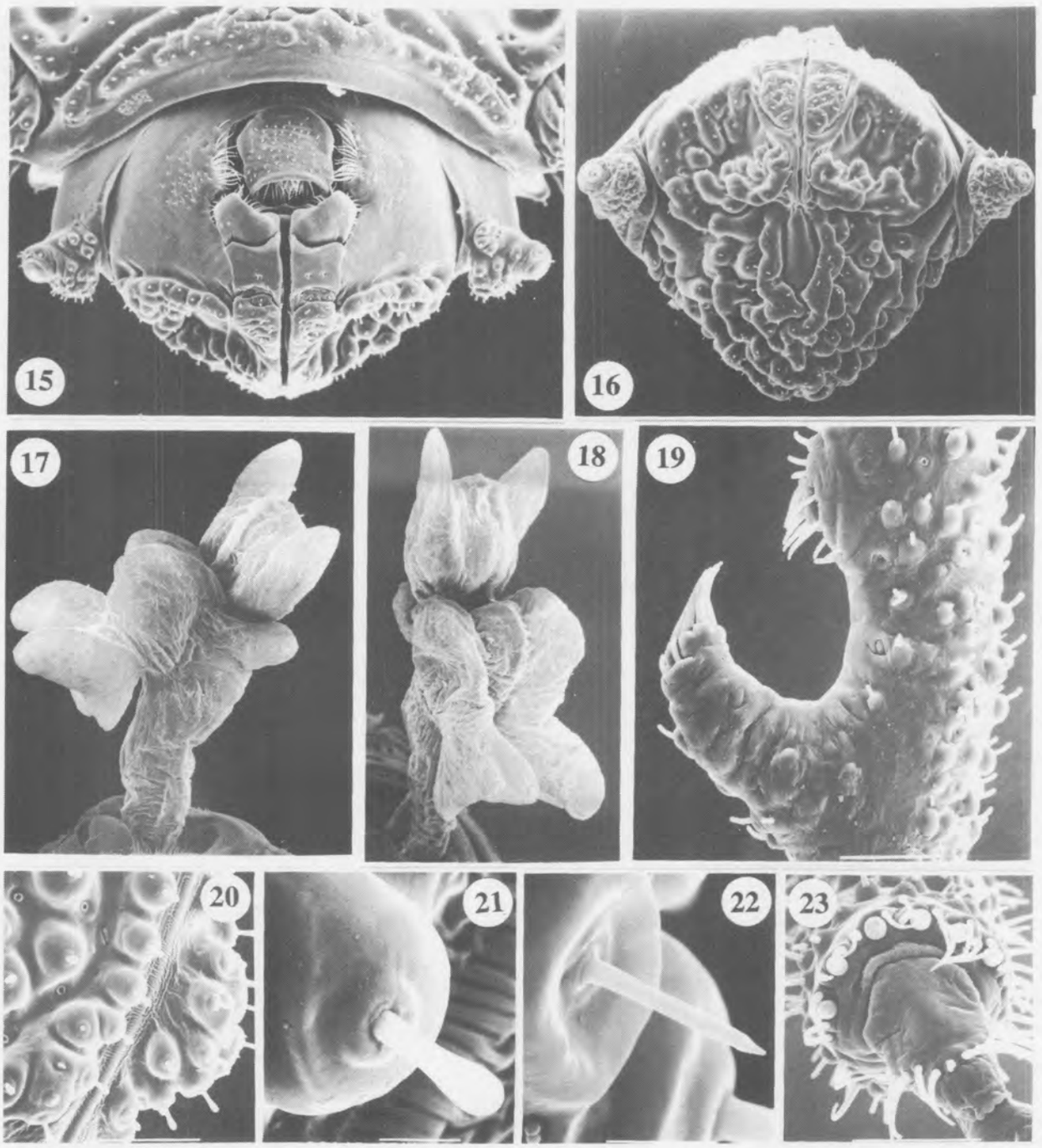


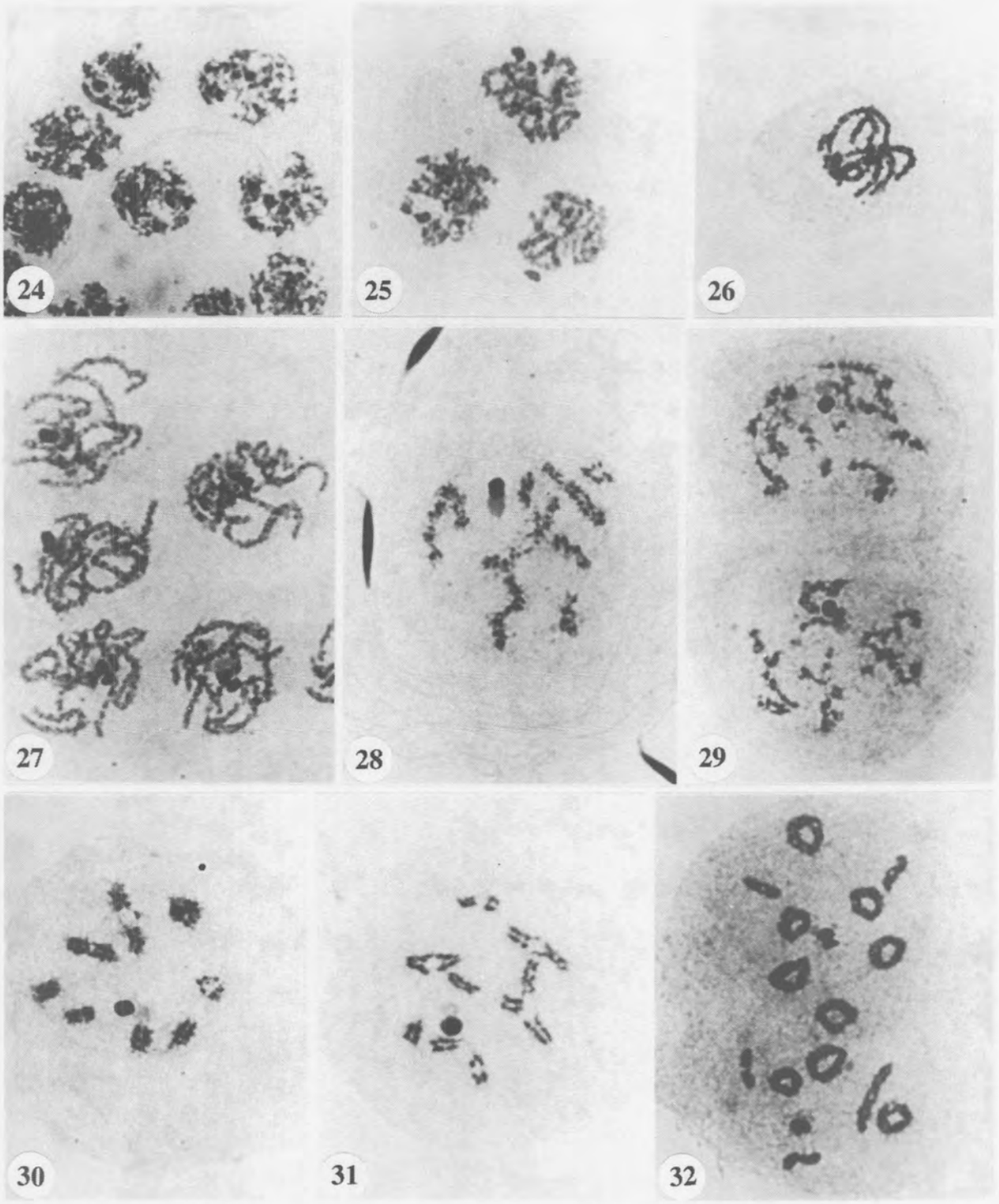
Fig. 4. Scanning electron photomicrograph of *Adamanotus uncotibialis* **gen. et spec. nov.**, dorsal aspect of male paratype.



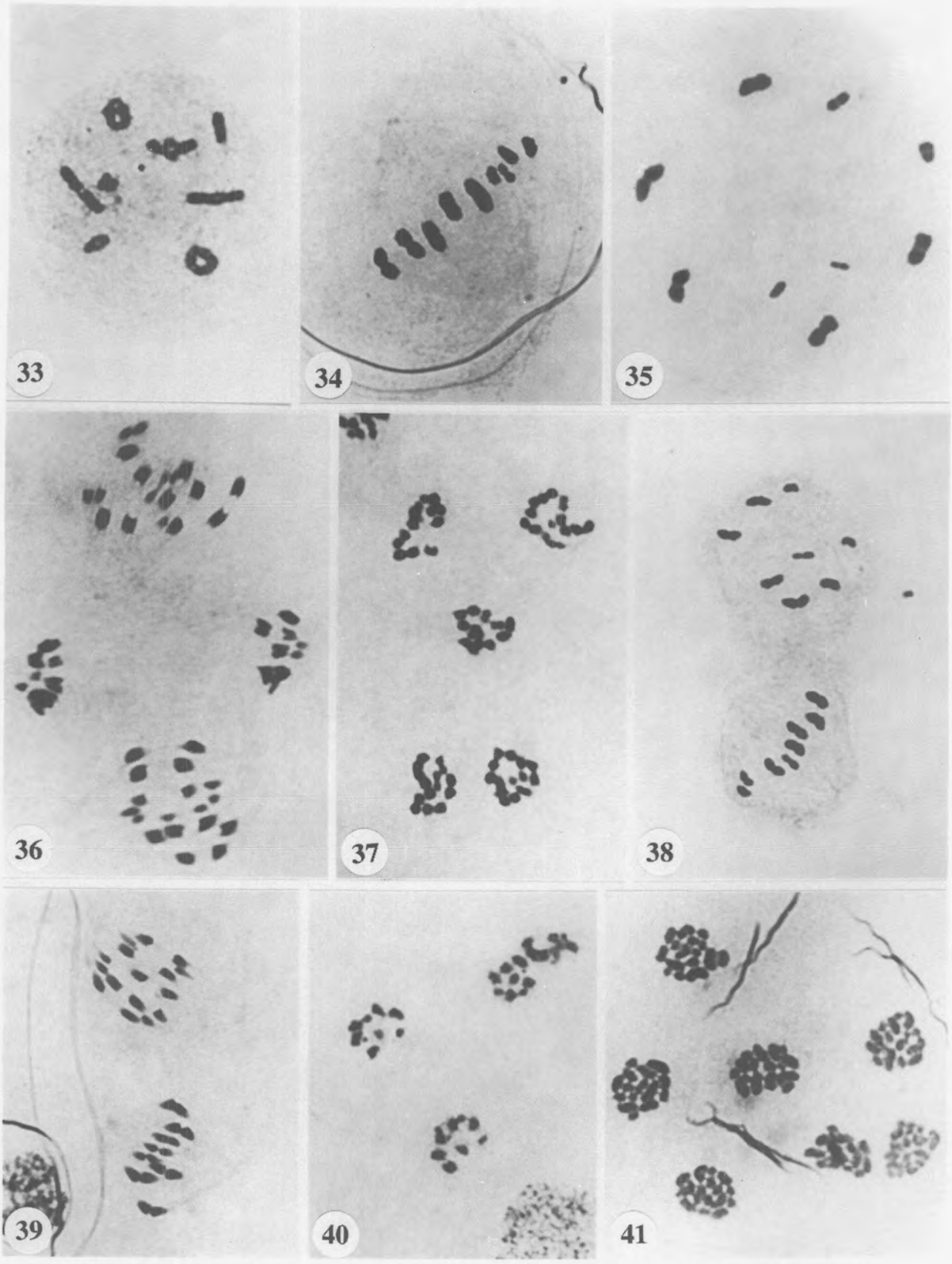
Figs 5-14. Scanning electron photomicrographs of *Adamanotus uncotibialis* **gen. et spec. nov.** 5. Female paratype, dorsal aspect. 6. Male paratype, ventral aspect. 7-12. Different aspects of the left paramere (scale bar = 50 μm). 13. Hind femur of male with protuberance (scale bar = 50 μm). 14. Close-up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



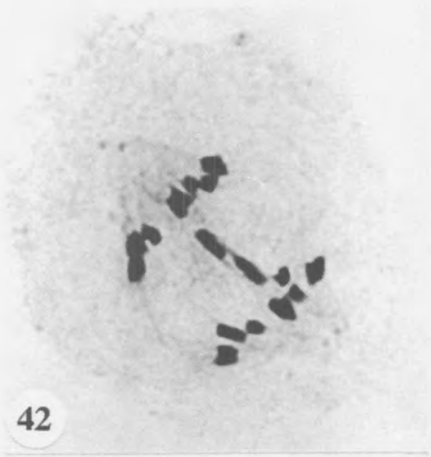
Figs 15-23. Scanning electron photomicrographs of *Adamanotus uncotibialis* **gen. et spec. nov.** 15-16. Pygophore. 15. Dorsal aspect (scale bar = 50 μm). 16. Caudal aspect (scale bar = 50 μm). 17-18. Inflated aedeagus. 17. Lateroposterior aspect. 18. Dorsoposterior aspect. 19. Unciform outgrowth of 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).

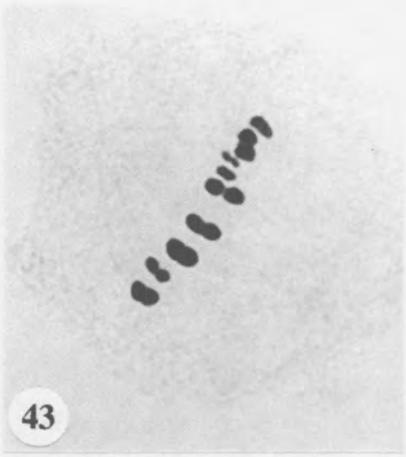


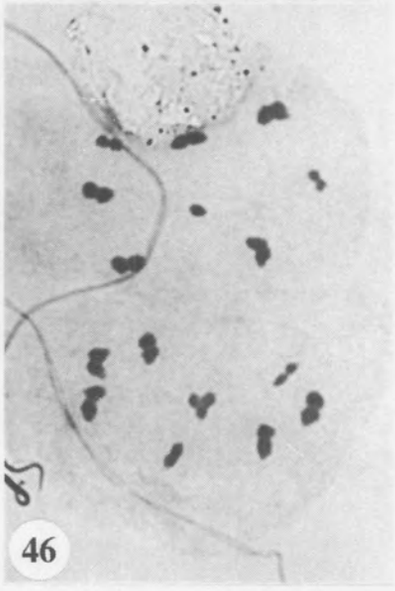
Figs 24-32. Meiotic stages in *A. uncotibialis*. 24-25. Pre-pachytene stages. 26. Pachytene displaying the typical bouquet formation. 27. Pachytene as appearing in well-spread cells. 28. Early diplotene/diffuse stage. 29. Diplotene/diffuse stage. 30. Early diplotene/diffuse stage in the Hawaan forest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

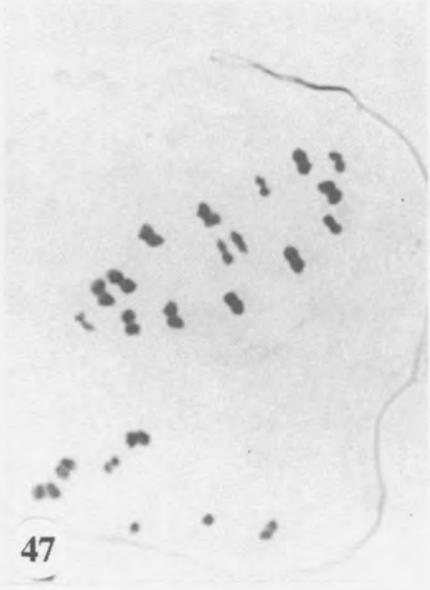


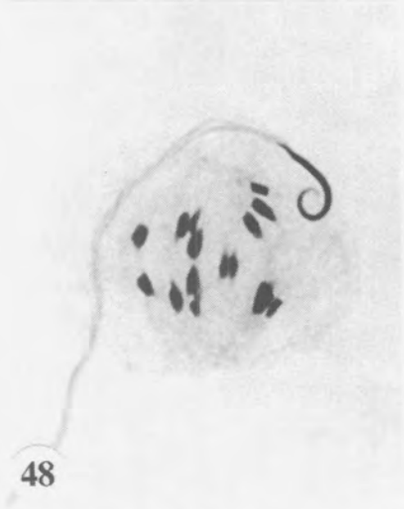
Figs 33-41. Meiotic stages in *A. uncotibialis*. 33. Diakinesis. 34-35. Metaphase I. 34. Equatorial view. 35. Polar view. 36. Anaphase I. 37. Late anaphase/telophase I. 38. Metaphase II. 39. Anaphase II. 40. Late anaphase/telophase II. 41. Spermatogonial metaphases.

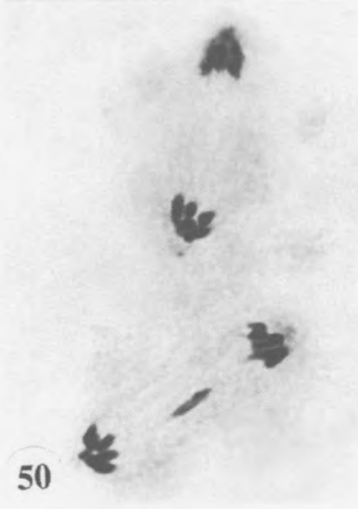












Figs 42-50. Examples of abnormal meiocytes observed in *A. uncotibialis*. 42. Anaphase I with late segregating autosome. 43. Metaphase I with malorientated bivalent. 44. Anaphase I with dicentrically attached lagging sex chromosome. 45. Metaphase II with malorientated sex chromosomes. 46. Unbalanced 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.

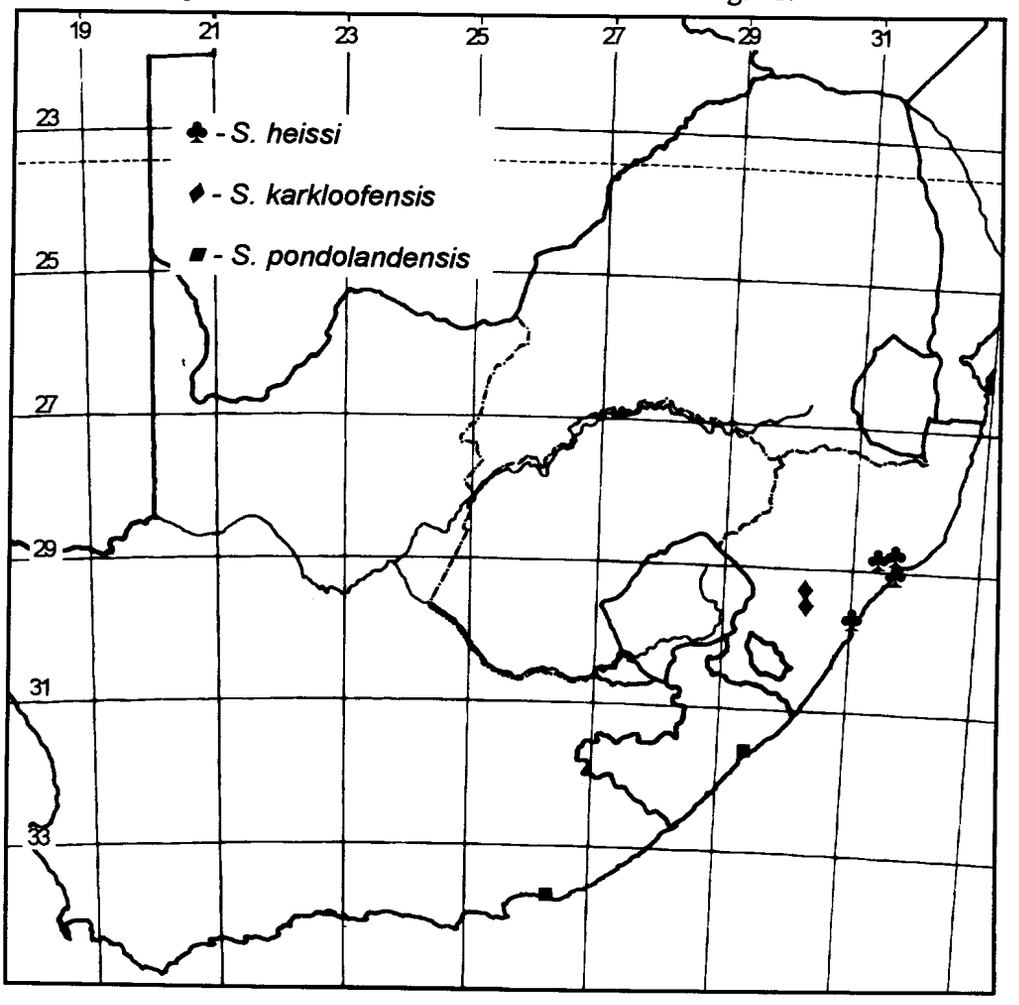


Fig. 51. Distribution map of the ***Silvacoris*** **species.**

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)			

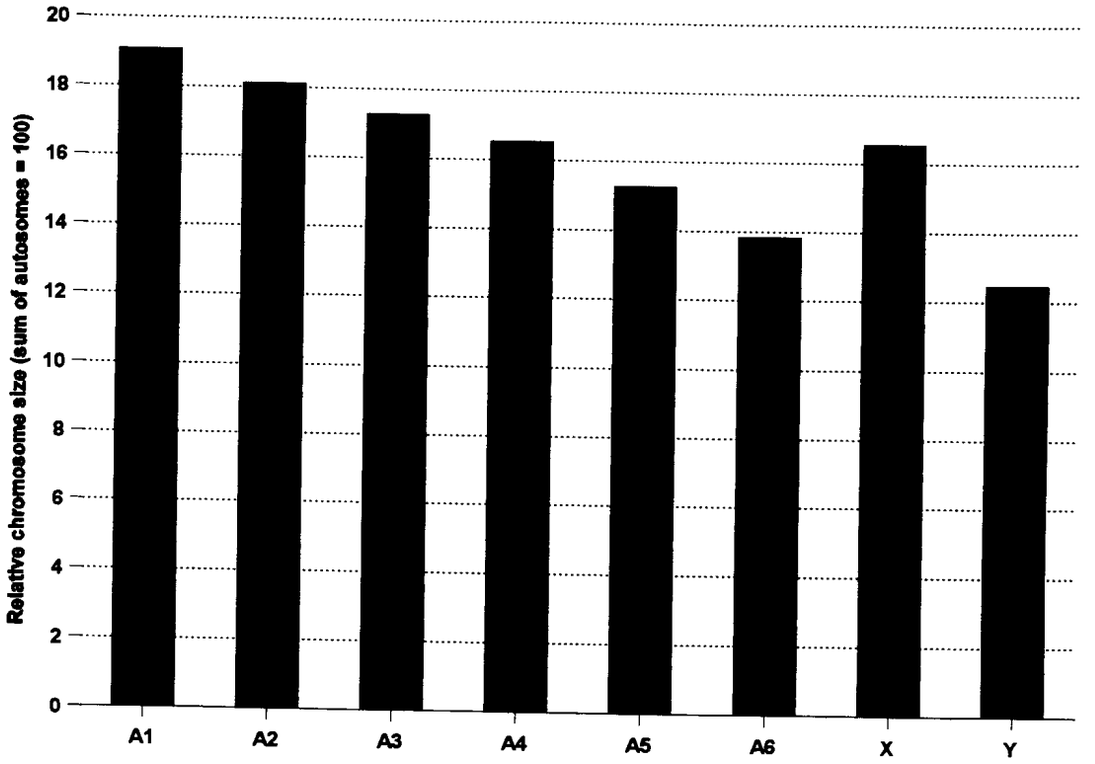


Figure 52. Idiogram of *Silvacoris heissi*.

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)			

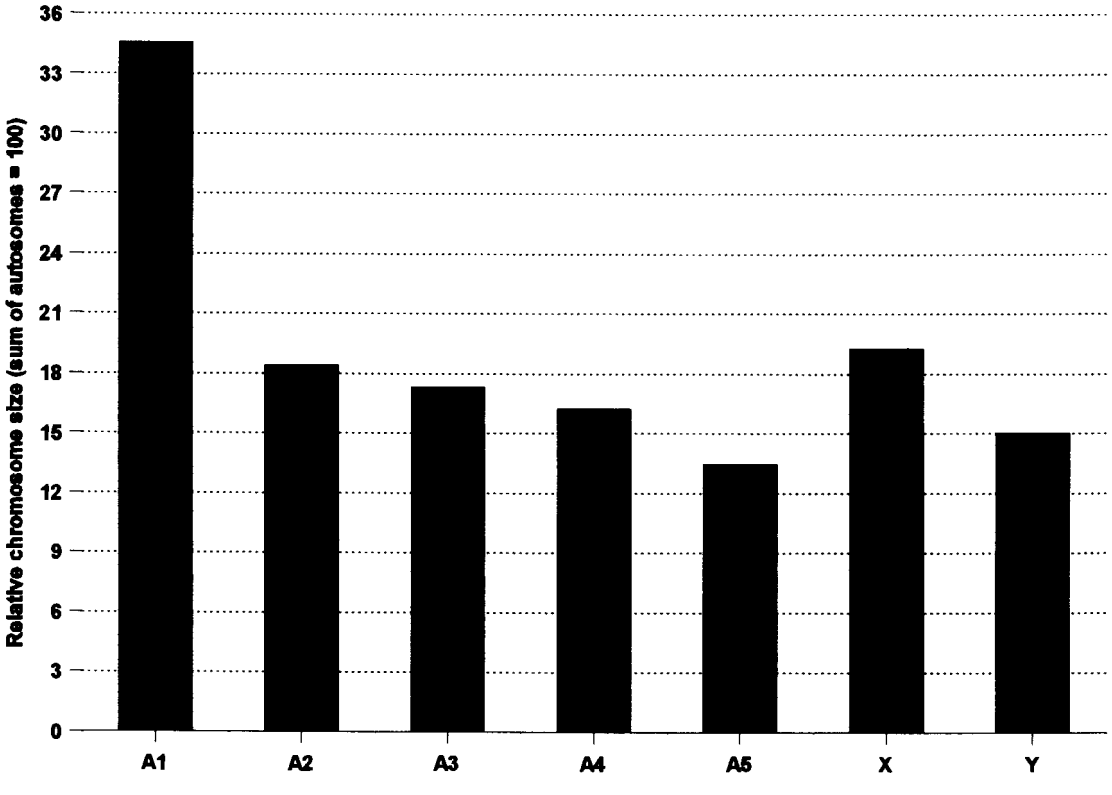


Figure 53. Idiogram of *Silvacoris karkloofensis*.

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)	

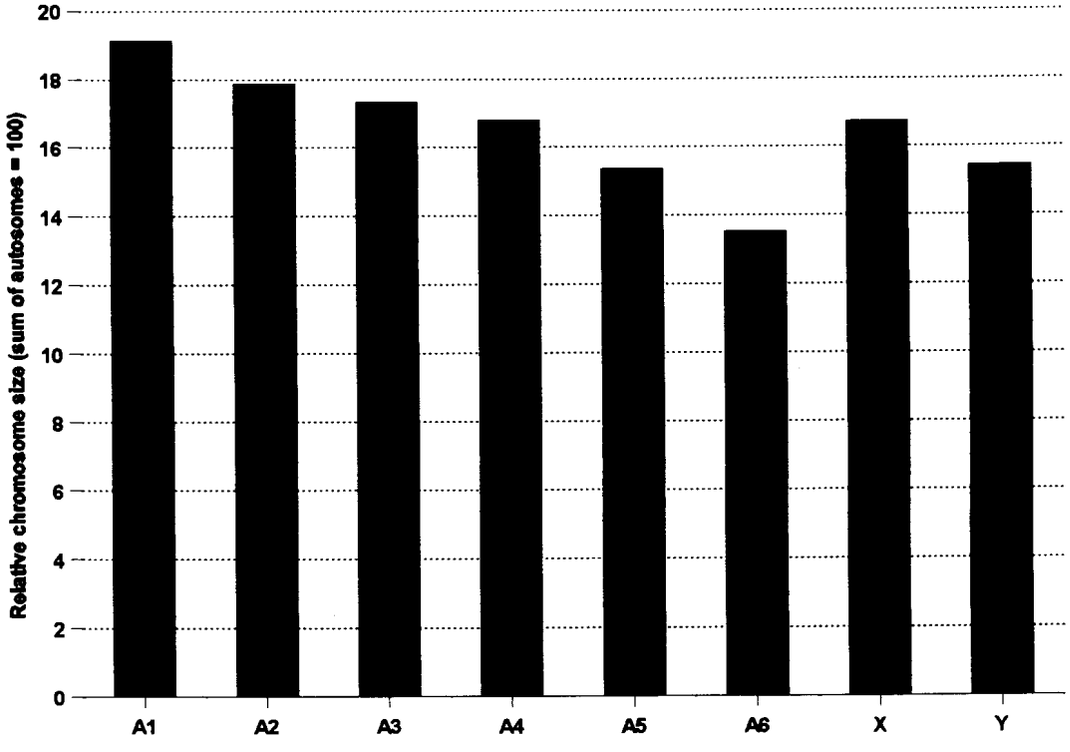


Figure 54. Idiogram of *Silvacoris pondolandensis*.

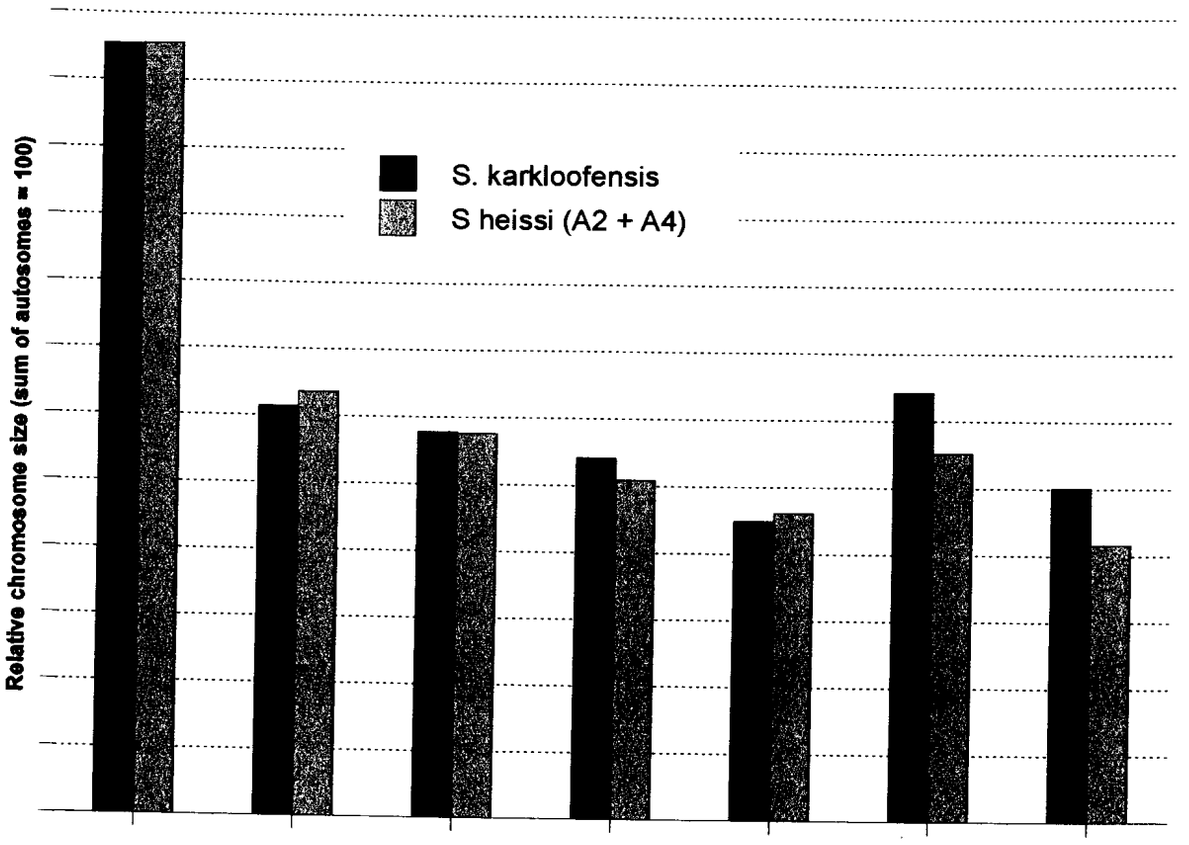


Figure 55. Comparison of the idiograms of *S. heissi* and *S. karkloofensis* with autosomes A2 and A4 of *S. heissi* added.

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).

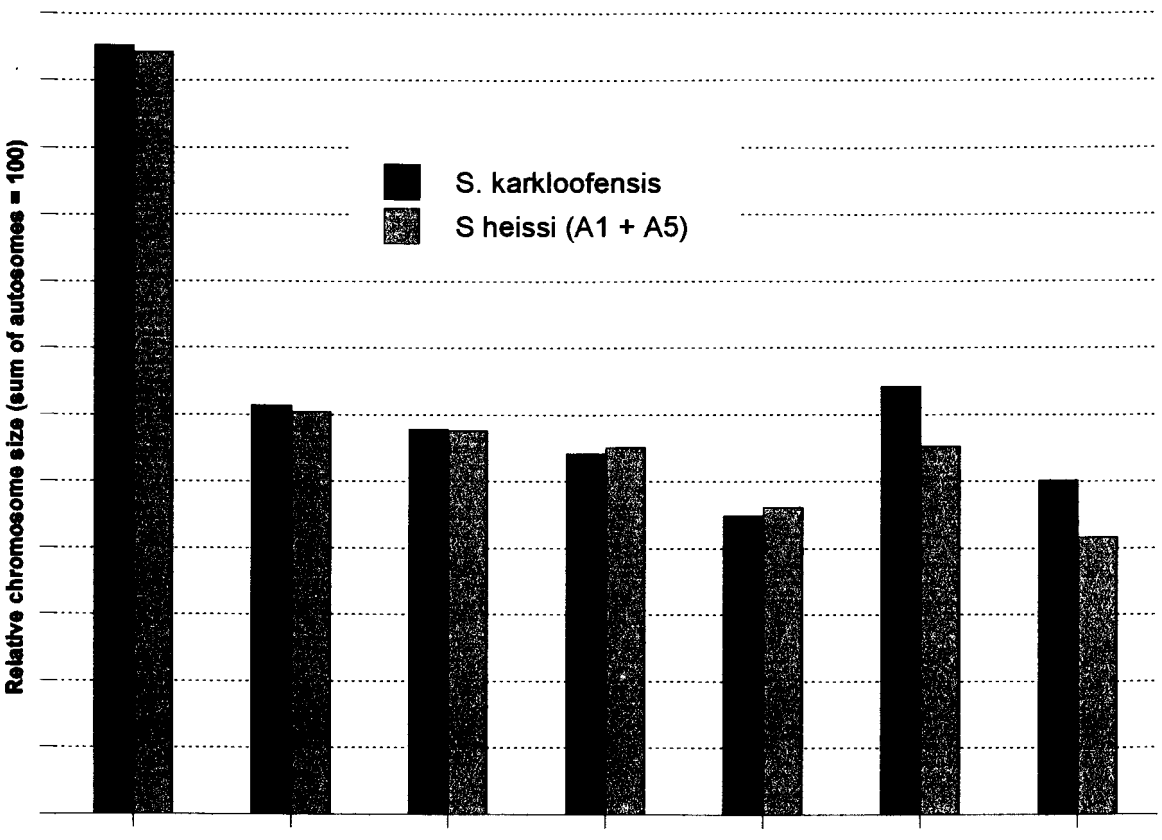


Figure 56. Comparison of the idiograms of *S. heissi* and *S. karkloofensis* with autosomes A1 and A5 of *S. heissi* added.

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.

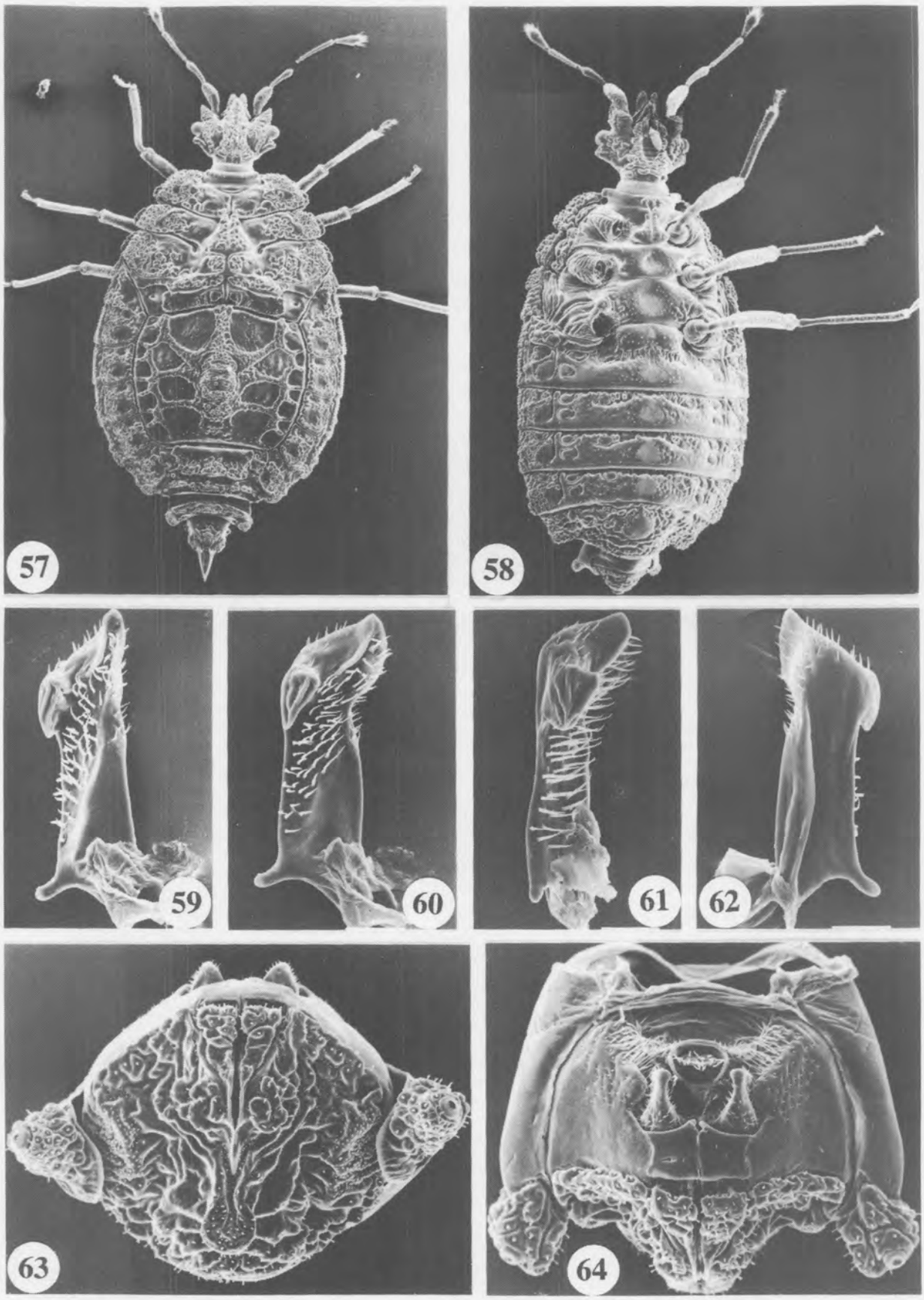
Table 5.8: Test statistics for testing the hypothesis that chromosomes A2 and A4 of *S. heissi* fused to form chromosome A1 of *S. karkloofensis*.

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

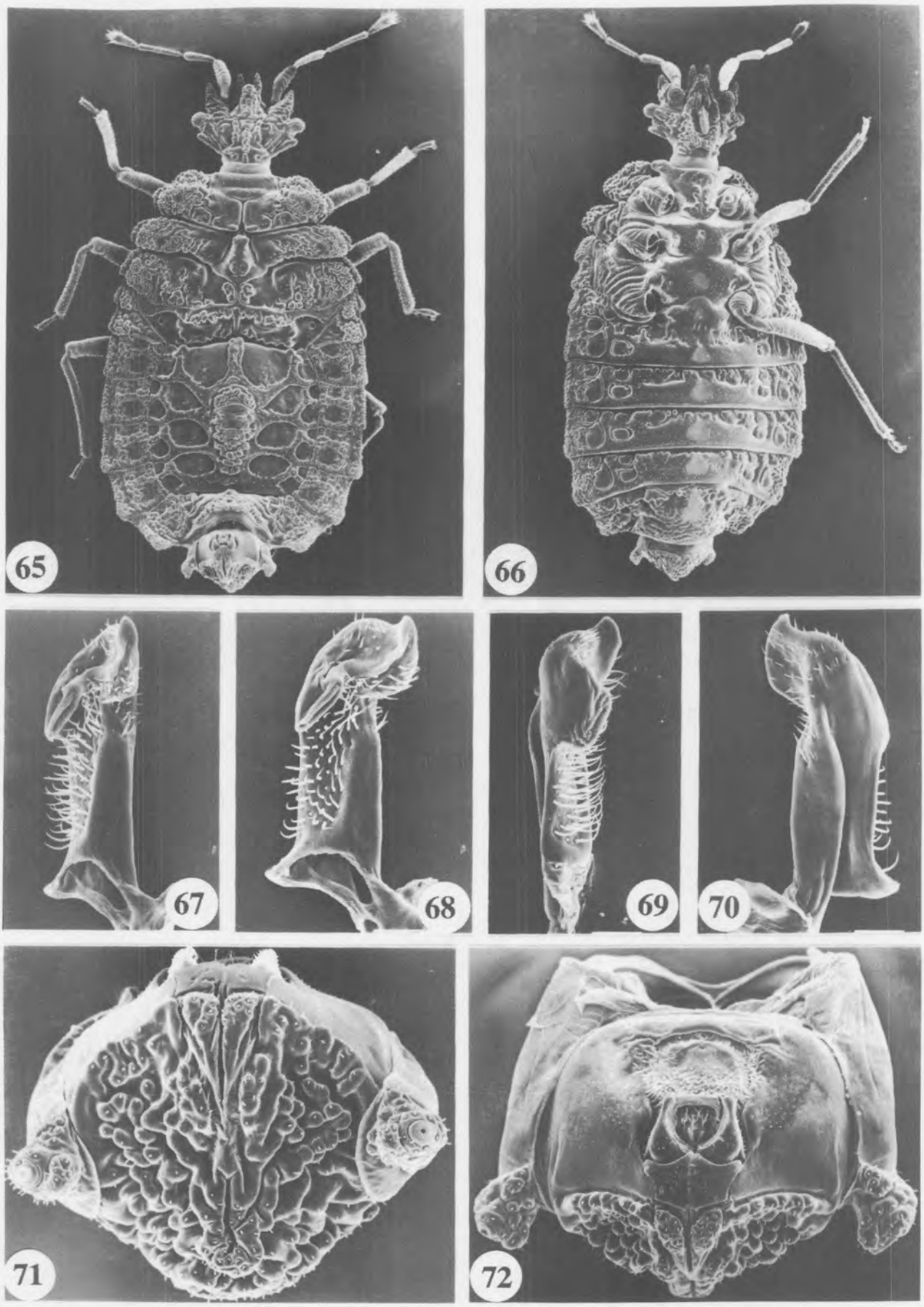
* Significant and ** highly significant values.

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*.

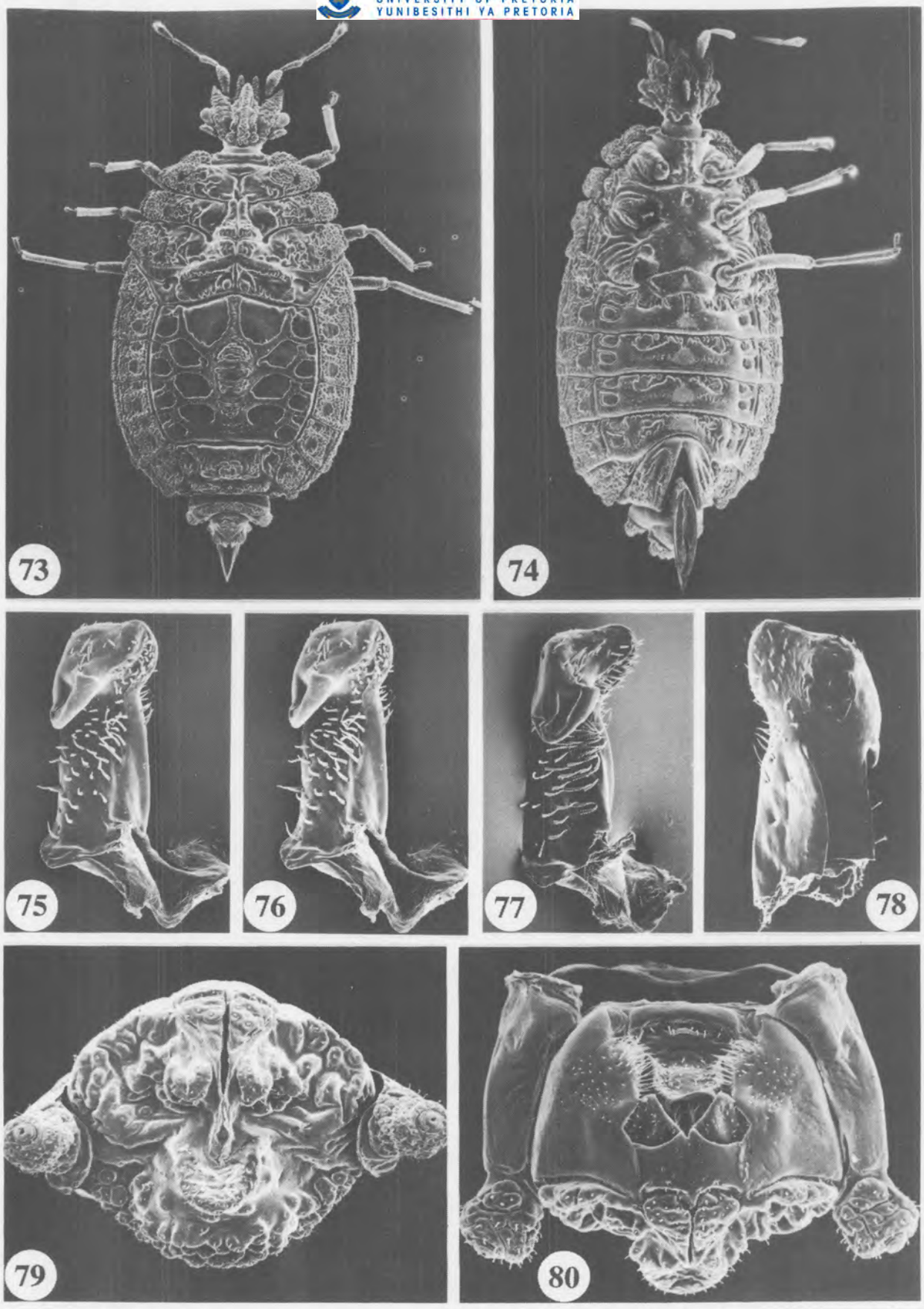
Relative chromosome areas (% of total area of autosomes).			
Chromosome	**95th percentile**	**99th percentile**	**Test statistics**
A1	1.1827	2.0140	0.0498
A2	0.3205	0.5741	0.1402
A3	0.3211	0.5354	0.0018
A4	0.5223	0.7590	0.1389
A5	0.5416	1.4318	0.0717
Sum of autosomes	2.1786	3.0507	0.4025
True chromosome 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



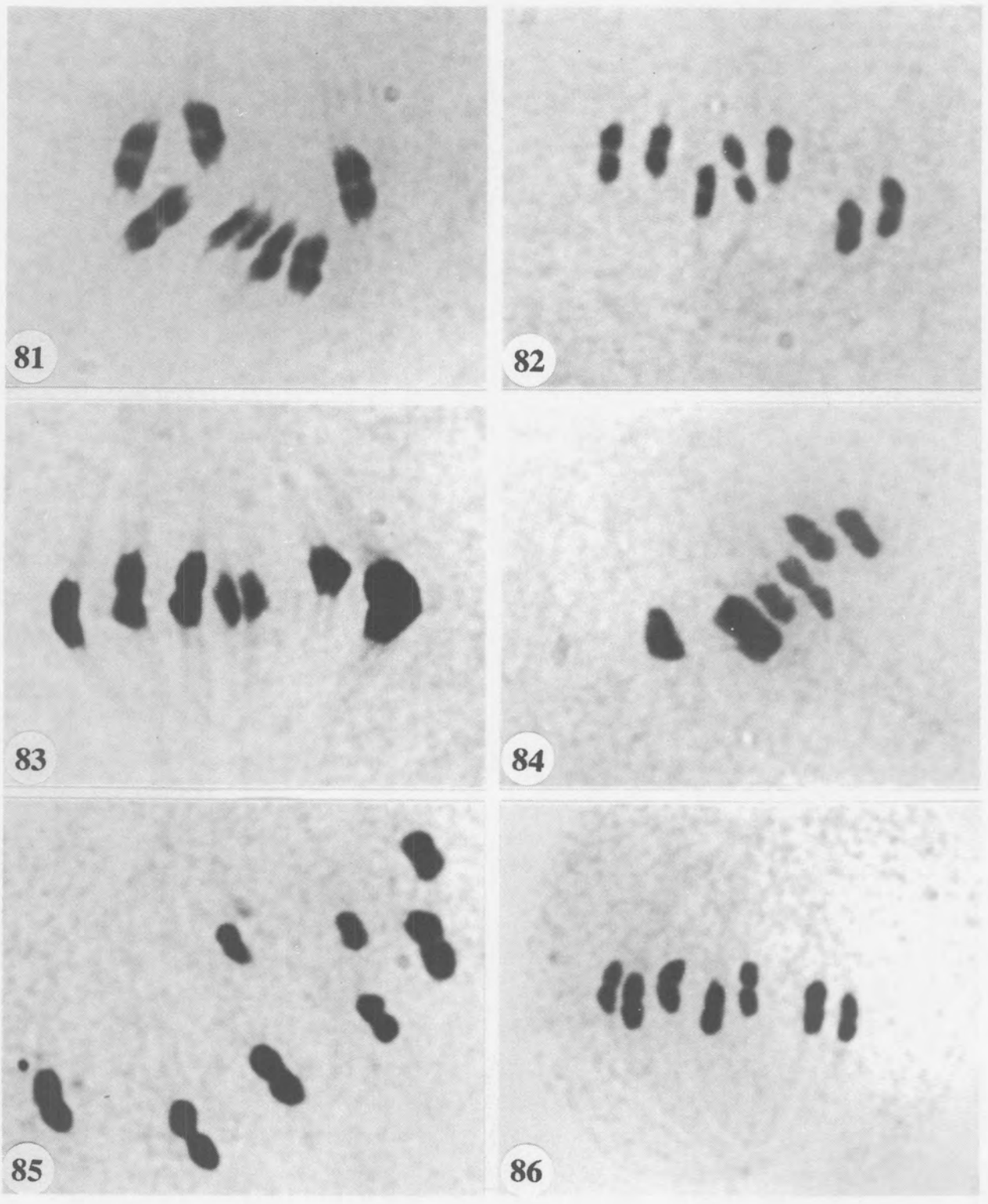
Figs 57-64. Scanning electron photomicrographs of *Silvacoris heissi* **gen. et spec. nov.** 57. Female paratype, dorsal aspect. 58. Male paratype, ventral aspect. 59-62. Different aspects of the left paramere (scale bar = 50 μm). 63-64. Pygophore. 63. Caudal aspect. 64. Dorsal aspect.



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.

Chapter 6

GENUS *PONDOCORIS* HEISS & JACOBS.

New records of specimens described earlier as *Dundocoris latebrosus* Hoberlandt and comparison with additional material of other *Dundocoris* species has revealed that *D. latebrosus* has distinctive characters which separate it from all other apterous Carventinae. The genus *Pondocoris* was therefore proposed by Heiss & Jacobs (1989).

6.1 *Pondocoris* Heiss & Jacobs.

Type species: *Dundocoris latebrosus* Hoberlandt 1959.

Etymology: From Pondoland (now in the Eastern Cape), the type locality of the type species.

Apterous, body elongate, oval, incrustate, shining and granular beneath the incrustation, granules with short, stiff bristles.

Head: Longer than its width across eyes, genae finger-like, produced beyond clypeus, divergent, not touching in front of clypeus. The latter with a prominent round tubercle anterodorsally. Antenniferous spines well developed, divergent. Postocular tubercles present. Eyes globular. Head constricted behind postocular tubercles to neck region. Antennae distinctly longer than width of head, first segment thickest, extending beyond apex of genae, second shorter and more slender, club shaped, third longest and cylindrical, slightly enlarged apically, fourth segment short, fusiform, conical apex pilose. Rostrum arising from a slit-like atrium, rostral groove deep and closed posteriorly.

Thorax. Pronotum trapezoidal, more than three times as wide as long with a very distinct, elevated ring-like collar, which bears 2(1+1) smaller tubercles dorsolaterally and 2(1+1) large prominent rounded tubercles laterally. Lateral lobes with dense granulation, deeply incised before collar, anterolateral angles subrectangular, posterolateral lobes rounded, projecting laterally, lateral margins upturned, concave. Lateral propleural margin visible from above expanding into small rounded lobes anteriorly and posteriorly, separated from pronotal margin by a distinct sulcus. Disk formed by 2(1+1) smooth plates, which are separated medially by a deep longitudinal groove which may reach the collar ring. Posterior margin convex, separated from mesonotum by a deep sulcus.

Mesonotum wider but shorter than pronotum, comprising 2(1+1) subrectangular plates which are separated by a sulcus from metanotum, and an elevated longitudinal median ridge which projects posteriorly over metanotum and half of fused MTg 1 and 2. This ridge bears a median sulcus and is split posteriorly into two ridges ending in a row of granules directed laterally. Lateral lobes granulate, margins slightly concave, tubercular mesonotal margin visible from above. Disk smooth with 2(1+1) comma-shaped elevations laterad of median ridge, separated from the latter by a deep groove.

Metanotum fused with MTg 1 and 2, forming a hexagonal plate. Anterolateral lobes granulate, its lateral margins also slightly concave, tuberculate margin of metapleuron visible from above. Disk with 2 (1 + 1) smooth comma-shaped elevations anteriorly, with coarse granulation and longitudinal

rugosities posteriorly. MTg 2 demarcated by irregular transverse rows of tubercles laterad of a wedge-like median elevation which reaches from posterior margin into the cleft median ridge. This elevated wedge-like sclerite is enlarged at base and longitudinally sulcate on posterior 2/3. Basolateral angles with 2 (1 + 1) short ridges delimiting the sublateral glabrous impressions.

Abdomen. Tergal disk formed by fused MTg 3 to 6 with convex lateral margins and depressed glabrous impressions delimited by elevated ridges. Disk elevated along median line which is highest on MTg 4. Dorsal external laterotergites with subparallel lateral margins, slightly enlarging posteriorly. DELTg 1 to 3 fused but marked by a notch on the narrow visible rim of ventral laterotergites, extending anteriorly to lateral lobes of metanotum. Posteroexterior angles of DELTg 3 to 7 increasingly protruding. Surface and lateral margins granular. MTg 7 in female with a transverse carina posteriorly. Paratergites 8 directed backward, conical, not reaching apex of tricuspidate tergite 9. MTg 7 in male raised medially for the reception of the pygophore. Paratergites 8 triangular, reaching level of posterior margin of DELTg 7.

Genitalia: Male genital structures. Visible portion of pygophore pyriform, with rugose surface, dorsally with a cleft median ridge which ends posteriorly in an oval pit with prominent carinate borders (Figs. 121-126). Parameres with anterolateral reflexed rounded lobe and a basal lateral projection, inner face with long setae (Figs. 101-120).

Venter. Pro-, meso- and metasterna flattened at middle, delimited by sutures. Male metasternum with 2(1+1) sublateral, rounded, prominent tubercles on anterior half which bear a small operculate opening subapically (Fig. 135-141, 144), their function not yet investigated. Pro-, meso- and metapleura with large suboval areas laterad of coxae, dorsally demarcated by a deep sulcate cleft and ventrally by a deep somewhat irregular furrow. Obtuse fingerlike setae which are thickened at their apices are present dorsally of both these clefts (Figs. 142-143). These areas are most probably evaporative surfaces and are unique to *Pondocoris* in the Carventinae. Sternites 1 to 3 fused, 4 to 7 separated by deep sulci. Spiracles 2 to 4 ventral, 5 to 7 lateral and visible from above, 8 subterminal.

Legs. Slender, trochanters fused with cylindrical femora, only on hind femora marked by a thin suture. Claws with two bristle-like parempodia and long, thin pseudopulvilli.

Discussion: The genus resembles *Dundocoris* Hoberlandt only superficially and can easily be separated by the elongate subparallel body outline; the presence and shape of the uninterrupted median ridge extending from mesonotum to MTg 2; the metanotum fused with MTg 1 and 2; the two conspicuous tubercles on metasternum; and by the peculiar pilose areas on the thoracic pleura, which are not known in other Carventinae.

Specimens of *Pondocoris* can be divided into two distinct morphological species. Cytogenetical studies have, however, shown that four different chromosome numbers are present in *Pondocoris latebrosus* (Hoberlandt).

All populations sampled are homogeneous regarding chromosome number and three of the four "cytoforms" seem to be associated with particular geographical areas as follows:

1. the 22XY populations occur from Umtamvuma forest at Port Edward southwards to Dwesa forest near the southern border of the former Transkei.

2. the 12XY populations occur in the coastal dune forests of northern Kwazulu-Natal from Maphelana near St. Lucia northwards to Manzengwenya.
3. the 10XY populations have been found in the central Kwazulu-Natal coastal forests from Umhlanga Rocks southwards to Scottburgh.

The 14XY populations are the exception as they seem to occur at isolated spots, usually montane forests, over a very large area. They are very common in the Dhlinsa and Ngoye forests in northern Kwazulu-Natal, but have also been found in the coastal forest at Umdoni Park near Scottburgh in central Kwazulu-Natal and more than 400 km southwest from there in the montane forest at Hogsback in the Eastern Cape.

The chances that viable and fertile offspring will be produced if for example the 22XY and 14XY forms are crossed is slim as many meiotic abnormalities would probably occur. Strictly according to the biological species concept these cytoforms should be regarded as good species which will leave us with a sibling species complex. I am not a proponent of the biological species concept and after careful consideration I have decided to describe these cytoforms as subspecies, as a better alternative does not presently exist. I shall defend and explain this decision more fully in Chapter 12.

Pondocoris latebrosus was described from a single male from "Pondoland" (now part of the Eastern Cape) by Hoberlandt (1959). From this fact as well as certain morphological traits I am convinced that the holotype belongs to the 22XY cytoform which will accordingly be described as the nominate subspecies. *Pondocoris latebrosus* is redescribed to bring the description in line with the others in this work and to facilitate the description of the other subspecies.

6.1.1 Redescription of *Pondocoris latebrosus* (Hoberlandt) (Figs. 93-126, 135-143).

Dundocoris latebrosus Hoberlandt 1959:91
Pondocoris latebrosus (Hoberlandt) Heiss & Jacobs 1989:48

Length ♂ 4,4 - 5,8 mm; ♀ 5,2 - 7,0 mm.
Width ♂ 1,7 - 2,6 mm; ♀ 2,2 - 3,4 mm.

Apterous. Body coated with a pale yellowish brown incrustation, resulting in a general brownish grey appearance of uncleaned specimens. The following description is based on specimens with the incrustation removed.

Head: Longer (not including neck area) than its width across the eyes. Genae usually slightly diverging anteriorly. Clypeus with a prominent subapical tubercle. Antennae 1,5-1,7 times as long as width across eyes, first segment thickest, slightly curved and tapering towards base, extending beyond apex of genae by less than half but more than a third of its length; second segment slightly curved basally, gradually thickened towards apex; third segment longest and thinnest, pedicellate; fourth segment fusiform, with a short pedicel, conical apex pilose; relative lengths of segments: 9,25:6:10:7,5.

Postocular tubercles usually not reaching to level of outer margins of the eyes. Neck slightly constricted just behind the head.

Thorax: Dorsum. Pronotum 2,8-3,0 times as wide as long (including collar). Lateral lobes prominent, elevated and reflexed, densely granulate, lateral margins strongly concave, produced anteriad to level of collar or beyond. Disk smooth and shining with some irregular excavations, mainly posterolaterally. Hind margin of pronotum reinforced with a transverse bar-like thickening which ends adjacent to median groove in 2(1+1) toothlike nodules.

Mesonotal disk with 2(1+1) smooth, comma-shaped areas laterad of median ridge, remainder irregularly excavated. Lateral lobes granulate and lateral margins straight or slightly concave, slightly converging anteriad. Median ridge fairly narrow, separated from disk by a longitudinal furrow which is crossed at posterior margin by a transverse row of nodules; median ridge split by a prominent longitudinal suture along its total length.

Metanotum completely fused with MTg 1 and 2, only sculpture indicates the relative positions of the different tergites. Metanotal disk with 2(1+1) smooth comma-shaped elevations anteriorly, lateral of median ridge, rest irregularly excavated but a transverse row of tubercles posteriorly indicates its border with MTg 1. Lateral lobes granulate and lateral margins straight or slightly concave, semiparallel. Median ridge fused with that of mesonotum, although a transverse (usually incomplete) suture may often indicate the border; the median ridge extends posteriorly on MTg 1 before it swerves laterally and continues as a transverse row of tubercles at the posterior margin of MTg 1.

MTg 2 with sublateral ridges prominent and usually with a wedge-like elevation medially which penetrates anteriorly between the split median ridge. The wedge-like elevation is enlarged at its base and longitudinally sulcate on its posterior two-thirds. In the subspecies *decimus* the wedge-like elevation is replaced by a slender median longitudinal bar which penetrates the split median ridge, flanked by 2(1+1) longitudinal ridges on MTg 2.

Venter: Collar present ventrally of lateral tubercles only as a very narrow rim on anterior margin. Prosternum with an inverted T-shaped elevation, bearing a longitudinal depression. Mesosternum with a large oval, finely rastrate area that is strongly depressed. Metanotum of female also with a finely rastrate, depressed oval area, that of male with an elongate oval, finely rastrate, depressed area, laterally delimited by 2(1+1) large, oval, strongly elevated, shining protuberances which usually bear a prominent tubercle with an operculate opening. (Only in *Pondocoris latebrosus decimus* the tubercle on the protuberance is absent). In the females only a small tubercle situated more laterally, anterior to the metacoxa, is usually present.

Legs: Trochanter of hind legs demarcated by a thin suture, completely fused with femur in other legs.

Abdomen: Dorsum. Tergal disk only slightly elevated along median line. Carinae separating glabrous impressions prominent. Surface between carinae and impressions areolate, especially along margins of carinae. Posterior nodulate transverse ridge on MTg 7 of females well developed but may be interrupted medially.

Venter: Intersegmental sutures 3/4, 4/5 5/6 and 6/7 complete, reaching lateral margins of body. Spiracle 2 ventral, 3 + 4 sublateral, placed between 1 and 2 spiracle widths from margin, 5-7 lateral and visible from above, 8 subterminal on paratergites.

Genitalia: Visible part of pygophore (Figs 121-126) broadly oval with a rugose surface, dorsally with 2(1+1) subtriangular ridges separated by a cleft which ends ventrally just dorsal of an oval pit with prominent carinate borders. Dorsally (the part usually obscured by MTg 7) as in Figs 122, 124 & 126. Parameres as in Figs 101 to 120.

Chromosome number: 2n(♂) = 10XY, 12XY, 14XY, or 22XY depending on the subspecies.

Habitat and distribution: Coastal and montane evergreen forests of Kwazulu-Natal and the Eastern Cape. (Fig. 87).

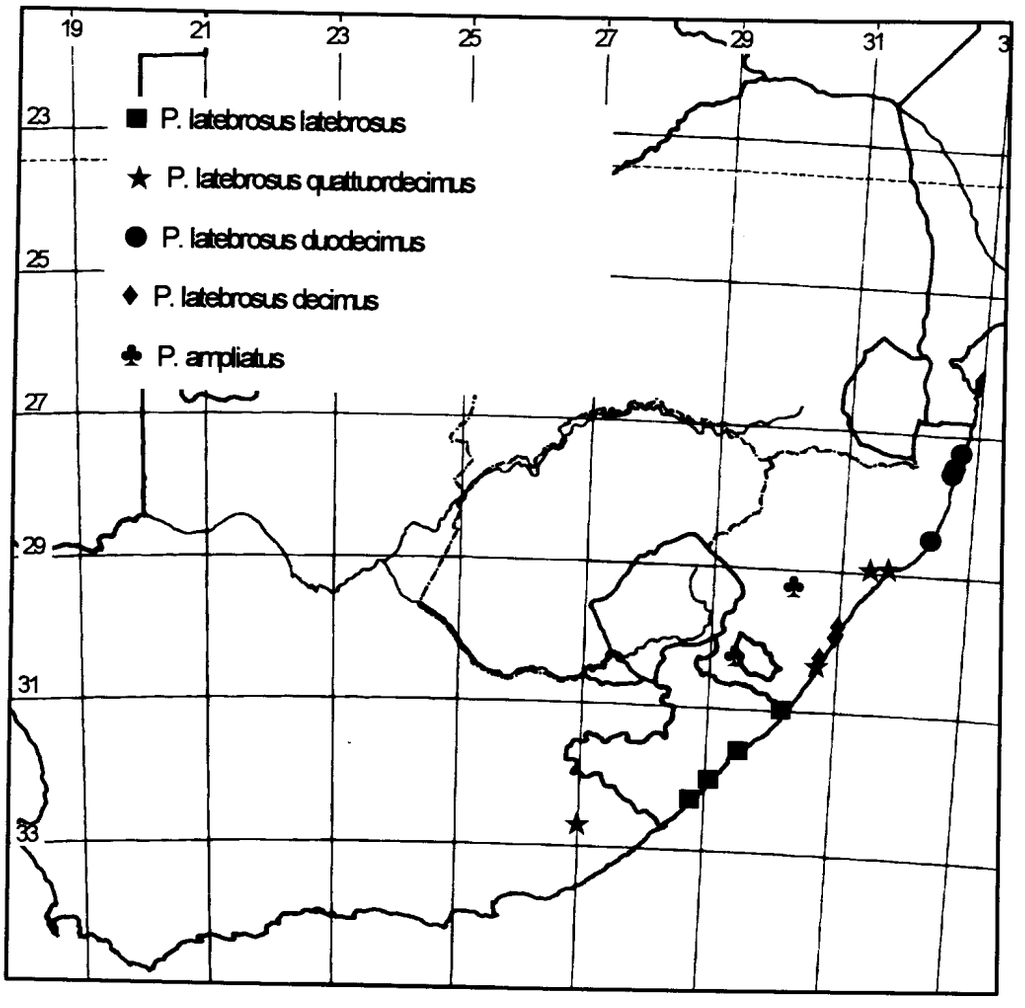


Figure 87. Distribution map of *Pondocoris* species and subspecies.

Discussion *Pondocoris latebrosus* can be distinguished from *Pondocoris ampliatus*, the only other species known in the genus, as discussed under the latter species. As mentioned before the four cytoforms of *Pondocoris latebrosus* are described as subspecies and they are very difficult to distinguish from one another without cytogenetical preparations. In each of them the chromosome number seems to be constant and no hybrid forms have been found.

6.1.1.1 *Pondocoris latebrosus latebrosus* (Hoberlandt) (Figs 93, 97, 101-105, 121-122, 135-138, 142-143).

Length ♂ 4,5 - 5,8 mm; ♀ 5,3 - 7,0 mm.

Width ♂ 1,9 -2,6 mm; ♀ 2,2 - 3,4 mm.

Diagnostic measurements are given in Table 6.1. The nominate subspecies is very similar to both *duodecimus* and *quattuordecimus* but can be distinguished from both by having its tergal disk distinctly wider than long (about 1,05 times as wide as long). It also has a stouter body form than the above-mentioned two subspecies, the males being about 2,3 times as wide as long and the females about 2,1 times. The males give the impression that the abdomen is widest over the posterior margin of the fifth segment but when measured this distance proves to be equal to the distance over the posterior margin of the fourth segment. In *duodecimus* and quattuordecimus, however, the abdomen is the wider over the posterior margin of the fourth segment than over the fifth segment.

Table 6.1. Measurements (in mm) of *Pondocoris latebrosus latebrosus* (Hoberlandt).

STRUCTURE		MALES				FEMALES			
		N♦	Mean	SD	Range§	N♦	Mean	SD	Range§
Total	length	20	5.23	0.381	4.52-5.78	20	6.08	0.459	5.33-6.94
	width	20	2.29	0.169	1.91-2.54	20	2.87	0.226	2.21-3.34
Head	length	20	1.00	0.051	0.87-1.09	20	1.09	0.065	0.99-1.24
	width	20	0.89	0.033	0.80-0.95	20	0.96	0.044	0.89-1.05
Pronotum	length	20	0.59	0.057	0.44-0.66	20	0.65	0.070	0.52-0.79
	width	20	1.66	0.126	1.32-1.86	20	1.92	0.138	1.61-2.20
Tergal disk	length	20	1.39	0.099	1.15-1.56	20	1.76	0.131	1.48-2.01
	width	20	1.49	0.106	1.27-1.68	20	1.84	0.136	1.50-2.15
Antennal segments	I	20	0.42	0.018	0.38-0.45	20	0.44	0.019	0.41-0.48
	II	20	0.27	0.013	0.24-0.31	20	0.29	0.015	0.26-0.33
	III	20	0.45	0.035	0.40-0.53	20	0.48	0.035	0.41-0.54
	IV	20	0.31	0.012	0.29-0.34	20	0.32	0.018	0.29-0.36

§ May include measurements of specimens other than those used for statistical analysis.
♦ Five individuals from each of the following localities: Port St. Johns, Dwesa forest, Mpame forest and Umtamvuma forest.

Although *decimus* also has the tergal disk wider than long it can easily be distinguished from *latebrosus* by lacking the wedge-like elevation on MTg 2, by not having a tubercle on the elevations of the metasternum in the males, and by being smaller.

There is a difference in the average size of individuals in different populations of the nominate subspecies: those from Umtamvuma forest at Post Edward seem to be larger than those from other localities.

Chromosome number: 2n(♂) = 22XY.

Habitat and distribution: Coastal forests at Port Edward, the southern border of Kwazulu-Natal and in the Eastern Cape.

MATERIAL EXAMINED: **SOUTH AFRICA: Kwazulu-Natal**. 74♂♂ 40♀♀: Umtamvuma forest, nr. Port Edward, 31°03′S 30°11′E, 28.i.1983, D.H. Jacobs (DHJS); **Eastern Cape**. 65♂♂ 48♀♀: Mount Thesiger Nature Reserve, Port St. Johns, 31°37′S 29°31′E, 4-5.xii.1981, D.H. Jacobs (DHJS); 50♂♂ 42♀♀: Port St. Johns, Transkei, 31°38′S 29°32′E, 2-6.xii.1981, D.H. Jacobs (DHJS); 2♀♀: Ntsubane forest, 31°27′S 29°44′E, 25.xi.1987, E-Y: 2537, fungi & forest litter, leg. Endrödy-Younga (TMSA); 48♂♂ 78♀♀: Mpame forest, Transkei, 32°05′S 29°02′E, 12.xii.1981, D.H. Jacobs (DHJS); 32♂♂ 89♀♀ Dwesa forest, Transkei, 32°18′S 28°50′E, 10-13.xii.1981, D.H. Jacobs (DHJS).

6.1.1.2 *Pondocoris latebrosus decimus* subspec. nov. (Figs 96, 100, 116-120, 138-139).

Length: ♂ 4,4 - 5,0 mm; ♀ 5,2 - 6,0 mm.

Width: ♂ 1,9 - 2,3 mm; ♀ 2,3 - 3,0 mm.

Diagnostic measurements are given in Table 6.2. *Pondocoris latebrosus decimus* is the subspecies which is easiest to recognize morphologically. It differs from all other subspecies by having the wedge-like elevation on MTg 2 replaced by a single longitudinal median, elongate fusiform bar, flanked by two parallel longitudinal ridges, and in the males, by the absence of the tubercles on the protuberances of the metasternum. It can also be distinguished from *duodecimus* and *quattuordecimus* by being more broadly oval in general facies (males about 2.25 times as long as wide and females 2,08 times) and having the tergal disk distinctly wider than long (about 1,06 times as wide as long).

Table 6.2. Measurements (in mm) of *Pondocoris latebrosus decimus* subspec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	N◆	Mean	SD	Range	AT#	N◆	Mean	SD	Range
Total	length	4.71	10	4.74	0.142	4.41-4.93	5.50	10	5.57	0.216	5.24-5.94
	width	2.06	10	2.10	0.078	1.97-2.24	2.61	10	2.68	0.147	2.35-2.92
Head	length	0.83	10	0.85	0.023	0.81-0.89	0.93	10	0.94	0.027	0.90-0.99
	width	0.80	10	0.81	0.021	0.78-0.86	0.88	10	0.88	0.037	0.82-0.95
Pronotum	length	0.55	10	0.55	0.028	0.51-0.62	0.60	10	0.62	0.029	0.55-0.67
	width	1.55	10	1.56	0.057	1.47-1.69	1.77	10	1.77	0.055	1.63-1.85
Tergal disk	length	1.26	10	1.30	0.052	1.19-1.38	1.60	10	1.62	0.047	1.53-1.70
	width	1.35	10	1.38	0.046	1.30-1.47	1.66	10	1.71	0.082	1.52-1.85
Antennal segments	I	0.37	10	0.37	0.011	0.34-0.39	0.39	10	0.38	0.017	0.35-0.42
	II	0.24	10	0.25	0.011	0.23-0.27	0.25	10	0.26	0.013	0.24-0.29
	III	0.39	10	0.40	0.017	0.38-0.44	0.41	10	0.44	0.023	0.40-0.48
	IV	0.30	10	0.29	0.013	0.27-0.32	0.30	10	0.32	0.013	0.30-0.35

* HT = holotype. # AT = allotype.
◆ 3♂♂,5♀♀ from Stainbank Nature Reserve and 7♂♂,5♀♀ from Umhlanga Rocks Nature Reserve.

Chromosome number: 2n(♂) = 10XY.

Habitat and distribution: So far it has only been collected in the coastal evergreen forests of central Kwazulu-Natal, from Scottburgh in the south to Umhlanga Rocks in the north (Fig. 87).

Etymology: decem (L) = ten, referring to the chromosome number of the subspecies.

MATERIAL EXAMINED: **SOUTH AFRICA, Kwazulu-Natal**. ♂ holotype: Umhlanga Rocks Nature Reserve, nr. Durban, 29°42′S 31°04′E, 11.ix.1991, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 36 paratypes as follows: 9♂♂ 9♀♀: Same data as holotype (DHJS, TMSA); 1♀: nr. Durban, 29°45′S 31°04′E, 4.iv.1980, D.H. Jacobs (DHJS); 5♂♂ 11♀♀: Stainbank Nature Reserve, Durban, 29°55′S 30°56′E, 2.xi.1989, D.H. Jacobs (DHJS, TMSA); 1♀: nr. Scottburgh, 30°15′S 30°46′E, 25.i.1983, D.H. Jacobs (DHJS).

6.1.1.3 *Pondocoris latebrosus duodecimus* subspec. nov. (Figs 95, 99, 111-115, 125-126, 137, 140-141).

Length: ♂ 4,5 - 5,3 mm; ♀ 5,6 - 6,3 mm.

Width: ♂ 1,7 - 2,2 mm; ♀ 2,4 - 3,0 mm.

Diagnostic measurements are given in Table 6.3. The differences of *duodecimus* with the previous two subspecies have been discussed under them. Although I have spent a long time comparing series of *duodecimus* and quattuordecimus I could find no clearcut and reliable morphological differences between them. The antennae of *duodecimus* in relation to the width of head seem on average to be shorter (1,56x in males and 1,50x in females versus 1,71x and 1,64x respectively), the antenniferous lobes seem to be shorter, DELTg 7 seems to be less produced and the tubercles on the metasterna of the males seem to be larger. However, there are many individual exceptions to this and it would only be helpful in identification if long series are available. The only reliable way of distinguishing between these subspecies at present is their different chromosome number and they also seem to be allopatric so that locality renders a good indication of identity.

Table 6.3. Measurements (in mm) of *Pondocoris latebrosus duodecimus* subspec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	♂N	Mean	SD	Range$	AT#	♀N	Mean	SD	Range$
Total	length	5.01	12	4.95	0.154	4.52-5.28	6.15	11	5.96	0.195	5.62-6.25
	width	1.98	12	2.01	0.078	1.79-2.14	2.69	11	2.69	0.132	2.41-2.96
Head	length	0.95	12	0.94	0.039	0.85-1.03	1.08	11	1.05	0.032	0.98-1.11
	width	0.83	12	0.83	0.027	0.77-0.90	0.94	11	0.93	0.034	0.86-0.99
Pronotum	length	0.54	12	0.54	0.029	0.45-0.59	0.62	11	0.61	0.032	0.56-0.66
	width	1.51	12	1.51	0.054	1.38-1.61	1.79	11	1.76	0.072	1,65-1.86
Tergal disk	length	1.32	12	1.35	0.048	1.22-1.48	1.81	11	1.77	0.085	1.68-1.90
	width	1.28	12	1.34	0.065	1.20-1.44	1.80	11	1.74	0.068	1.63-1.86
Antennal segments	I	0.38	12	0.37	0.012	0.33-0.39	0.41	11	0.41	0.013	0.38-0.45
	II	0.25	12	0.25	0.008	0.23-0.27	0.27	11	0.26	0.008	0.24-0.28
	III	0.39	12	0.40	0.020	0.35-0.44	0.42	11	0.44	0.018	0.39-0.50
	IV	0.29	12	0.28	0.015	0.25-0.31	0.29	11	0.29	0.010	0.27-0.32

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.
♦ 4♂♂,4♀♀ from Manzengwenya, 4♂♂,4♀♀ from Lake Sibayi and 4♂♂,3♀♀ from Sordwana Bay.

Chromosome number: 2n(♂) = 12XY.

Habitat and distribution: Coastal forest in Northern Kwazulu-Natal from Maphelana just south of St. Lucia northwards to Manzengwenya forest (Fig. 87).

Etymology: Duodecem (L) = twelve, referring to the chromosome number of the subspecies.

MATERIAL EXAMINED: **SOUTH AFRICA: Kwazulu-Natal**. ♂ holotype: Manzengwenya, Kwazulu, 27°16′S 32°46′E, 3-7.xii.1980, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 92 paratypes as follows: 3♂♂ 3♀♀: Manzengwenya forest, 27°13′S 32°47°E, 7.xii.1980, D.H. Jacobs (DHJS); 32♂♂ 22♀♀: Same data as holotype (TMSA, DHJS); 11♂♂ 5♀♀: Lake Sibayi, Kwazulu, 27°25′S 32°43′E, 5.xii.1980, D.H. Jacobs (DHJS, TMSA); 6♂♂ 3♀♀: Sordwana Bay, Natal, 27°32′S 32°40′E, 23.vii.1977, D.H. Jacobs (DHJS, TMSA); 4♂♂ 3♀♀: nr. Maphelana, Natal, 28°26′S 32°25′E, 10.xii.1980, D.H. Jacobs (DHJS, TMSA).

6.1.1.4 *Pondocoris latebrosus quattuordecimus* subspec. nov. (Figs 94, 98, 106-110, 123-124, 136).

Length: ♂ 4,7 - 5,8 mm; ♀ 5,5 - 7,0 mm.
Width: ♂ 1,9 - 2,5 mm; ♀ 2,3 - 3,1 mm.

Table 6.4. Measurements (in mm) of *Pondocoris latebrosus quattuordecimus* subspec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	N♦	Mean	SD	Range$	AT#	N♦	Mean	SD	Range$
Total	length	5.44	10	5.36	0.254	4.71-5.76	6.34	10	6.40	0.348	5.59-6.92
	width	2.21	10	2.19	0.133	1.92-2.44	2.97	10	2.85	0.153	2.39-3.09
Head	length	1.06	10	1.04	0.040	0.96-1.11	1.21	10	1.16	0.067	0.92-1.25
	width	0.88	10	0.88	0.037	0.82-0.96	1.02	10	0.98	0.043	0.82-1.03
Pronotum	length	0.57	10	0.58	0.037	0.49-0.66	0.66	10	0.64	0.028	0.56-0.69
	width	1.69	10	1.67	0.086	1.46-1.80	1.95	10	1.90	0.109	1.66-2.06
Tergal disk	length	1.45	10	1.43	0.089	1.27-1.59	1.90	10	1.86	0.102	1.65-2.04
	width	1.38	10	1.39	0.073	1.24-1.51	1.86	10	1.80	0.093	1.60-1.98
Antennal segments	I	0.44	10	0.43	0.015	0.39-0.45	0.48	10	0.47	0.032	0.38-0.53
	II	0.29	10	0.29	0.008	0.27-0.31	0.32	10	0.30	0.023	0.25-0.33
	III	0.48	10	0.47	0.020	0.43-0.51	0.51	10	0.50	0.024	0.41-0.54
	IV	0.32	10	0.32	0.010	0.29-0.34	0.34	10	0.34	0.013	0.28-0.36

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.
♦ Five individuals from each of the following localities: Dhlinsa forest and Ngoye forest.

Diagnostic measurements are given in Table 6.4. Refer to the previous subspecies for differences with them.

Chromosome number: 2n(♂) = 14XY.

Habitat and distribution: Where the previous subspecies seems to be restricted to a particular geographic area, *quattuordecimus* seems to occur at selected spots, often montane forests, over a very large area from Hogsback in the Eastern Cape to Ngoye forest in northern Kwazulu-Natal (Fig. 87).

Etymology: Quattuordecem (L) = fourteen, referring to the chromosome number of the subspecies.

MATERIAL EXAMINED: **SOUTH AFRICA, Kwazulu-Natal**. ♂ holotype: Dhlinsa forest, Eshowe, 28°54′S 31°27′E, 12.iv.1980, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 278 paratypes as follows: 84♂♂ 32♀♀: Ngoye Forest Reserve, nr. Empangeni, 28°50′S 31°43′E, 11-12.xii.1980, D.H. Jacobs (DHJS, TMSA); 10♂♂ 4♀♀: ditto, 22.viii.1985, (DHJS, TMSA); 59♂♂ 75♀♀: Same data as holotype (DHJS, TMSA); 1♂ 1♀: ditto, 21.viii.1985 (DHJS); 2♂♂ 9♀♀: Umdoni Park, nr. Scottburgh, 30°24′S 30°41′E, 27.i.1983, D.H. Jacobs (DHJS); **Eastern Cape**. 1♀: Schwarzwald forest, nr. Hogsback, 32°39′S 27°00′E, 16.xii.1981, D.H. Jacobs (DHJS).

6.1.2 *Pondocoris ampliatus* spec. nov. (Figs 127-134, 144).

Length: ♂ 5,1 - 5,5 mm; ♀ 5,5 - 6,4 mm.
Width: ♂ 2,3 - 2,7 mm; ♀ 2,8 - 3,2 mm.

Diagnostic measurements are given in Table 6.5. Apterous. Ovate body coated with a pale yellowish brown incrustation, resulting in a general brownish grey appearance. The following description is based on specimens with the incrustation removed.

Table 6.5. Measurements (in mm) of *Pondocoris ampliatus* spec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	N♂	Mean	SD	Range	AT#	N♂	Mean	SD	Range
Total	length	5.38	10	5.34	0.080	5.18-5.45	6.16	10	6.13	0.213	5.59-6.40
	width	2.49	10	2.55	0.084	2.38-2.64	3.02	10	3.04	0.100	2.85-3.19
Head	length	1.00	10	1.03	0.042	0.96-1.11	1.09	10	1.09	0.035	1.02-1.14
	width	0.90	10	0.92	0.027	0.88-0.97	0.97	10	0.97	0.026	0.92-1.01
Pronotum	length	0.62	10	0.62	0.018	0.58-0.65	0.62	10	0.63	0.029	0.57-0.67
	width	1.66	10	1.70	0.041	1.63-1.78	1.91	10	1.86	0.064	1.71-1.92
Tergal disk	length	1.39	10	1.39	0.043	1.32-1.44	1.78	10	1.78	0.070	1.61-1.87
	width	1.68	10	1.66	0.050	1.58-1.73	2.01	10	1.97	0.068	1.79-2.04
Antennal segments	I	0.44	10	0.45	0.011	0.43-0.47	0.46	10	0.45	0.013	0.43-0.48
	II	0.33	10	0.33	0.024	0.28-0.36	0.36	10	0.35	0.015	0.32-0.37
	III	0.42	10	0.43	0.012	0.40-0.46	0.45	10	0.44	0.019	0.39-0.46
	IV	0.33	10	0.33	0.009	0.31-0.35	0.34	10	0.33	0.007	0.32-0.35

* HT = holotype. # AT = allotype.
♦ 7♂♂,10♀♀ from Shaws Wood farm, 2♂♂ from Sneezewood forest and 1♂ from Ehlatini farm.

Head: About 1,1 times as long (not including neck area) as width across eyes. Genae stout, straight or diverging anteriorly. Clypeus with a prominent subapical tubercle. Antenniferous lobes short, directed anterolaterally. Antennae 1,6-1,7 times as long as width across eyes; first segment thickest and subequal in length or very slightly longer than the third segment, slightly curved and tapering towards base; second segment slightly curved basally, gradually thickening towards apex, slightly longer than segment four; third segment thinnest, slightly and evenly thickening towards apex, pedicellate; fourth segment fusiform, with a short pedicel, conical apex pilose; relative lengths of segments: 10,3:7,8:10:7,5. Postocular tubercles small, not reaching to level of outer margins of eyes. Neck slightly constricted just behind the head.

Thorax: Dorsum. Pronotum 2,75-3 times as wide as long. Lateral lobes elevated and reflexed, densely granulate, produced anteromesad to level of collar, or slightly beyond, lateral margins concave. Disk smooth and shining, with uneven surface. Longitudinal median groove narrow and usually shallow.

Mesonotum shorter and wider than pronotum. Disk with 2(1+1) comma-shaped smooth areas lateral of median ridge, remainder irregularly excavated. Lateral lobes granulate, lateral margins straight, converging anteriad. Median ridge separated from disk by longitudinal furrow which is posteriorly crossed by a transverse row of nodules; median ridge split by a prominent median suture or furrow along its total length, deeper and wider than that of the previous species.

Metanotum completely fused with MTg 1 and 2 and even sculpture does not usually indicate the position of the different tergites Lateral lobes granulate, lateral margins straight, converging anteriad. Disk with 2(1+1) comma- or S-shaped smooth elevations anteriorly, rest irregularly excavated. Median ridge more or less fused with that of mesonotum, although dorsally and laterally it sometimes seems to be built up by a series of irregular longitudinal elongate elevations. The ridge curves laterad just posterior of the metanotum and fade into a transverse, irregularly nodulate, elevated part which presumably represents MTg 1. Medially on MTg 2 a longitudinal furrow is present which is flanked by elevated areas. This median furrow is continuous with the median sulcus of the median ridge of the meso- and metanotum, forming a straight prominent furrow which stretches from the anterior margin of the mesonotum to the posterior margin of MTg 2. In the vicinity of MTg 1 a bar-like elevation is usually present medially in the furrow, fading posteriorly in females but usually reaching the posterior margin of MTg 2 in males. (In some specimens this bar may be split by a median longitudinal fossula). Sublateral ridges on MTg 2 triangular, usually not prominent.

Venter. As in the previous species except that the longitudinal depression on the T-shaped elevation of the prosternum is not well defined and the tubercles on the metasternal protuberances of the male are very small or absent, somewhat reminiscent of the situation in *Pondocoris latebrosus decimus*.

Legs: Trochanters of all legs demarcated by a suture.

Abdomen: Dorsum. Tergal disk distinctly broader than long (1,2x in males, 1,1 in females), moderately elevated along median line. Carinae separating glabrous impressions prominent. Surface between carinae and impressions areolate, especially along margins of carinae. DELTg 1+2+3 and 4 in males strongly sloping lateroventrally (or, in dried specimens, the part posterior to the tergal disk is strongly upturned), DELTg 5 posteriorly widened and protuberant resulting that the abdomen is widest over posterior margin of tergite 5 and that lateral margin of body is concave. Lateral margin of the body of females convex, DELTg 1+2+3 and 4 not exceptionally sloping and abdomen widest across posterior part of tergite 4. Posterior nodulate transverse ridge on MTg 7 of female usually interrupted medially, anteriorly of this ridge 2(1+1) prominent elevations are usually present.

Venter. All intersegmental sutures complete, reaching lateral margin of body. Spiracle 2 ventral, 3-4 sublateral, placed between 1 and 2 spiracle widths from lateral margin; 5 just off the lateral margin and usually visible from above in females but not in males; 6-7 lateral and visible from above, 8 subterminal on paragites.

Genitalia: Pygophore as in Figs 133-134. Parameres as in Figs 129 to 132.

Chromosome number: 2n(♂) = 10XY.

Habitat and distribution: Inland montane evergreen forests in Kwazulu-Natal and the Eastern Cape (Fig 87).

Discussion: The males of *Pondocoris ampliatus* can easily be distinguished from the previous species by having either DELTg 1+2+3 & 4 sloping lateroventrally, resulting that the lateral margin of the body in concave (usually in fresh or alcohol preserved specimens), or having the abdomen behind the tergal disk strongly turned up (usually in dried mounted specimens); the carinate margin of the caudal pit on the pygophore is also more elongate oval, the tubercle on the metasternal protuberances is very small or obsolete and spiracle 5 is usually not clearly visible from above. Both sexes can be

distinguished by the relative lengths of the antennal segments where segment 1 is subequal or longer than 3 and 2 is longer than 4, the prominent median longitudinal furrow on the tergum stretching back to the posterior margin of MTg 2 (thus lacking the wedge-like elevation on Mtg 2), the broadly ovate form of the body which is on average less than 2,1x as long as wide in males and less than 2,02 times in females and the posterior external angle of DELTg 3-6 which is much more produced. The only subspecies of *Pondocoris latebrosus* with which it may be confused is *decimus* but apart from differences mentioned above it has the median bar on MTg 1 and 2 not as prominent and it is larger and more rugged.

MATERIAL EXAMINED: **SOUTH AFRICA, Kwazulu-Natal**. ♂ holotype: Shaws Wood Farm, Karkloof, 29°19′S 30°18′E, 1.ii.1983, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 45 paratypes as follows: 1♂: Ehlantini Farm, Karkloof, 29°19′S 30°17′E, 1.ii.1983, D.H. Jacobs (DHJS, TMSA). **Eastern Cape**. 5♂♂ 5♀♀: Sneezewood forest, nr. Umzimkulu, 30°15′S 29°27′E, 1.xii.1981, D.H. Jacobs (DHJS).

Table 6.6. Locality and numbers of individuals of *Pondocoris* taxa cytogenetically studied.

Locality	Co-ordinates	Date collected	No. of individuals cytogenetically studied
Pondocoris latebrosus latebrosus			
Umtamvuma forest, nr. Port Edward	31°03′S 30°11′E	28/i/1983	12
Mount Thesiger Nature Reserve, nr. Port St. Johns, Transkei	31°37′S 29°31′E	4-5/xii/1981	4
nr. Port St. Johns, Transkei	31°38′S 29°32′E	2-6/xii/1981	7
Mpame forest, Transkei	32°05′S 29°02′E	12/xii/1981	5
Dwesa forest, Transkei	32°18′S 28°50′E	10-13/xii/1981	6
Pondocoris latebrosus quattuordecimus			
Ngoye forest, nr. Empangeni	28°50′S 31°43′E	11-12/xii/1980	5
Dhlinza forest, Eshowe	28°54′S 31°27′E	12/iv/1980	8
Tugela river mouth	29°14′S 31°39′E	7/iv/1980	1
Umdoni Park, nr. Scottburgh	30°24′S 30°41′E	27/i/1983	4
Schwarzwald forest, nr. Hogsback	32°39′S 27°00′E	16/xii/1981	1
Pondocoris latebrosus duodecimus			
Manzengwenya, Kwazulu	27°13′S 32°47′E	7/xii/1980	2
Manzengwenya forest, Kwazulu	27°16′S 32°46′E	3-7/xii/1980	12
Lake Sibayi, Kwazulu	27°25′S 32°43′E	5/xii/1980	3
nr. Maphelana, Natal	28°26′S 32°25′E	10/xii/1980	4
Pondocoris latebrosus decimus			
nr. Durban	29°45′S 31°04′E	4/iv/1980	1
Stainbank Nature Reserve, Durban	29°55′S 30°56′E	2/xi/1989	4
nr. Scottburgh	30°15′S 30°46′E	25/i/1983	2
Pondocoris ampliatus			
Shaws Wood farm, Karkloof	29°19′S 30°18′E	1/ii/1983	10
Sneezewood forest, nr. Umzimkulu	30°15′S 29°27′E	1/xii/1981	3

6.2 Cytogenetics of the genus Pondocoris..

The localities and number of individuals of *Pondocoris* taxa that were cytogenetically studied are presented in Table 6.6. The course of meiosis is similar to that of *Adamanotus uncotibialis* and a true diffuse stage is present.

6.2.1 ***Pondocoris latebrosus*** (Figs 88-91, 145-152).

The four subspecies of *P. latebrosus* have different chromosome numbers, ranging from 2n = 10XY to 2n = 22XY. It is evident from the different chromosome numbers as well as the size distribution of the chromosomes that extensive karyotype evolution took place in this species and, as will be discussed later, the phylogenetic relationship between the subspecies is not clear.

6.2.1.1 ***Pondocoris latebrosus latebrosus*** (Figs 88, 145-146).

The chromosome number of *P. latebrosus latebrosus* is 2n = 22XY. The true and relative chromosome areas for *P. latebrosus latebrosus* are presented in Table 6.7 and an idiogram in Fig. 88. Two of the ten autosomes is markedly larger than the other eight which form a gradual size series. The larger sex chromosome (presumably the X) is slightly smaller than the largest autosome while the Y-chromosome is slightly larger than the third largest autosome.

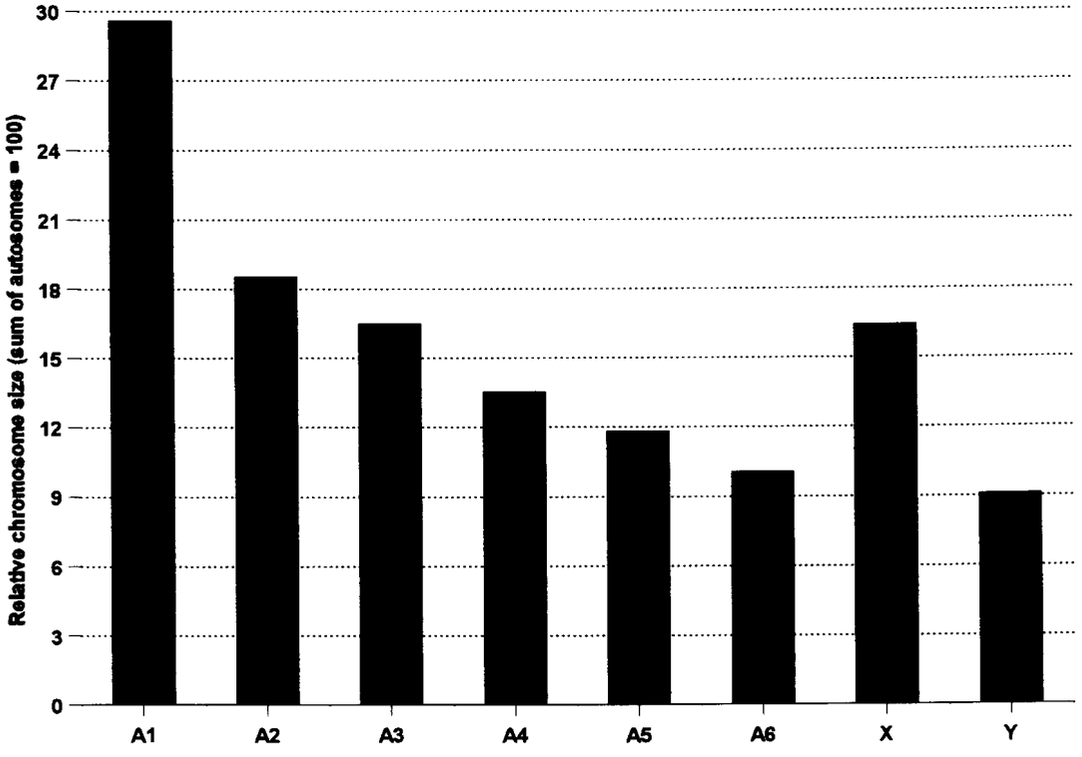


Figure 89. Idiogram of *Pondocoris latebrosus quattuordecimus*.

Table 6.7: True and relative chromosome areas of *P. latebrosus latebrosus*.

True chromosome areas (μm²) and standard deviation.				Relative chromosome areas (% of total area of autosomes) and standard deviation.		
Chromosome	Port St. Johns	Dwesa forest	TOTAL	Port St. Johns	Dwesa forest	TOTAL
Individuals	3	2	5	3	2	5
Cells	11	7	18	11	7	18
A1	2.96(±0.49)	3.18(±0.50)	3.05(±0.49)	16.54(±0.68)	16.78(±0.93)	16.63(±0.77)
A2	2.28(±0.37)	2.54(±0.34)	2.38(±0.37)	12.76(±1.05)	13.47(±0.84)	13.03(±1.01)
A3	1.98(±0.25)	2.06(±0.37)	2.01(±0.30)	11.13(±0.49)	10.83(±0.54)	11.01(±0.52)
A4	1.83(±0.26)	1.96(±0.40)	1.88(±0.32)	10.28(±0.35)	10.27(±0.62)	10.27(±0.46)
A5	1.73(±0.20)	1.82(±0.33)	1.76(±0.25)	9.72(±0.51)	9.55(±0.37)	9.66(±0.46)
A6	1.60(±0.22)	1.71(±0.29)	1.64(±0.25)	8.97(±0.49)	9.01(±0.22)	8.98(±0.40)
A7	1.48(±0.21)	1.58(±0.30)	1.52(±0.25)	8.29(±0.30)	8.27(±0.37)	8.28(±0.32)
A8	1.43(±0.21)	1.51(±0.28)	1.46(±0.23)	8.02(±0.39)	7.94(±0.45)	7.99(±0.40)
A9	1.34(±0.18)	1.39(±0.19)	1.36(±0.18)	7.50(±0.36)	7.38(±0.51)	7.45(±0.42)
A10	1.22(±0.19)	1.24(±0.24)	1.23(±0.20)	6.80(±0.23)	6.50(±0.50)	6.68(±0.38)
X	2.67(±0.39)	2.84(±0.53)	2.74(±0.44)	14.97(±0.61)	14.97(±0.96)	14.97(±0.73)
Y	1.98(±0.26)	2.22(±0.39)	2.07(±0.33)	11.19(±1.44)	11.66(±0.53)	11.37(±1.17)
Autosomes	17.86(±2.43)	18.98(±3.09)	18.30(±2.68)			
All chromosomes	22.51(±2.94)	24.04(±3.97)	23.11(±3.35)			

6.2.1.2 *Pondocoris latebrosus quattuordecimus* (Figs 89, 147-149).

The chromosome number of *P. latebrosus quattuordecimus* is 2n = 14XY. The true and relative chromosome areas for *P. latebrosus quattuordecimus* are presented in Table 6.8 and an idiogram in Fig. 89.

One of the autosomes is markedly larger than the other 5 which form a gradual series.

Slight differences in the karyotype are present between the different localities, but the total pattern remain the same. For example: the five smaller autosomes form a more gradual series in the Dhlinsa forest and Umdoni Park populations while the larger two of these chromosomes is distinctly larger than the other three in the Ngoye and Schwarzwald populations (Figs 147-149). When interpreting the idiograms the reader should keep in mind that the size difference between two chromosomes that are more or less of equal size are usually amplified in the idiogram because of reversal in the order of chromosomes that is unavoidable in compiling these idiograms.

The X-chromosome is about the same size as the third largest autosome while the Y-chromosome is usually the smallest the smallest chromosome (except in the case of the specimens from Dhlinsa forest). As will be pointed out repeatedly and discussed later, large size differences in the sex chromosomes is common between localities and even between individuals from the same locality.

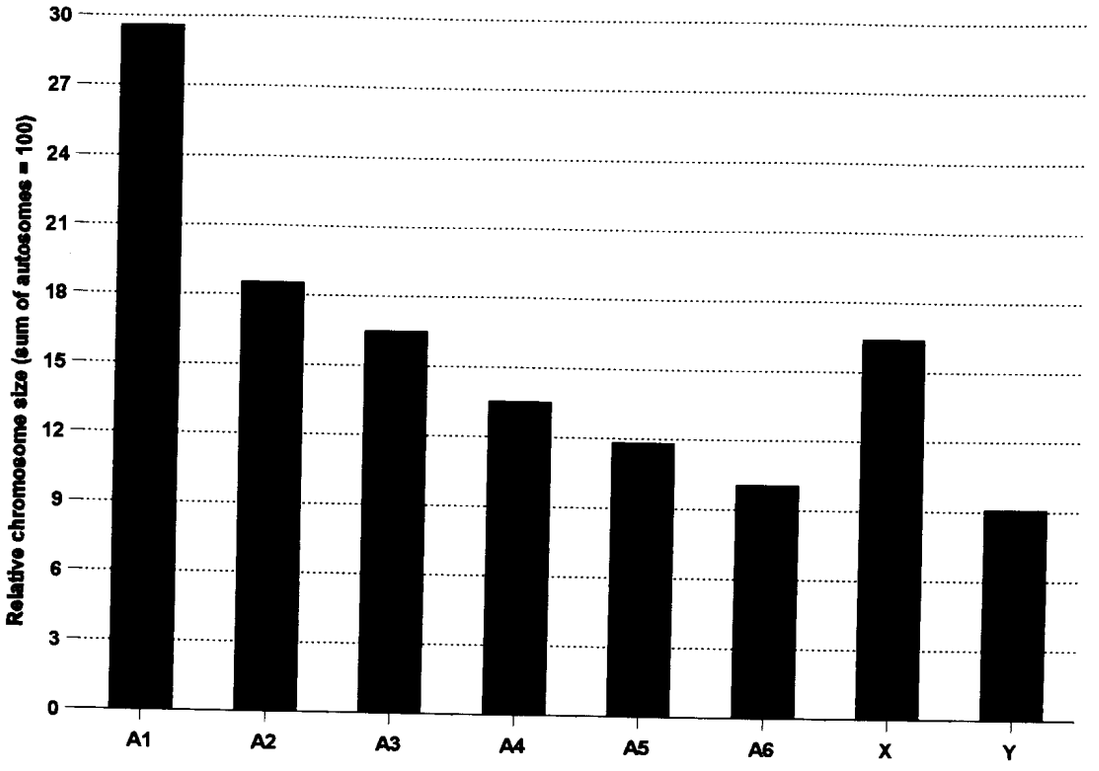


Figure 89. Idiogram of *Pondocoris latebrosus quattuordecimus*.

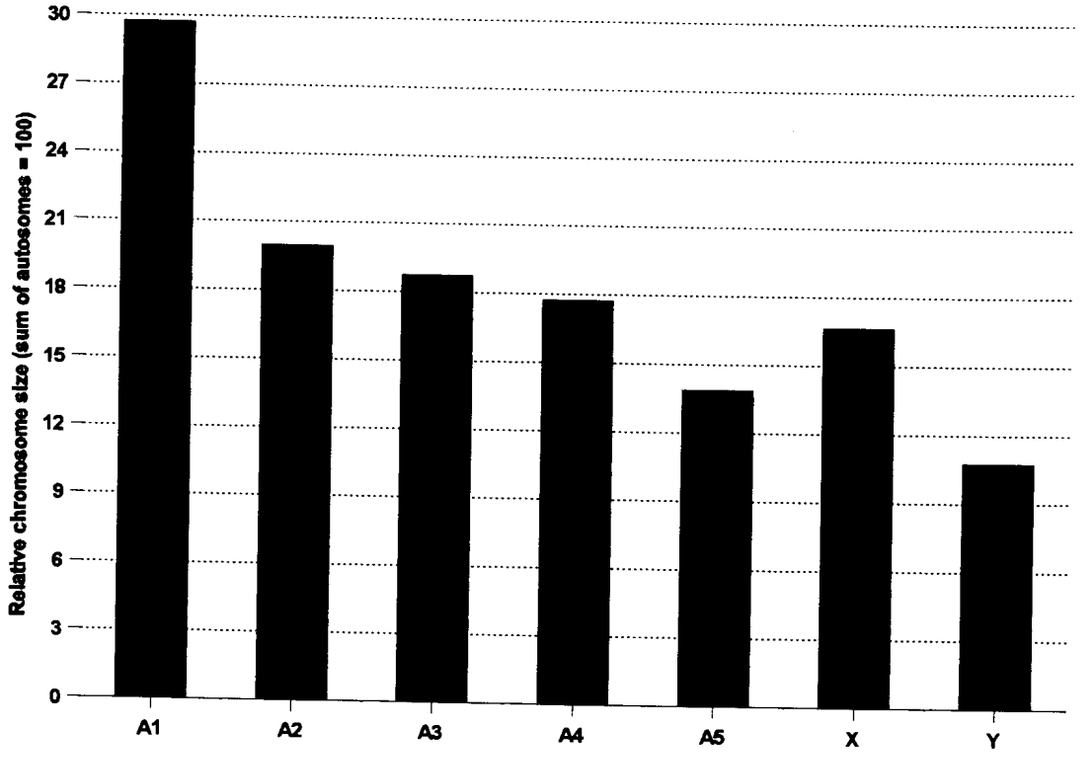


Figure 90. Idiogram of *Pondocoris latebrosus duodecimus*.

Table 6.9. True and relative chromosome areas of *P. latebrosus duodecimus*.

Relative chromosome areas (μm^2) and standard deviation.				
Chromosome	**Manzengwenya forest**	**Maphelana**	**Lake Sibayi**	**TOTAL**
Individuals	**3**	**3**	**1**	**7**
Cells	**13**	**10**	**4**	**27**
A1	**5.89(±1.27)**	**5.55(±0.78)**	**6.98(±0.80)**	**5.92(±1.12)**
A2	**3.91(±0.71)**	**3.67(±0.56)**	**5.01(±0.67)**	**3.99(±0.77)**
A3	**3.69(±0.72)**	**3.38(±0.45)**	**4.88(±0.61)**	**3.75(±0.78)**
A4	**3.51(±0.76)**	**3.15(±0.56)**	**4.79(±0.62)**	**3.57(±0.85)**
A5	**2.68(±0.51)**	**2.63(±0.39)**	**3.40(±0.50)**	**2.77(±0.52)**
X	**3.21(±0.49)**	**2.96(±0.40)**	**4.62(±0.60)**	**3.33(±0.72)**
Y	**2.04(±0.36)**	**1.87(±0.40)**	**3.34(±0.45)**	**2.17(±0.62)**
Autosomes	**19.68(±3.88)**	**18.37(±2.63)**	**25.05(±3.04)**	**19.99(±3.92)**
All chromosomes	**24.94(±4.62)**	**23.21(±3.38)**	**33.00(±4.05)**	**25.49(±5.15)**
Relative chromosome areas (% of total area of autosomes) and standard deviation.				
A1	**29.88(±1.50)**	**30.25(±1.58)**	**27.92(±1.65)**	**29.73(±1.68)**
A2	**19.94(±0.80)**	**19.98(±0.58)**	**19.98(±0.52)**	**19.96(±0.67)**
A3	**18.73(±0.67)**	**18.41(±0.61)**	**19.47(±0.42)**	**18.73(±0.69)**
A4	**17.80(±0.98)**	**17.06(±1.07)**	**19.11(±0.54)**	**17.72(±1.16)**
A5	**13.64(±0.62)**	**14.30(±0.65)**	**13.52(±0.52)**	**13.87(±0.69)**
X	**16.50(±1.57)**	**16.15(±0.91)**	**18.42(±0.68)**	**16.65(±1.44)**
Y	**10.45(±1.13)**	**10.10(±1.00)**	**13.30(±0.55)**	**10.74(±1.48)**

6.6.1.3 ***Pondocoris latebrosus duodecimus*** (Figs 90, 151-152).

The chromosome number of *P. latebrosus duodecimus* is 2n = 12XY. The true and relative chromosome areas for this species are presented in Table 6.9 and an idiogram in Fig. 90. The largest autosome is markedly larger than the other four while the smallest one is distinctly smaller than the intermediate three which form a gradual series. The X-chromosome is somewhat smaller than the second smallest autosome while the Y-chromosome is the smallest chromosome in the complement.

6.2.1.4 ***Pondocoris latebrosus decimus*** (Figs 91, 150, 153-154).

The chromosome number of *P. latebrosus decimus* is 2n = 10XY. The true and relative chromosome areas for this subspecies are presented in Table 6.10 and an idiogram in Fig. 91. The four autosomes form a gradual series while both sex chromosomes are smaller than the smallest autosome. The Y-chromosome is distinctly smaller than the X-chromosome. The Y-chromosome in the specimen from Durban is markedly smaller than in the Scottburgh specimen.

Table 6.10. True and relative chromosome areas of *P. latebrosus decimus*.

True chromosome areas (µm²) and standard deviation.				Relative chromosome areas (% of total area of autosomes) and standard deviation.		
Chromosome	Durban	Scottburgh	TOTAL	Durban	Scottburgh	TOTAL
Individuals	1	1	2	1	1	1
Cells	6	7	13	6	7	13
A1	6.28(±0.37)	5.28(±0.88)	5.74(±0.84)	29.67(±0.72)	30.41(±1.11)	30.07(±0.99)
A2	5.97(±0.58)	4.75(±0.77)	5.31(±0.92)	28.20(±1.49)	27.35(±0.64)	27.74(±1.15)
A3	4.92(±0.42)	4.01(±0.67)	4.43(±0.72)	23.24(±1.36)	23.05(±0.77)	23.14(±1.04)
A4	3.99(±0.37)	3.33(±0.56)	3.64(±0.57)	18.89(±1.46)	19.19(±1.13)	19.05(±1.25)
X	3.63(±0.35)	2.94(±0.42)	3.26(±0.52)	17.13(±0.74)	17.00(±1.10)	17.06(±0.91)
Y	1.61(±0.19)	1.77(±0.29)	1.70(±0.25)	7.63(±0.80)	10.18(±0.81)	9.00(±1.53)
Autosomes	21.16(±1.36)	17.36(±2.81)	19.11(±2.93)			
All chromosomes	26.40(±1.78)	22.07(±3.46)	24.07(±3.52)			

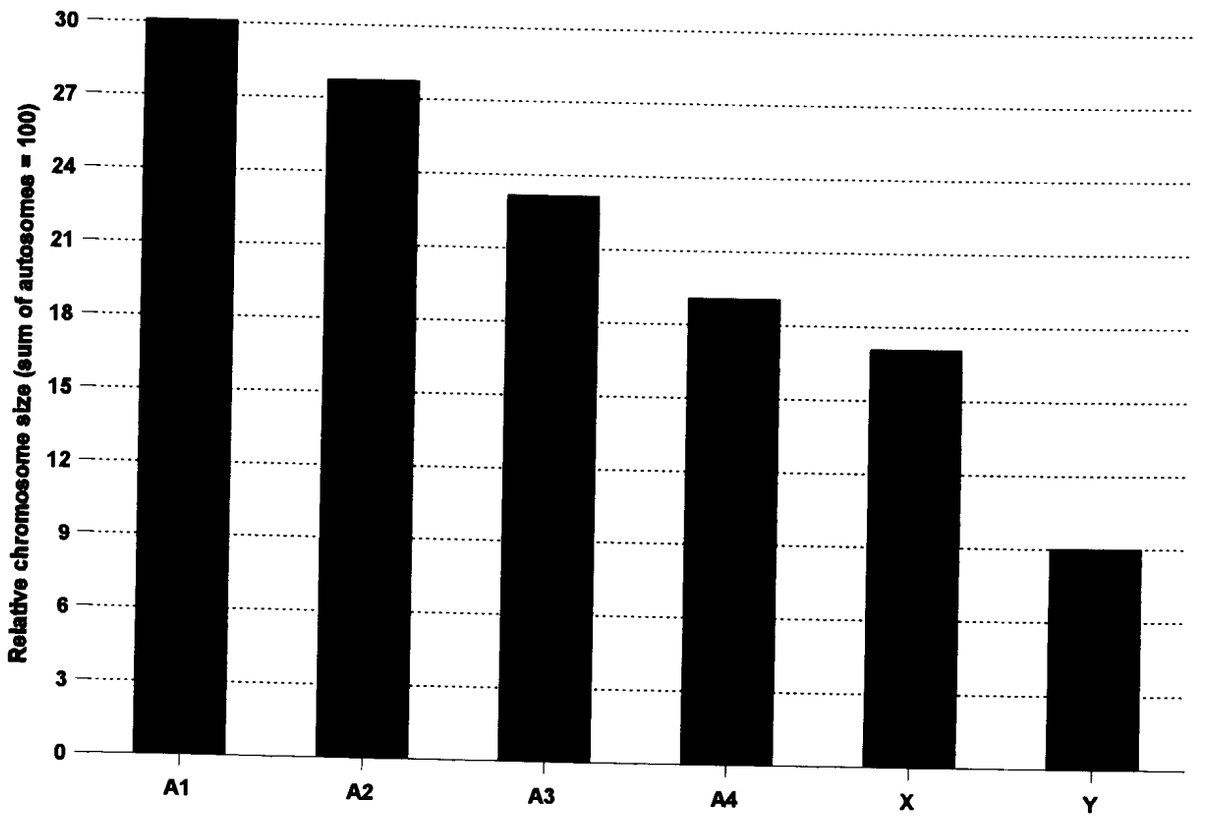


Figure 91. Idiogram of *Pondocoris latebrosus decimus*.

6.2.2 *Pondocoris ampliatus* (Figs 92, 155-156).

The chromosome number of P. ampliatus is 2n = 10XY. The true and relative chromosome areas for this species are presented in Table 6.11 and an idiogram in Fig. 92. The karyotype of this species is quite different from that of *P. latebrosus decimus* which has the same chromosome number. Two of the four autosomes are markedly larger than the other two while the X- and Y-chromosomes are the smallest two in the complement.

Table 6.11. True and relative chromosome areas of *P. ampliatus*.

True chromosome areas (μm²) and standard deviation.				Relative chromosome areas (% of total area of autosomes) and standard deviation.		
Chromosome	Karkloof	Sneezewood forest	TOTAL	Karkloof	Sneezewood forest	TOTAL
Individuals	3	1	4	3	1	4
Cells	12	4	16	12	4	16
A1	5.24(±0.74)	5.06(±1.00)	5.19(±0.78)	36.04(±1.57)	36.32(±0.80)	36.11(±1.39)
A2	4.34(±0.49)	3.95(±0.81)	4.24(±0.58)	29.93(±1.38)	28.33(±0.73)	29.53(±1.42)
A3	2.65(±0.43)	2.66(±0.35)	2.65(±0.40)	18.18(±0.94)	19.30(±1.45)	18.46(±1.15)
A4	2.30(±0.29)	2.24(±0.46)	2.28(±0.32)	15.85(±0.86)	16.05(±0.70)	15.90(±0.81)
X	2.06(±0.27)	2.01(±0.30)	2.04(±0.27)	14.23(±1.81)	14.55(±1.50)	14.31(±1.69)
Y	1.29(±0.20)	1.53(±0.19)	1.35(±0.22)	8.93(±1.13)	11.18(±1.51)	9.49(±1.55)
Autosomes	14.53(±1.83)	13.90(±2.60)	14.37(±1.97)			
All chromosomes	17.87(±2.13)	17.44(±2.96)	17.76(±2.26)			

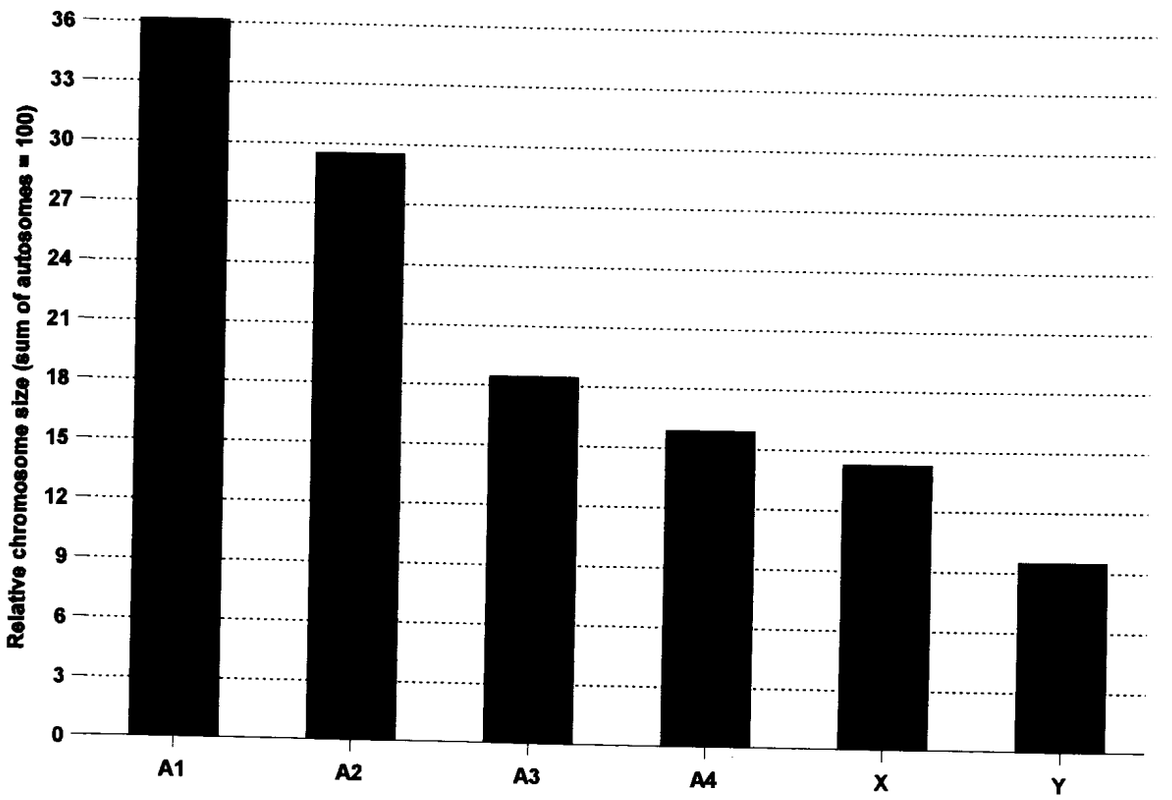


Figure 92. Idiogram of *Pondocoris ampliatus*.

6.2.3 Discussion:

Although the five taxa of Pondocoris belong to only two species, karyotype evolution has been extensive in this genus. *P. latebrosus quattuordecimus* exhibit the primitive chromosome number of 2n = 14XY but its karyotype is actually derived with the large autosome probably originated from the fusion of two smaller ones (also refer to 12.1.1 and 12.1.5). This would imply that an intermediate 16XY karyotype probably existed which could have arisen from the primitive 14XY by the fission of a autosome (probably the largest autosome in order to explain the chromosome size distribution in *P. latebrosus quattuordecimus*) or from an ancestor with a higher chromosome number.

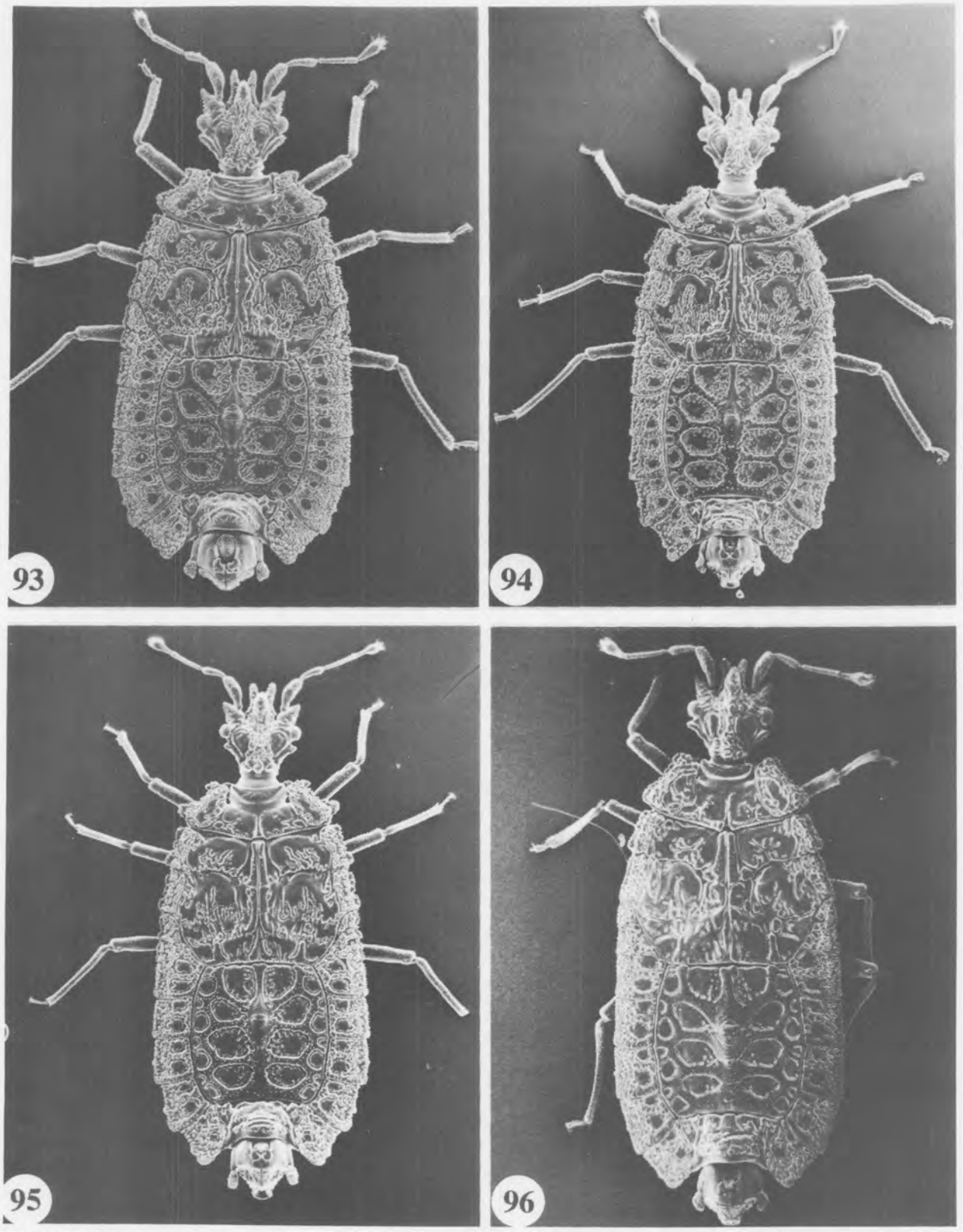
The karyotype of *P. latebrosus decimus* could have originated by fusion of autosomes A3 + A5 and A4 + A6 of *quattuordecimus*.

From the size distribution of the chromosomes of *P. ampliatus* it seems unlikely that it originated from *quattuordecimus* or *duodecimus*, but more probably from the postulated primitive 14XY karyotype by two fusions.

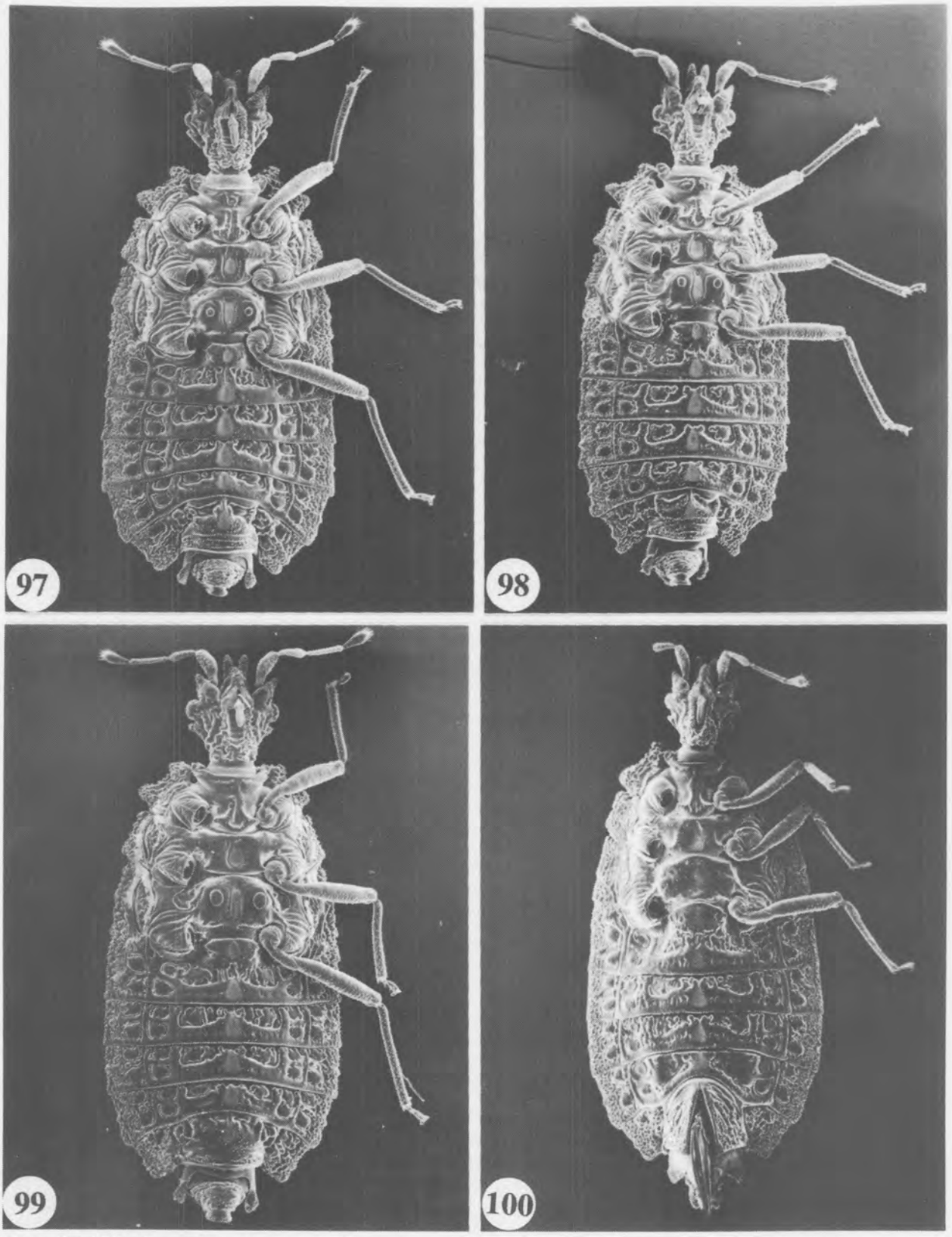
The origin of the karyotypes of *duodecimus* and *latebrosus* is more difficult to envisage. Although *duodecimus* has a large autosome which could have originated by the fusion of two autosomes of the primitive 14XY karyotype, the size distribution of its chromosomes does not fit into the scheme that can explain the origin of *quattuordecimus, decimus* and *ampliatus* from the same primitive 14XY karyotype. This implies that more than mere fusions and fissions took place in the karyotype evolution of these taxa or that more fusions and fissions took place or that the ancestral chromosome number for the genus is higher. The 22XY karyotype of *latebrosus* supports the latter view as it could possible have originated by 4 fissions from a 14XY karyotype or in one step by pseudoploidy from a 12XY karyotype or by pseudoploidy followed by two fusions of a 14XY karyotype. The unequal size of the two larger chromosomes in the *latebrosus* karyotype support the latter of these possibilities as they would have been expected to be of equal size if they originated by chromatid autonomy alone. (There have been many arguments against pseudoploidy and the whole issue will be discussed in 12.1.2)

The genus *Pondocoris* seems to be characterized by a low chromosome number and relatively small sex chromosomes. There is usually also a marked difference in the size of the X- and Y-chromosomes. The exception to all the above is *P. latebrosus latebrosus* with 2n = 22XY and the sex chromosome larger than most autosomes.

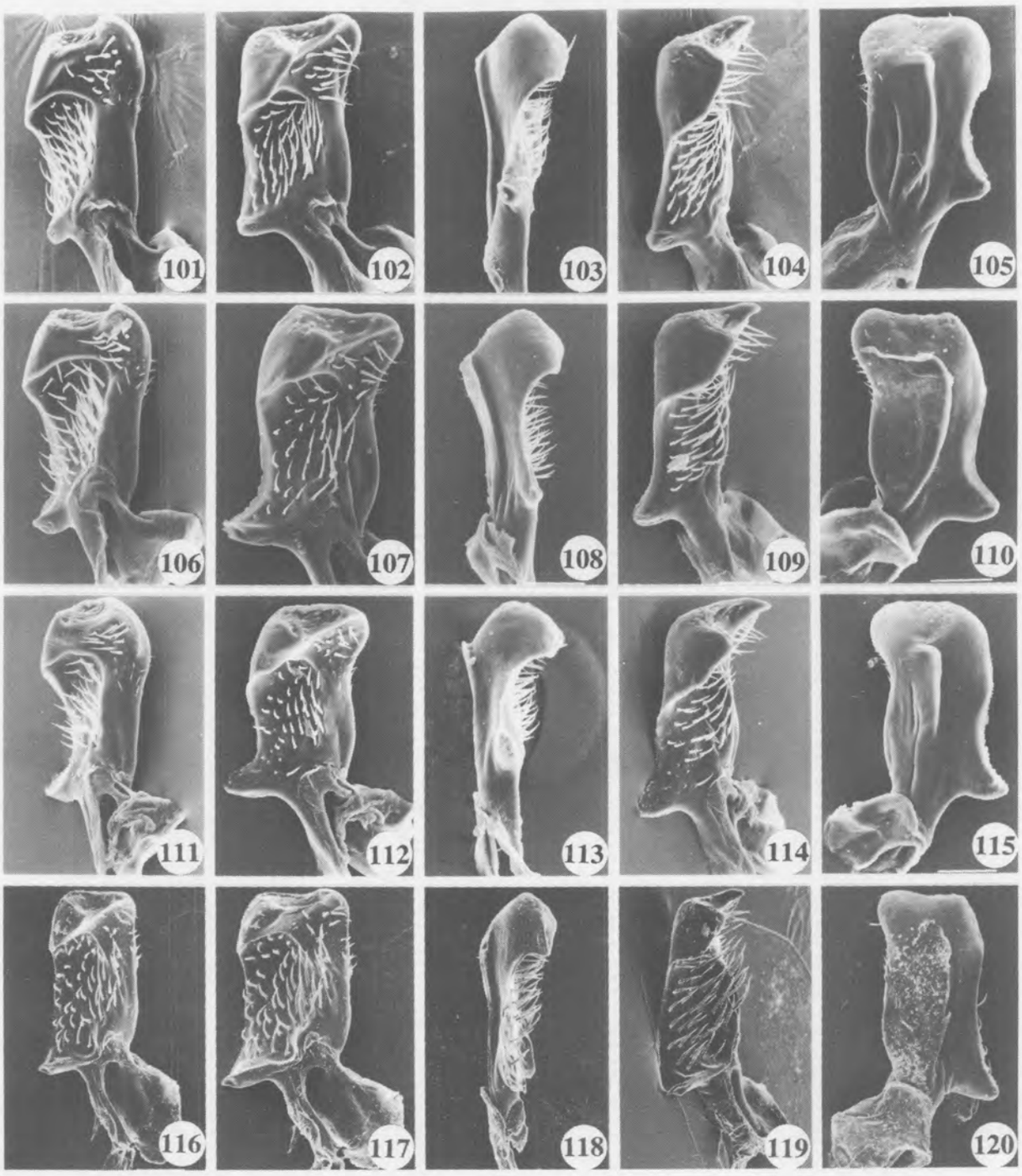
Karyotype evolution has outpaced morphological evolution in *Pondocoris* and this has led to some interesting problems in the classification of these taxa. Strictly according to the Biological Species Concept (BSC) the four subspecies of *P. latebrosus* should all have been described as separate species as it is not likely that these "chromosomal races" or "cytoforms" would be reproductively compatible as previously stated. The BSC has several weaknesses and I don't accept it unconditionally. I shall discuss this briefly and motivate and defend taxonomic decisions I took in 12.1.4.



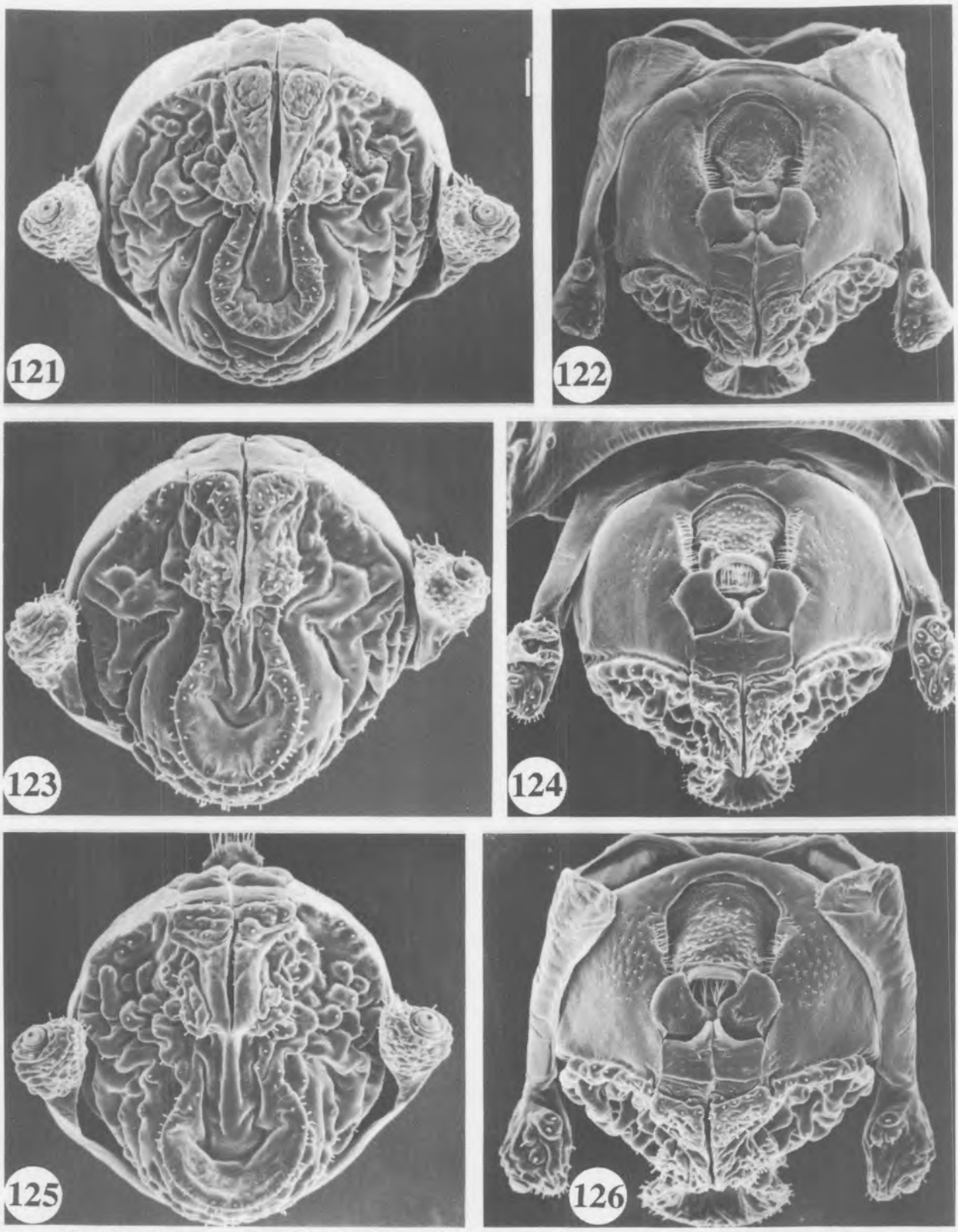
Figs 93-96. Scanning electron photomicrographs of the dorsal aspects of the subspecies of *Pondocoris latebrosus* (Hoberlandt). 93. *P. latebrosus latebrosus* (Hoberlandt), male. 94. *P. latebrosus quattuordecimus* **subspec. nov.**, male paratype. 95. *P. latebrosus duodecimus* **subspec. nov.**, male paratype. 96. *P. latebrosus decimus* **subspec. nov.**, male paratype.



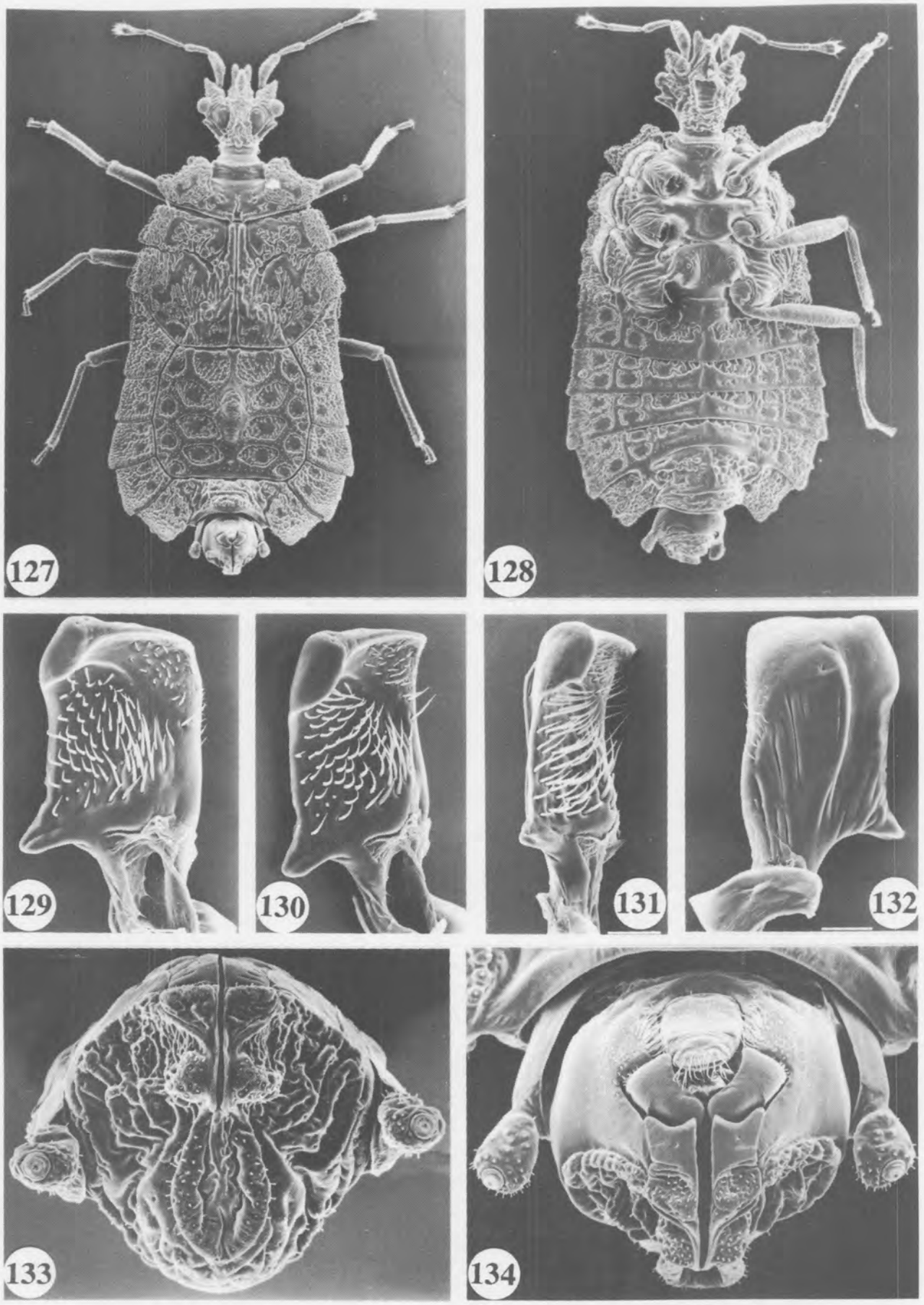
Figs 97-100. Scanning electron photomicrographs of the ventral aspects of the subspecies of *Pondocoris latebrosus* (Hoberlandt). 97. *P. latebrosus latebrosus* (Hoberlandt), male. 98. *P. latebrosus quattuordecimus* **subspec. nov.**, male paratype. 99. *P. latebrosus duodecimus* **subspec. nov.**, male paratype. 100. *P. latebrosus decimus* **subspec. nov.**, female paratype.



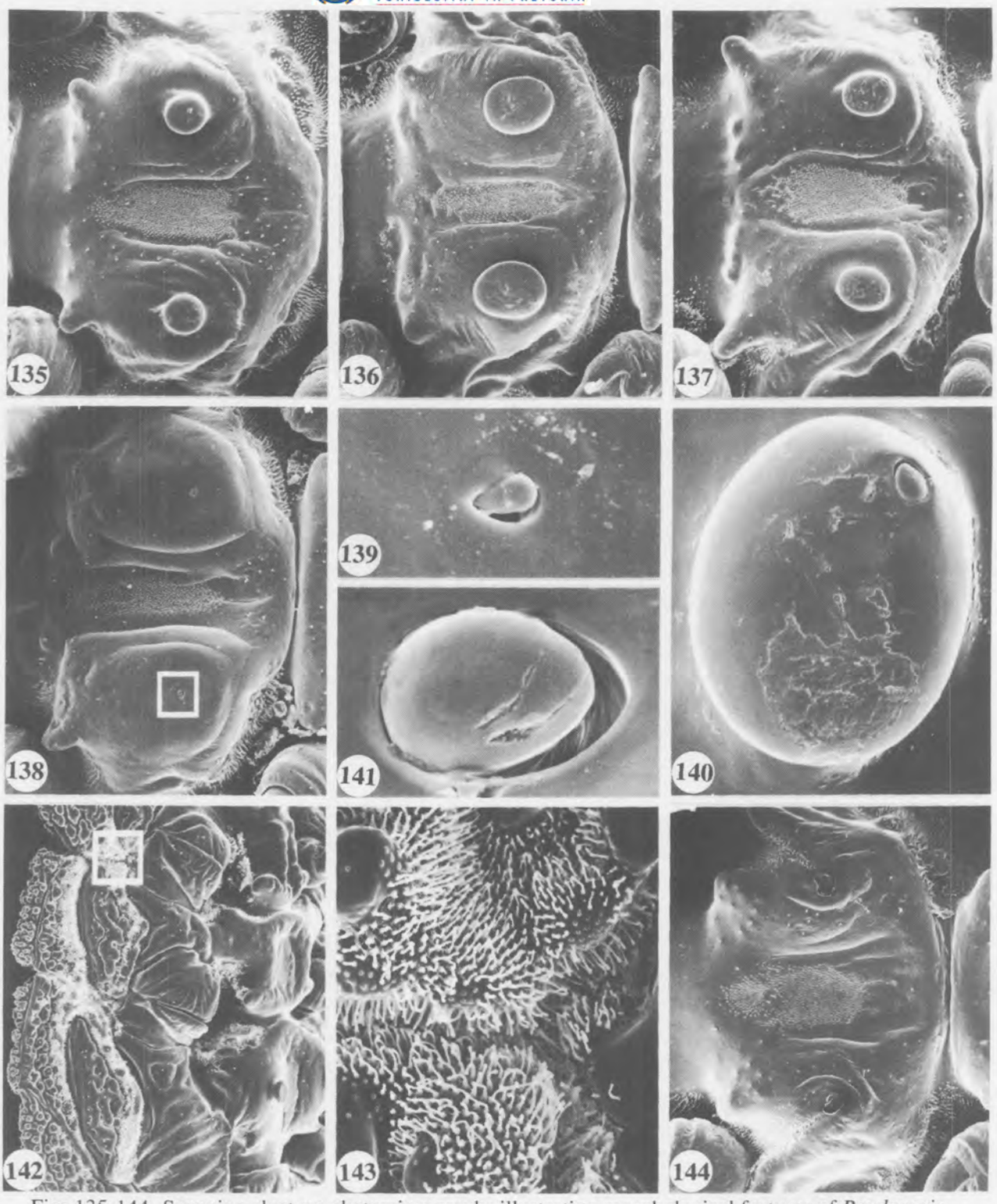
Figs 101-120. Scanning electron photomicrographs of different aspects of the left parameres of the subspecies of *Pondocoris latebrosus* (Hoberlandt). 101-105. *P. latebrosus latebrosus* (Hoberlandt). 106-110. *P. latebrosus quattuordecimus* **subspec. nov.** 111-115. *P. latebrosus duodecimus* **subspec. nov.** 116-120. *P. latebrosus decimus* **subspec. nov.**



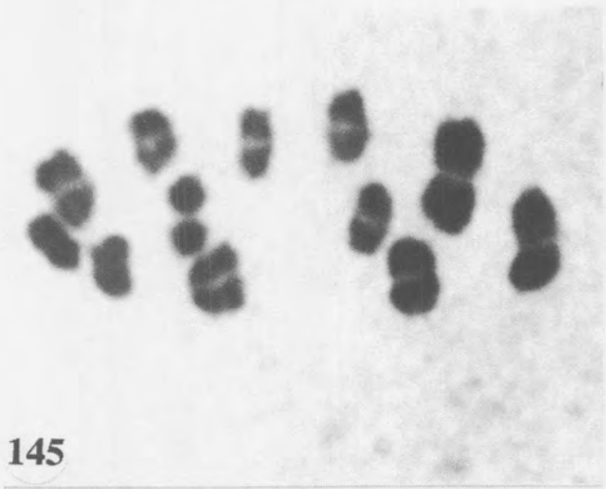
Figs 121-126. Scanning electron photomicrographs of the pygophores of some subspecies of *Pondocoris latebrosus* (Hoberlandt). 121-122. *P. latebrosus latebrosus* (Hoberlandt). 121. Caudal aspect. 122. Dorsal aspect. 123-124. *P. latebrosus quattuordecimus* **subspec. nov.** 123. Caudal aspect. 124. Dorsal aspect. 125-126. *P. latebrosus duodecimus* **subspec. nov.** 125. Caudal aspect. 126. Dorsal aspect.

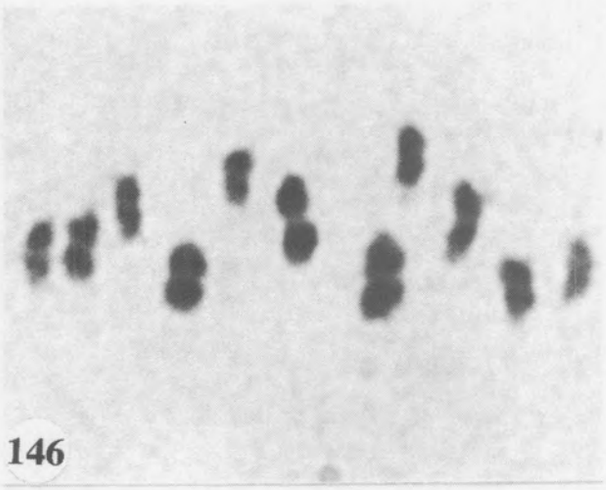


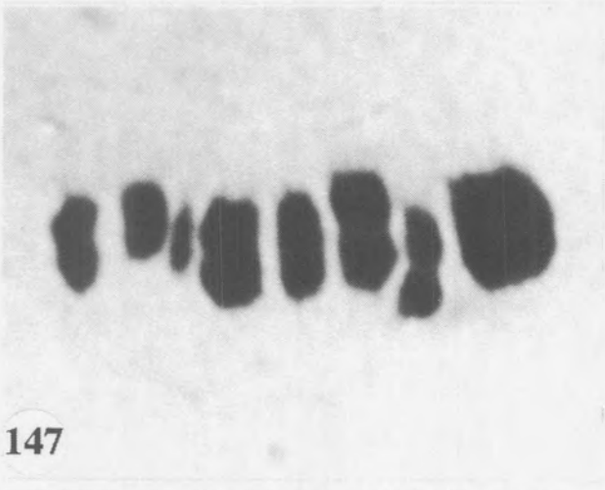
Figs 127-134. Scanning electron photomicrographs of *Pondocoris ampliatus* **spec. nov.** 127. Male paratype, dorsal aspect. 128. Male paratype, ventral aspect. 129-132. Different aspects of the left paramere (scale bar = 50 μm). 133-134. Pygophore. 133. Caudal aspect. 134. Dorsal aspect.

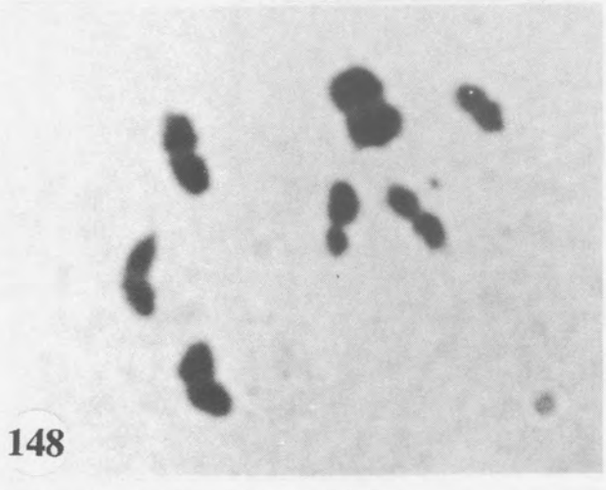


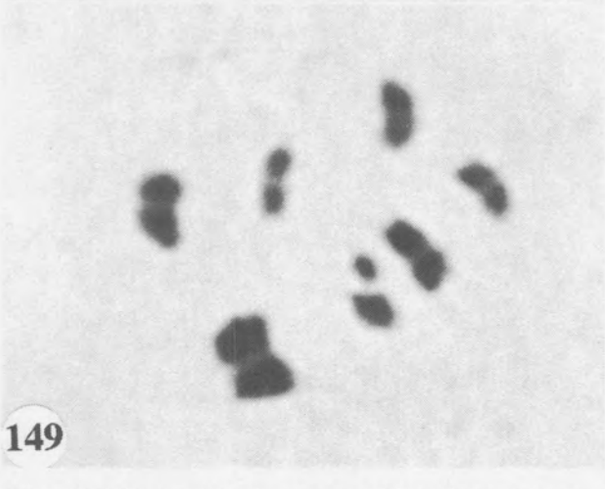
Figs 135-144. Scanning electron photomicrographs illustrating morphological features of *Pondocoris* species. 135-138. Metasterna of males of the subspecies of *Pondocoris latebrosus* (Hoberlandt) showing the protuberances and associated tubercles. 135. *P. latebrosus latebrosus* (Hoberlandt). 136. *P. latebrosus quattuordecimus* **subspec. nov.** 137. *P. latebrosus duodecimus* **subspec. nov.** 138. *P. latebrosus decimus* **subspec. nov.** 139. Enlargement of indicated area of Fig. 138 showing the operculate opening. 140. Metasternal tubercle of *P. latebrosus quattuordecimus* **subspec. nov.** showing the operculate opening (enlargement of Fig. 137). 141. Same, showing detail of operculate opening. 142. Lateroventral aspect of the male of *P. latebrosus latebrosus* (Hoberlandt) showing the evaporative areas. 143. Enlargement of the indicated area of Fig. 142 showing the capitate hairs on the surface of the evaporative area. 144. Metasternum of the male of *P. ampliatus* **spec. nov.** showing the protuberances and operculate opening.

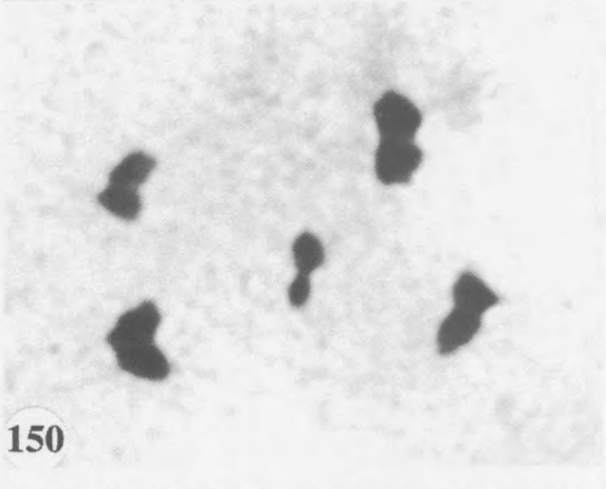




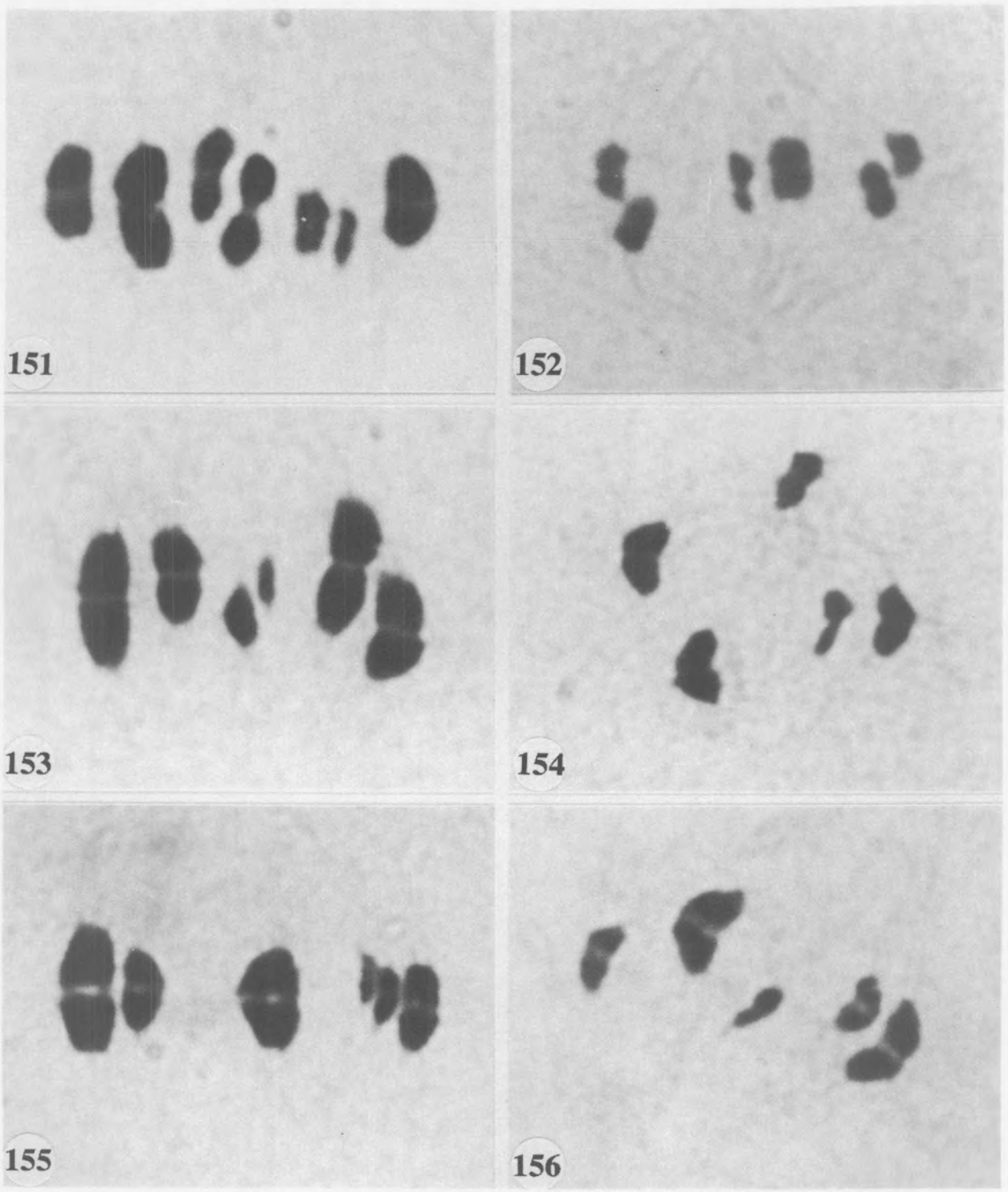








Figs 145-150. Meiotic stages of *Pondocoris* taxa. 145-146. *P. latebrosus latebrosus*. 145. Metaphase I. 146. Metaphase II. 147-149. *P. latebrosus quattuordecimus*. 147. Metaphase I. 148-149. Metaphase II. 150. *P. latebrosus decimus*, metaphase II.



Figs 151-156. Meiotic stages of *Pondocoris* taxa. 151-152. *P. latebrosus duodecimus*. 151. Metaphase I. 152. Metaphase II. 153-154. *P. latebrosus decimus*. 153. Metaphase I. 154. Metaphase II. 155-156. *P. ampliatus*. 155. Metaphase I. 156. Metaphase II.

Chapter 7

GENUS *TRICHOCARVENTUS* HEISS & JACOBS

7.1 ***Trichocarventus*** **Heiss & Jacobs**, Figs 161-176.

Trichocarventus Heiss & Jacobs, 1989 p. 50.

Type species: *Trichocarventus klapperichi* Heiss & Jacobs.

Etymology: From greek trichotos, meaning pilose.

Apterous. Body oval, coated with incrustation, beneath shining, surface including appendages and eyes covered with erect pilosity.

Head: Distinctly shorter than width across eyes, genae straight, produced beyond clypeus. Antenniferous spines acute, divergent. Eyes stylate. Postocular tubercles developed, ridge-like, strongly converging posteriorly to constricted collar. At base of head 2(1+1) prominent elevated sublateral tubercles. Antennae slender, distinctly longer than width of head; first segment stout, thickened, second shorter and cylindrical, third longest, cylindrical, fourth fusiform, conical apex pilose. Rostrum shorter than head, arising from a slit-like atrium. Rostral groove deep, closed posteriorly.

Thorax: Pronotum considerably wider than long, collar ring-like with 2(1+1) prominent tubercles laterally and 2(1+1) small tubercles dorsolaterally. Lateral lobes granulate, with 2(1+1) prominent tubercles laterally, deeply incised before collar, anterolateral angles subrectangular, posterolateral lobes rounded, projecting laterally, lateral margin concave. Disk with a longitudinal groove.

Mesonotum as long as pronotum but wider, at middle with an elevated triangular ridge which extends anteriorly into a cleft of gaping pronotal groove, its apex rounded, medially with a longitudinal sulcus. Lateral lobes granular, projecting, lateral margins converging anteriorly. Mesonotum is separated from metanotum by a transverse sulcus.

Metanotum shorter than mesonotum but wider, with an elevated subrectangular median ridge, also bearing a longitudinal sulcus, lateral margins straight, converging anteriorly. Metanotum separated from MTg 1 by a sulcus. MTg 1 forming 2(1+1) elevated transversal ridges, which meet at middle and are curved anteriorly. It is separated from depressed, strongly transversal Mtg 2 by a deep cleft. MTg 2 with an elongate median elevation, which is also longitudinally sulcate and 2(1+1) sublateral longitudinal elevations.

Legs: Slender, trochanters fused with femora, claws with two bristle-like parempodia and thin, long pseudopulvilli.

Abdomen: Tergal disk formed by fused MTg 3 to 6 with slightly convex lateral margins and depressed glabrous impressions. Disk slightly elevated along median line. DELTg 1 to 3 fused, anteriorly reaching posterolateral angle of metanotum. Posteroexterior angles of DELTg 4 to 7 with small but increasing rounded lobes, originating from reflexed ventral laterotergites.

MTg 7 in female with a transversal elevated ridge before posterior margin. Paratergites 8 conical, produced posteriorly, as long as tricuspidate tergite 9. MTg 7 in male strongly raised medially for the reception of the pygophore. Paratergites 8 slender, reaching apex of pygophore.

Ventral side: Pro-, meso- and metasterna flattened at middle and delimited by sutures. Sternites 1 to 3 fused, 4 to 7 separate. Spiracles 2 ventral, far from lateral margin, 3 and 4 ventral, close to margin, 5 to 7 lateral and visible from above, 8 subterminal.

Male genital structures: visible part of pygophore pyriform, surface rugose, dorsally with a split elevated median ridge which forms posteriorly a small oval pit with carinate borders (Figs 167-168, 175-176). Parameres with an anterolateral reflexed rounded lobe, inner face with long setae (Figs 163-166, 171-174).

Discussion: *Trichocarventus* superficially seems related to *Pondocoris,* resembling it in general shape of body and pronotum, but in fact is closer to *Dundocoris,* sharing the same pattern of median thoracal ridges. From both genera it is at once distinguished by its transverse head, stylate eyes and conspicuous hairy surface. It furthermore lacks the metasternal tubercles of *Pondocoris.*

7.1.1 *Trichocarventus klapperichi* Heiss & Jacobs, Figs 161-168.

Trichocarventus klapperichi Heiss & Jacobs, 1989 p. 51 (Or. descr.).

Body elongate with subparallel sides, covered on dorsal and ventral surface with long, erect pilosity. Colour reddish-brown, darker are the anterolateral angles of DELTg 2 to 7, lateral half of MTg 2, MTg 7 and 8 and tergite 9 in female, MTg 7 and pygophore in male; the median elevation of tergal disk is yellowish on posterior half.

Head: Length including neck/width across eyes 1,02/1,12; anterior process of genae straight, producing well beyond apex of clypeus, reaching 2/3 of antennal segment 1, its apices rounded. Antenniferous spines diverging anteriorly, apices acute. Eyes granular, stalked, strongly produced laterally. Postocular tubercles forming a rounded lobe, by far not reaching lateral margin of eyes, posteriorly carinate and strongly converging. Vertex with a longitudinal elevation flanked by 2(1+1) granulate carinae, laterad of them with 2(1+1) round impressions and 2(1+1) prominent tubercles posteriorly. Antennae 1,51 times as long as width across eyes, length of segments 1 to 4 = 0,47:0,32:0,55:0,35; first segment thickest, slightly curved and tapering towards base, second shorter and thinner, third longest and thin, fourth fusiform, its conical apex pilose. Rostrum short, not reaching posterior margin of head, arising from a slit-like atrium. Rostral groove wide, closed posteriorly, its lateral borders granulate.

Thorax: Pronotum length/width across posterior lobe 0,57/1,95 with a well developed ring-like collar, which bears 2(1+1) smaller tubercles dorsolaterally and 2(1+1) strong projecting ones laterally on a lower level. Collar thickened between dorsolateral tubercles. Lateral lobes slightly upturned, surface densely granular, incised before collar anteriorly, then angularly produced, lateral margin concave, posterolateral angle produced and rounded. Disk depressed and smooth with a longitudinal groove medially, which separates also the transversal ridge behind collar. Posterior margin feebly sinuate, marked by a transversal carina.

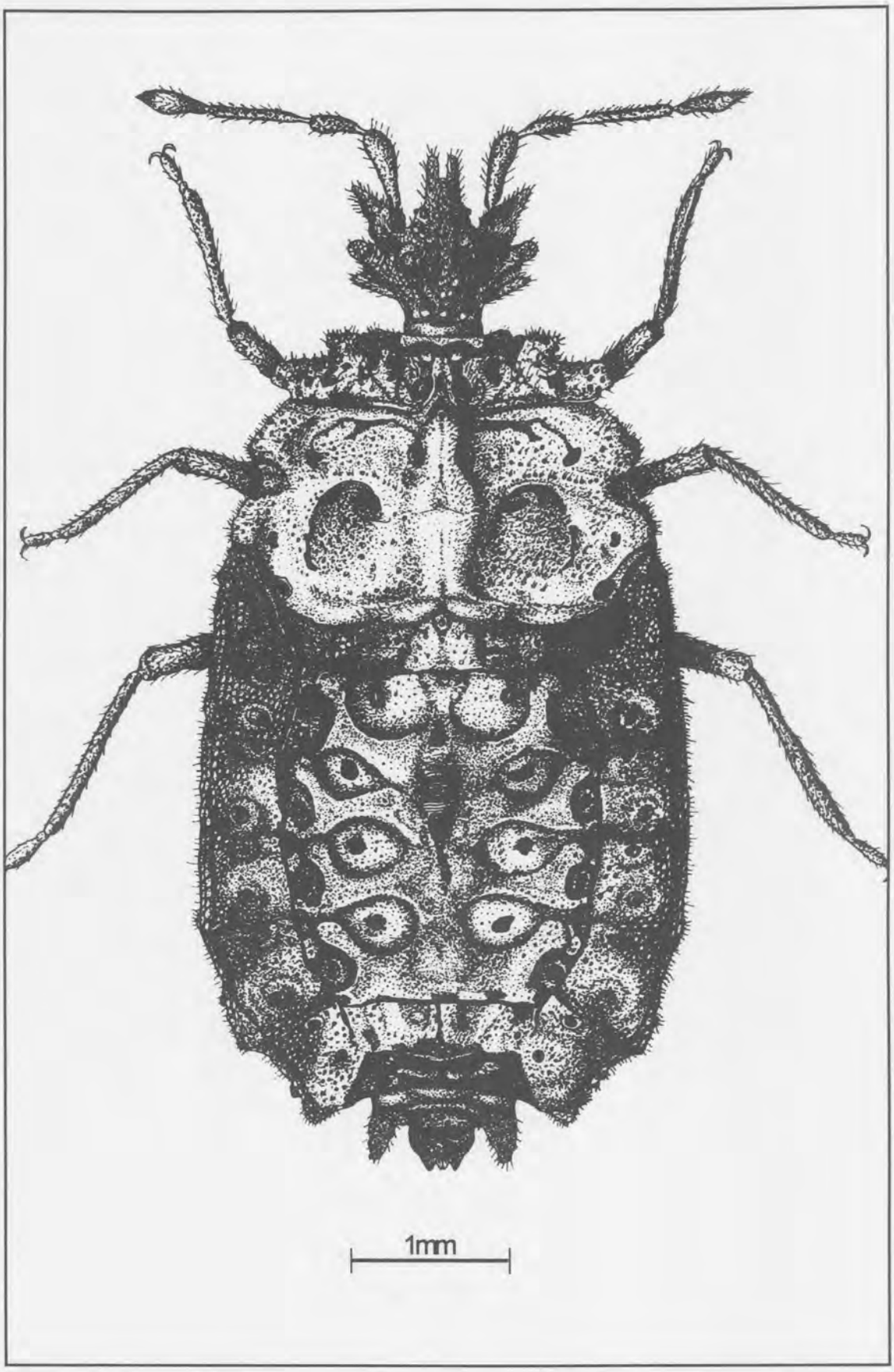


Figure 157. Dorsal view of *Trichocarventus klapperichi* Heiss & Jacobs.

Mesonotum length/width 0,55/1,80, slightly reflexed and lobately produced laterally, roundedly produced posteriorly with a triangular median elevation bearing a longitudinal sulcus. Lateral lobes subrectangular, densely granular, lateral margins converging anteriorly. Disk less granular with 2(1+1) smooth rounded plates. Mesonotum separated from metanotum by a distinct transversal groove which is projected backwards medially.

Metanotum shorter medially, but longer laterally than mesonotum, length/width 0,32/2,30, lateral lobes thickened but not produced and densely granular, lateral margins straight, converging anteriorly. Posterior margin delimited by a bisinuate sulcus which separates metanotum from MTg 1. Median subrectangular elevation with a longitudinal sulcus, surface roughly granular. Disk comprising 2(1+1) rounded plates laterad of median elevation, its surface smooth anteriorly and roughly granulate on posterior 2/3.

MTg 1 forming an elevated bisinuate transversal ridge with a shallow median groove, separated from MTg 2 by a deep groove. MTg 2 depressed with a median groove and 2(1+1) short ridges flanking the groove and 2(1+1) longitudinal ridges on posterolateral angles.

Abdomen: Tergal plate formed by fused MTg 3 to 6 with convex lateral margins, glabrous impressions deep, surface granular, the submedian ones separated by Y-shaped carinae; feebly elevated along median line. DELTg 1 to 3 fused and converging anteriorly, DELTg 4 to 7 subrectangular, 7 angularly produced posteriorly. Posteroexterior angles of all segments marked by small rounded lobes which increase in size posteriorly and represent the reflexed ventral laterotergites. Surface rugose.

MTg 7 in male raised medially with 2(1+1) prominent tubercles anterolaterally. Pygophore pyriform with rugose surface, dorsally with a cleft ridge which forms a pit with carinate borders posteriorly. (Figs 167-168). Parameres as Figs 163-166. paratergites 8 slender reaching apex of pygophore.

MTg 7 in female only slightly elevated, smooth anteriorly, with a transverse carina before posterior margin. Paratergites 8 projecting as conical lobes with acute apices, reaching apex of trilobate tergite 9.

Ventral side. Pro-, meso- and metasternum flattened at middle, separated by sulci. Sternites 1 to 2 fused. Spiracles 2 ventral, far from lateral margin, 3 and 4 ventral and close to margin, 5 to 7 lateral and visible from above, 8 subterminal.

Legs: Slender with long erect hairs, trochanters fused. Claws with bristle-like parempodia and long pseudopulvilli.

Chromosome number: 2n(♂) = 28XY.

Measurements: length of holotype ♂ 5,25; width of abdomen across tergite 4 2,50; female similar to male but larger, length 5,5 to 6,7 mm, male paratypes vary in size from 4,3 to 5,3 mm.

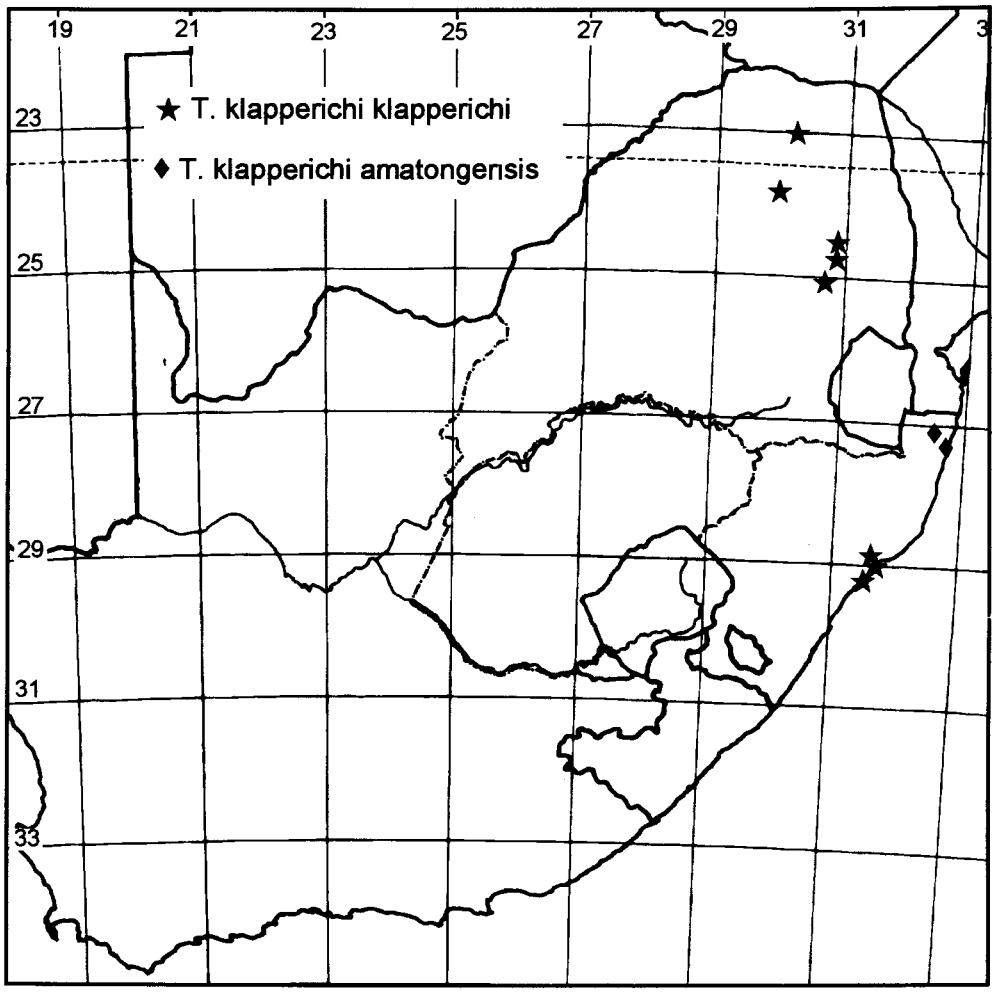


Figure 158. Distribution of the subspecies of *Trichocarventus klapperichi* Heiss & Jacobs.

MATERIAL EXAMINED: **SOUTH AFRICA. Kwazulu-Natal**. ♂ holotype: Natal, Ngoye Forest Reserve, nr. Mtunzini, 28°50′S, 31°43′E, viii.1985 (BMNH); paratypes: 2♂♂ 2♀♀: collected with holotype (EHIA); 2♂♂ 1♀: Natal, St. Lucia, 25.x.1980, leg. Klapperich (EHIA); **Northern Province**. 19♂♂ 37♀♀: Transvaal, Hanglip Forest, Louis Trichardt, 23°00′S, 30°16′E, 7-9.v.1978, D.H. Jacobs (DHJS); 1♂ 2♀♀: Transvaal, Woodbush Forest, 23°50′S 30°00′E, 9.v.1978, D.H. Jacobs (DHJS); 6♂♂ 14♀♀: Transvaal, Magoebaskloof, nr. Tzaneen, 23°52′S 30°00′E, 9.xi.1980, D.H. Jacobs (DHJS); **Mpumalanga**. 17♂♂ 17♀♀: Transvaal, Mariepskop Forest, nr. Hoedspruit, 24°33′S 30°54′E, 6.x.1981, Liebenberg & Jacobs (DHJS); 2♂♂ 2♀♀: Transvaal, Mariepskop Forest ZA.8, viii.1960, humus, no collector given (TMSA); 6♂♂ 2♀♀: Transvaal, Blyderivierspoort Nature Reserve, 24°39′S 30°54′E, 28-30.i.1989, D.H. Jacobs (DHJS); 1♂ 2♀♀: Transvaal, Welgevonden Forest, nr. Hoedspruit, 24°43′S 30°56′E, 8.x.1981, Liebenberg & Jacobs (DHJS); 3♂♂: Transvaal, Mac-Mac Falls, nr. Sabie, x.1983, C.H. Scholtz (DHJS); 1♂: Transvaal, Bridal Veil Falls, nr. Sabie, 25°05′S 30°44′E, 5.xi.1988, D.H. Jacobs (DHJS); **Kwazulu-Natal**. 17♂♂ 14♀♀: Natal, Ngoye Forest, nr. Empangeni, 28°50′S 31°43′E, ll-12.xii.1980, D.H. Jacobs (DHJS); 3♂♂ 2♀♀: Natal, Umlalazi Nature

Reserve, nr. Mtunzini, 28°58′S 31°46′E, 21-23.viii.1985, D.H. Jacobs (DHJS); 1♀: Tugela River mouth, 29°14′S 31°39′E, 7.iv.1980, D.H. Jacobs (DHJS).

Table 7.1. Measurements (in mm) of *Trichocarventus klapperichi amatongensis* subspec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	N♦	Mean	SD	Range	AT#	N♦	Mean	SD	Range$
Total	length	4.91	7	4.87	0.168	4.64-5.19	5.76	10	5.79	0.241	5.39-6.15
	width	2.17	7	2.21	0.045	2.16-2.29	2.64	10	2.71	0.068	2.60-2.84
Head	length	0.85	7	0.88	0.016	0.84-0.91	0.99	10	0.98	0.036	0.93-1.03
	width	0.99	7	1.01	0.017	0.98-1.04	1.08	10	1.08	0.041	1.03-1.14
Pronotum	length	0.50	7	0.50	0.015	0.47-0.53	0.56	10	0.57	0.031	0.50-0.63
	width	1.70	7	1.72	0.042	1.67-1.79	1.92	10	1.90	0.086	1.77-2.02
Tergal disk	length	1.33	7	1.34	0.035	1.31-1.42	1.79	10	1.81	0.087	1.69-1.96
	width	1.44	7	1.46	0.035	1.42-1.52	1.83	10	1.83	0.092	1.71-1.99
Antennal segments	I	0.39	7	0.41	0.009	0.39-0.42	0.44	10	0.44	0.019	0.41-0.47
	II	0.27	7	0.27	0.010	0.26-0.29	0.27	10	0.28	0.011	0.26-0.31
	III	0.43	7	0.41	0.016	0.38-0.44	0.46	10	0.46	0.025	0.40-0.49
	IV	0.30	7	0.31	0.009	0.29-0.33	0.34	10	0.33	0.019	0.28-0.35

* HT = holotype. # AT = allotype.
♦ 2♂♂ 3♀♀ from Sileza forest, 5♂♂ 4♀♀ from Sibayi Lake and 3♀♀ from Manzengwenya.

7.1.2 *Trichocarventus klapperichi amatongensis* subspec. nov., Figs 169-176.

Length: ♂ 4,6 - 5,2 mm; ♀ 5,3 - 6,2 mm.

Width: ♂ 2,1 - 2,3 mm; ♀ 2,6 - 2,9 mm.

Diagnostic measurements are given in Table 7.1.

This subspecies is extremely similar to the nominate subspecies except for its different chromosome number of 2n(♂) = 24XY. On the average it is smaller and its third antennal segment is relatively shorter. This is not true for all specimens and, for example, specimens of the nominate subspecies from Umlalazi Nature Reserve seem to be smaller or subequal in size to *T. klapperichi amatongensis*. Although the third antennal segment of *amatongensis* is relatively shorter than that of the nominate subspecies, it is quite variable and individual exceptions occur frequently.

T. klapperichi amatongensis has so far only been collected in a limited area in the coastal forests of Zululand (northern Kwazulu-Natal) and it is likely that it has a very limited distribution in contrast to the nominate subspecies (Fig. 158).

Etymology: From Amatonga, an old name for the area where the subspecies occurs.

MATERIAL EXAMINED: **SOUTH AFRICA, Kwazulu-Natal.** ♂ holotype: Sileza forest, nr. Manzengwenya, 27°05′S 32°36′E, 7.xii.1980, Jacobs, Kündig & Filter (TMSA); ♀ allotype: ditto (TMSA); paratypes as follows: 3♂♂ 5♀♀: Same data as holotype (DHJS, TMSA); 1♂ 5♀♀:

Manzengwenya, Kwazulu, 27°16′S 32°46′E, 3-7.xii.1980, D.H. Jacobs (DHJS, TMSA); 5♂♂ 4♀♀: Lake Sibayi, Natal, 27°19′S 32°45′E, 21.vii.1977, D.H. Jacobs (DHJS, TMSA).

7.2 Cytogenetics of the genus Trichocarventus

The locality and number of individuals of *Trichocarventus klapperichi*, the only species in the genus, that were cytogenetically studied are presented in Table 7.2. The course of meioses is of the regular Carventid type.

Table 7.2. Locality and numbers of individuals of *Trichocarventus* taxa cytogenetically studied.

Locality	Co-ordinates	Date collected	No. of individuals cytogenetically studied
Trichocarventus klapperichi klapperichi			
Entabeni forest, nr. Louis Trichardt	23°00′S 30°16′E	7-9/xii/1978	2
Magoebaskloof, nr. Tzaneen	23°52′S 30°00′E	9/xi/1980	5
Mariepskop forest, nr. Hoedspruit	24°33′S 30°54′E	4-8/x/1981	11
Welgevonden forest, nr. Hoedspruit	24°43′S 30°56′E	8/x/1981	4
Ngoye forest, nr. Empangeni	28°50′S 31°43′E	11-12/xii/1980	5
Umlalazi Nature Reserve, nr. Mtunzini	28°58′S 31°46′E	21-23/viii/1985	2
Tugela River mouth	29°14′S 31°39′E	7/iv/1980	1
Trichocarventus klapperichi amatongiensis			
Sileza forest, nr. Manzengwenya	27°05′S 32°36′E	7/xii/1980	4
Manzengwenya, Kwazulu	27°16′S 32°46′E	3-7/xii/1980	2
Sibayi Lake, Kwazulu	27°19′S 32°45′E	21/vii/1977	4

7.2.1 *Trichocarventus klapperichi klapperichi* (Figs 159, 177-179).

The chromosome number of the nominate subspecies is 2n(♂) = 28XY. The true and relative chromosome areas for *T. klapperichi klapperichi* of different localities are presented in Table 7.3 and an idiogram in Fig. 159. Autosomes A1-A12 form a more or less gradual series although a slight step in the series seems to be present between A1 and A2 and a more pronounce one between A11 and A12. Autosomes A12 and A13 thus seem to be distinctly smaller than the rest of the complement. The sex chromosomes are by far the largest chromosomes in the complement - the X-chromosome is about twice and the Y-chromosome usually more than 1.5x as large as the largest autosome.

Table 7.3. True and relative chromosome areas of *T. klapperichi klapperichi*.

True chromosome areas (μm²) and standard deviation.				
Chromosome	Magoebaskloof	Mariepskop	Ngoye forest	TOTAL
Individuals	3	3	2	8
Cells	9	10	7	26
A1	1.82(±0.13)	2.16(±0.27)	1.70(±0.18)	1.92(±0.28)
A2	1.68(±0.13)	1.91(±0.23)	1.56(±0.12)	1.74(±0.22)
A3	1.58(±0.14)	1.82(±0.18)	1.52(±0.13)	1.66(±0.20)
A4	1.53(±0.14)	1.76(±0.14)	1.47(±0.10)	1.60(±0.18)
A5	1.44(±0.12)	1.66(±0.17)	1.39(±0.10)	1.51(±0.18)
A6	1.41(±0.10)	1.60(±0.14)	1.37(±0.10)	1.47(±0.15)
A7	1.37(±0.10)	1.56(±0.13)	1.33(±0.11)	1.43(±0.15)
A8	1.34(±0.11)	1.51(±0.14)	1.30(±0.10)	1.39(±0.15)
A9	1.30(±0.10)	1.43(±0.12)	1.26(±0.13)	1.34(±0.14)
A10	1.24(±0.12)	1.40(±0.14)	1.17(±0.12)	1.28(±0.16)
A11	1.16(±0.15)	1.34(±0.13)	1.07(±0.12)	1.20(±0.17)
A12	0.97(±0.15)	1.08(±0.10)	0.91(±0.09)	1.00(±0.13)
A13	0.85(±0.11)	0.96(±0.10)	0.81(±0.07)	0.88(±0.11)
X	3.65(±0.25)	4.20(±0.65)	3.85(±0.44)	3.91(±0.53)
Y	3.37(±0.38)	3.24(±0.37)	2.67(±0.25)	3.13(±0.44)
Autosomes	17.70(±1.38)	20.19(±1.78)	16.86(±1.28)	18.43(±2.06)
All chromosomes	24.71(±1.91)	27.63(±2.66)	23.38(±1.82)	25.47(±2.80)
Relative chromosome areas (% of total area of autosomes) and standard deviation.				
A1	10.29(±0.66)	10.71(±0.65)	10.08(±0.55)	10.39(±0.66)
A2	9.52(±0.35)	9.46(±0.50)	9.28(±0.25)	9.43(±0.39)
A3	8.90(±0.39)	9.02(±0.26)	9.02(±0.31)	8.98(±0.31)
A4	8.67(±0.46)	8.74(±0.34)	8.70(±0.24)	8.70(±0.35)
A5	8.14(±0.27)	8.21(±0.32)	8.27(±0.15)	8.20(±0.26)
A6	7.98(±0.24)	7.91(±0.17)	8.11(±0.13)	7.99(±0.20)
A7	7.76(±0.20)	7.72(±0.29)	7.88(±0.12)	7.77(±0.23)
A8	7.54(±0.24)	7.49(±0.23)	7.70(±0.06)	7.57(±0.21)
A9	7.35(±0.20)	7.10(±0.27)	7.46(±0.43)	7.29(±0.33)
A10	7.02(±0.18)	6.92(±0.33)	6.93(±0.32)	6.96(±0.28)
A11	6.54(±0.45)	6.61(±0.28)	6.33(±0.50)	6.51(±0.41)
A12	5.48(±0.66)	5.33(±0.28)	5.39(±0.34)	5.40(±0.45)
A13	4.81(±0.45)	4.78(±0.40)	4.84(±0.44)	4.80(±0.41)
X	20.66(±1.19)	20.78(±1.94)	22.82(±1.57)	21.29(±1.82)
Y	19.03(±1.34)	16.06(±1.12	15.85(±1.21)	17.03(±1.89)

T. klapperichi klapperichi has a very wide and disjunct distribution, including isolated forested areas in the Northern Province, Mpumalanga and Kwazulu-Natal. Although some of the populations have been isolated for very long their karyotypes are extremely similar with only very slight and insignificant differences between them in the autosomes. The differences between the sex chromosomes (especially the Y-chromosome) of the different localities (Table 7.3) are more pronounced, following the general trend in many Heteroptera.

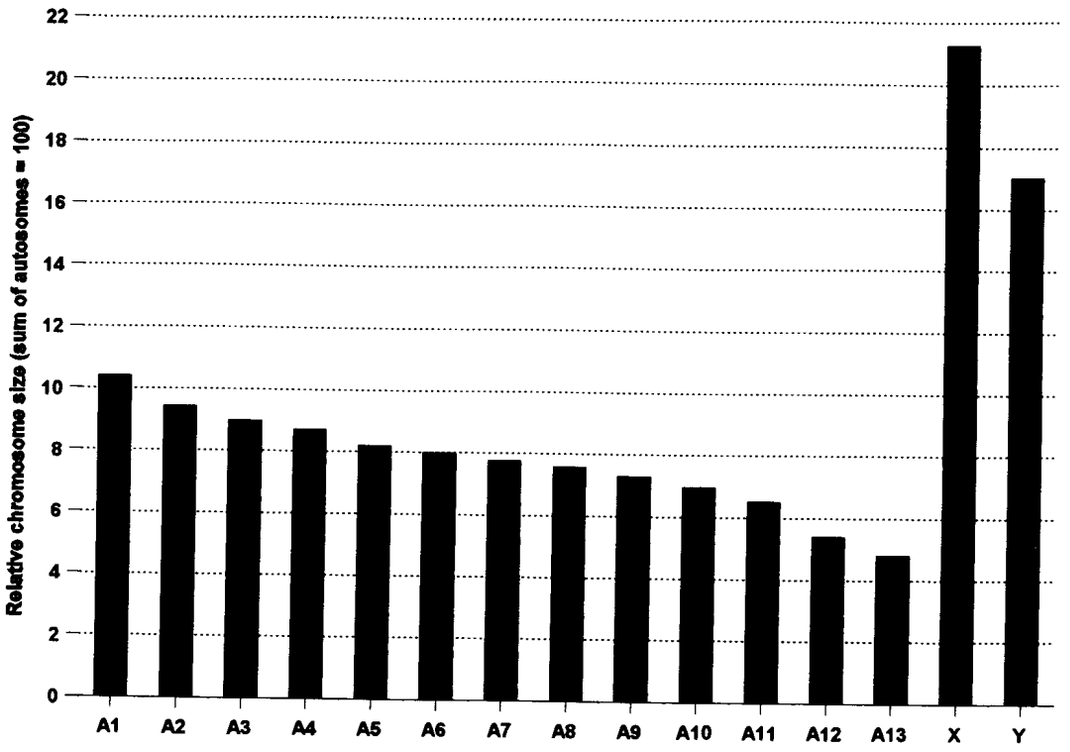


Figure 159. Idiogram of *Trichocarventus klapperichi klapperichi*.

7.2.2 ***Trichocarventus klapperichi amatongensis*** (Figs 160, 180-182).

The chromosome number of this subspecies, which is morphologically indistinguishable from the nominate subspecies, is 2n(♂) = 24XY. The true and relative chromosome areas for *T. klapperichi amatongensis* are presented in Table 7.4 and an idiogram in Fig 160. Two of the autosomes are distinctly larger than the rest. Autosomes A3-A11 form a more or less gradual series but as in the case of the nominate subspecies, the two smallest ones seem to be set apart by a small step in the series. The sex chromosomes are also very large, but because of the presence of the two large autosomes, the X-chromosomes is only subequal in size to the largest autosome while the Y-chromosome is smaller than these two autosomes but somewhat larger than the next one.

Table 7.4. True and relative chromosome areas of *T. klapperichi amatongensis*.

True chromosome areas (µm²) and standard deviation.				Relative chromosome areas (% of total area of autosomes) and standard deviation.		
Chromosome	Sileza forest	Manzengwenya	TOTAL	Sileza forest	Manzengwenya	TOTAL
Individuals	3	1	4	3	1	4
Cells	9	5	14	9	5	14
A1	4.00(±0.29)	2.78(±0.14)	3.56(±0.65)	16.07(±0.89)	15.55(±0.61)	15.88(±0.82)
A2	3.76(±0.32)	2.62(±0.14)	3.35(±0.62)	15.07(±0.75)	14.68(±0.57)	14.93(±0.70)
A3	2.59(±0.18)	1.90(±0.14)	2.34(±0.38)	10.39(±0.48)	10.62(±0.71)	10.47(±0.55)
A4	2.36(±0.21)	1.71(±0.09)	2.13(±0.36)	9.47(±0.54)	9.58(±0.40)	9.51(±0.48)
A5	2.26(±0.19)	1.56(±0.05)	2.01(±0.38)	9.06(±0.65)	8.70(±0.22)	8.93(±0.56)
A6	2.06(±0.19)	1.48(±0.04)	1.85(±0.33)	8.27(±0.51)	8.29(±0.36)	8.28(±0.45)
A7	1.89(±0.17)	1.39(±0.05)	1.71(±0.28)	7.57(±0.30)	7.75(±0.34)	7.64(±0.32)
A8	1.78(±0.16)	1.30(±0.08)	1.61(±0.28)	7.15(±0.36)	7.27(±0.49)	7.19(±0.40)
A9	1.63(±0.17)	1.17(±0.11)	1.47(±0.27)	6.54(±0.40)	6.57(±0.61)	6.55(±0.46)
A10	1.37(±0.13)	1.01(±0.05)	1.24(±0.21)	5.47(±0.27)	5.62(±0.16)	5.52(±0.24)
A11	1.23(±0.10)	0.96(±0.07)	1.13(±0.16)	4.93(±0.27)	5.37(±0.28)	5.09(±0.34)
X	4.35(±0.29)	2.77(±0.18)	3.79(±0.82)	17.48(±0.49)	15.53(±1.10)	16.78(±1.21)
Y	2.98(±0.28)	2.00(±0.13)	2.63(±0.54)	11.94(±0.55)	11.20(±0.75)	11.68(±0.71)
Autosomes	24.92(±1.63)	17.88(±0.49)	22.40(±3.73)			
All chromosomes	32.25(±2.15)	22.65(±0.57)	28.82(±5.07)			

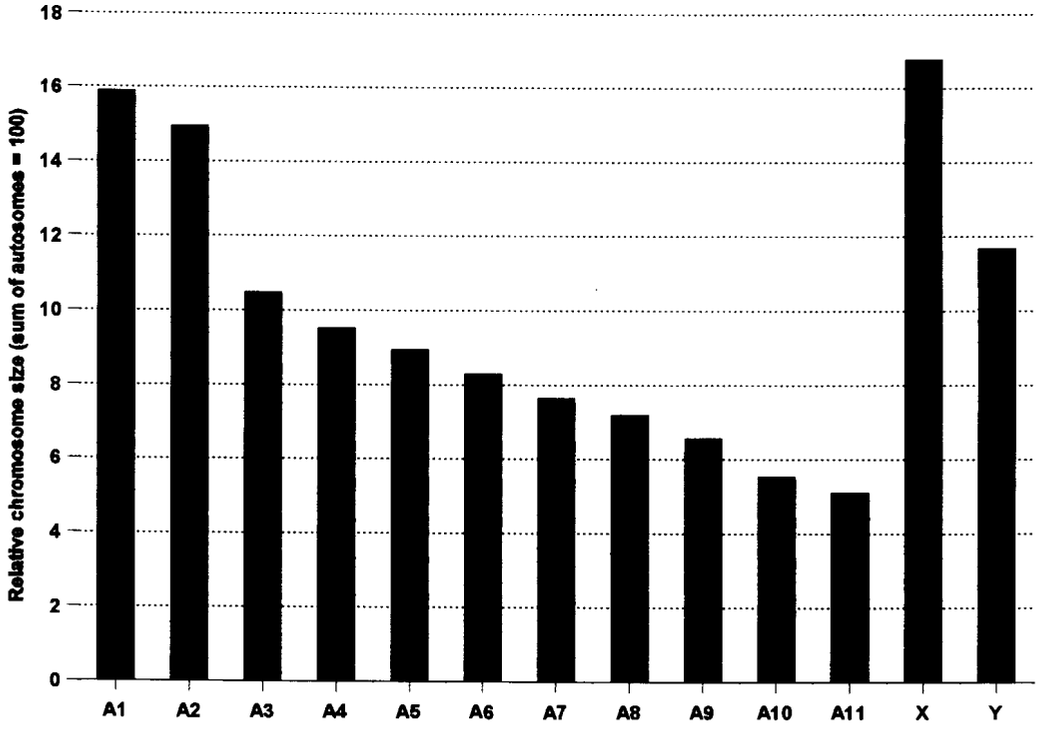
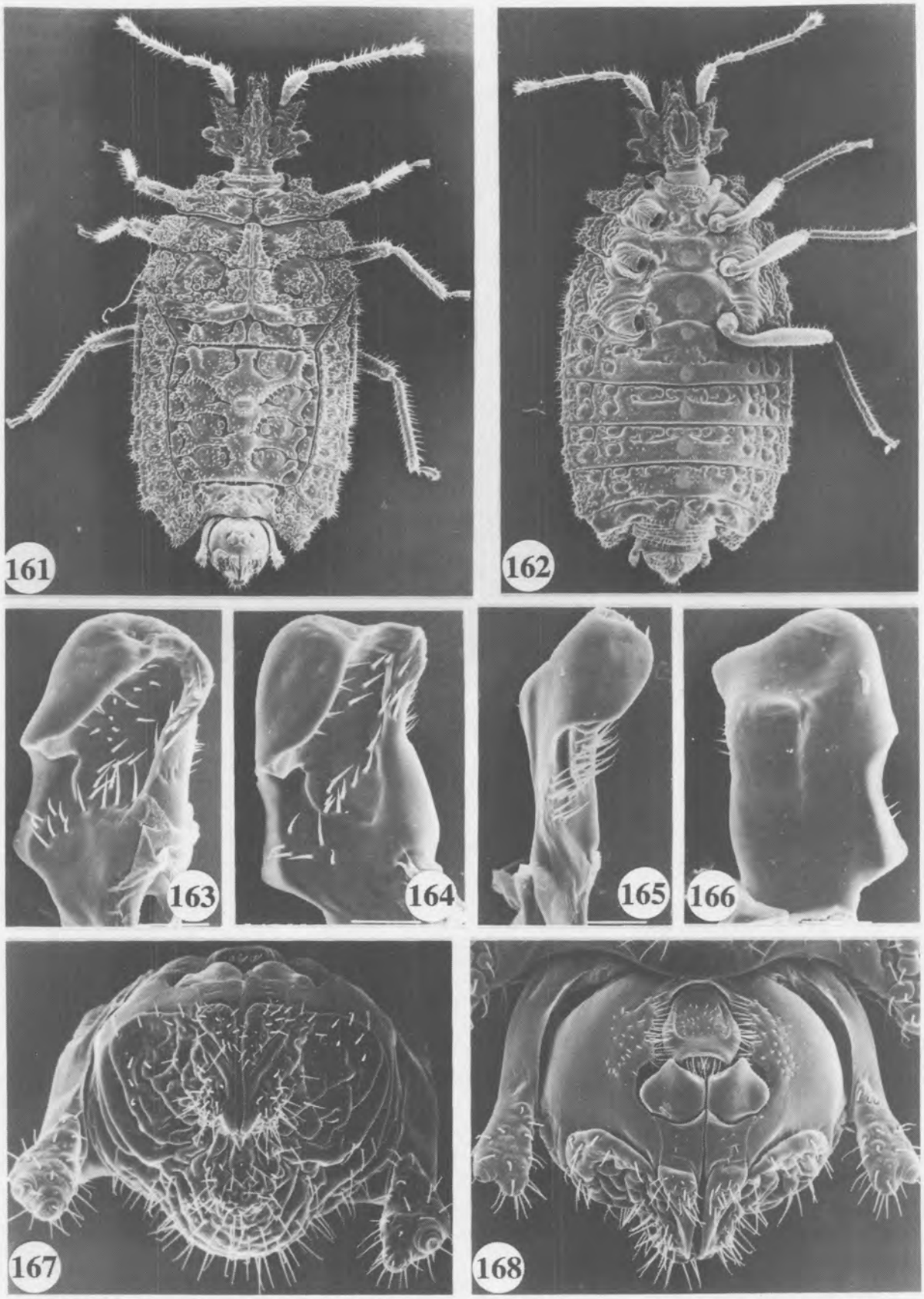


Figure 160. Idiogram of *Trichocarventus klapperichi amatongensis*.

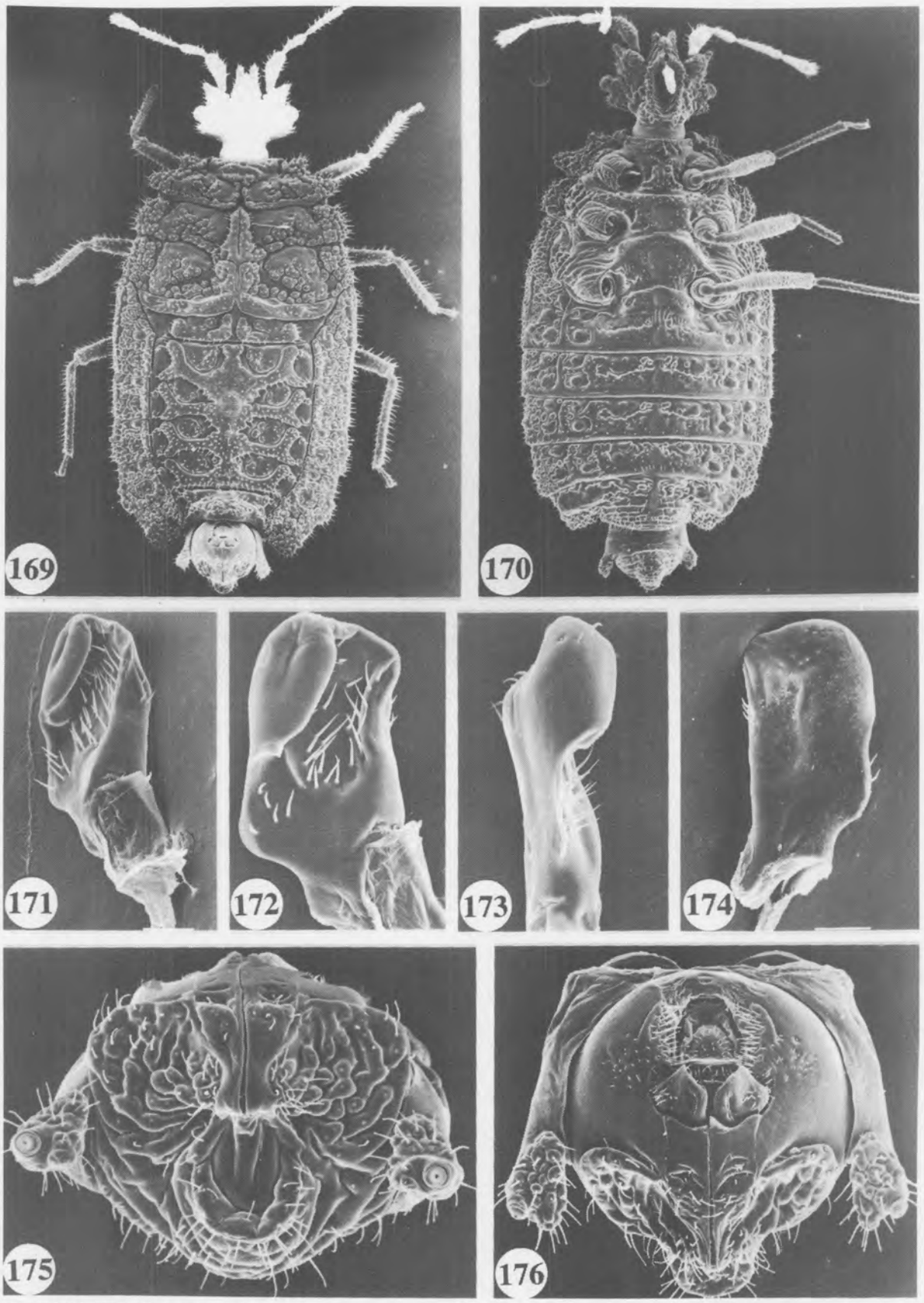
7.2.3 Discussion.

It is obvious that either *T. klapperichi amatongensis* originated from *T. klapperichi klapperichi* by two chromosome fusions or vice versa by two fissions. To my mind, the most likely steps in karyotype evolution from a hypothetical 14XY ancestor for these taxa would have been as follows:

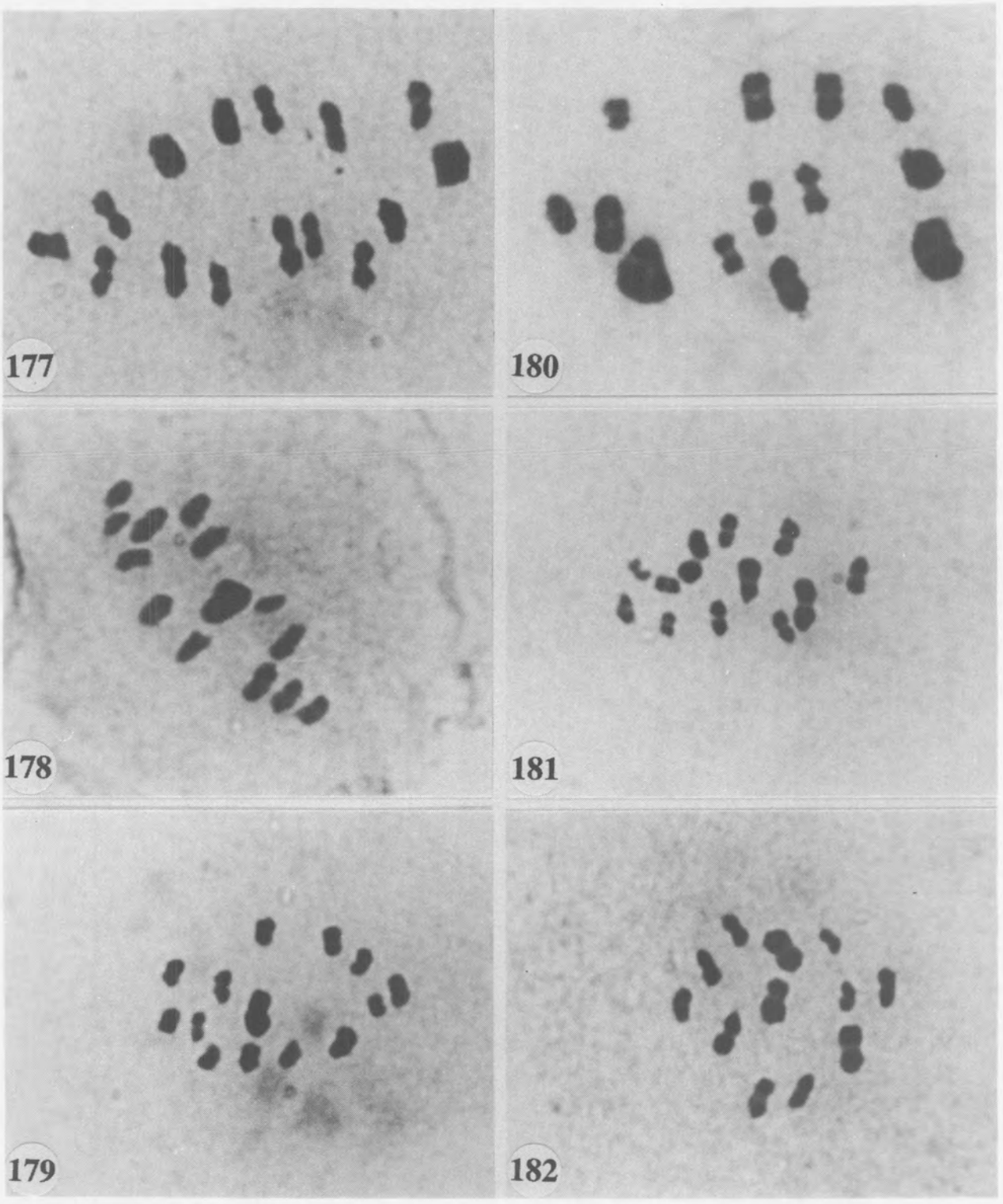
1. Pseudoploidy gave rise to a 26XY karyotype
2. Fission of one of the largest autosome led to the origin of the two smallest autosomes. This led to the 28XY karyotype of *T. klapperichi klapperichi*. The slight step between the largest and second largest autosome and the step setting apart the two smallest chromosomes support this hypothesis.
3. Two fusions, possibly autosomes A4+A8 and A6+A10 of *T. klapperichi klapperichi* led to the 24XY karyotype of *T. klapperichi amatongensis*.



Figs 161-168. Scanning electron photomicrographs of *Trichocarventus klapperichi klapperichi* Heiss & Jacobs. 161-162. Male paratype. 161. Dorsal aspect. 162. Ventral aspect. 163-166. Different aspects of the left paramere (scale bar = 50 μm). 167-168. Pygophore. 167. Caudal aspect. 168. Dorsal aspect.



Figs 169-176. Scanning electron photomicrographs of *Trichocarventus klapperichi amatongaensis* **subspec. nov.** 169-170. Male paratype. 169. Dorsal aspect. 170. Ventral aspect. 171-174. Different aspects of the left paramere (scale bar = 50 μm). 175-176. Pygophore. 175. Caudal aspect. 176. Dorsal aspect.



Figs 177-182. Meiotic stages in *Trichocarventus* taxa. 177-179. *T. klapperichi klapperichi*. 177. Metaphase I. 178-179. Metaphase II. 180-182. *T. klapperichi amatongaensis*. 180. Metaphase I. 181-182. Metaphase II.

Chapter 8

GENUS *MITERONOTUS* GEN. NOV.

8.1 *Miteronotus* gen. nov.

Type species: *Miteronotus labeosus* spec. nov.

Etymology: From greek miteros = pointed and notum = dorsal thoracal plate, referring to the pointed median ridge.

Apterous. Body elongate oval, incrustate, shining and granular beneath incrustation. The following description is based on cleaned individuals.

Head: Wider across eyes than length (excluding neck area). Genae produced beyond apex of clypeus. Subapical dorsal tubercle on clypeus absent. Antenniferous lobes well developed, diverging anteriorly. Ocelli absent. Postocular tubercles present. Antennae 4-segmented, first segment the longest and thickest, extending beyond apex of head, third segment always pedicellate, fourth segment fusiform, usually set on a short pedicel, conical apex pilose. Labium 3-segmented, only apical two segments visible externally, shorter than head, leaving head through a slit-like atrium. Labium not discernable. Rostral groove well developed, closed posteriorly.

Thorax: Dorsum. Pronotum 2-3x as wide as long. Collar very prominent with 2(1+1) large lateral tubercles and 2(1+1) smaller dorsolateral ones. Pronotum constricted behind the collar. Lateral lobes granulate, elevated and slightly reflexed so that propleural margins visible from above in most species. Disk formed by 2(1+1) smooth, shining plates which are medially separated by a deep and wide longitudinal furrow. A slight transverse elevation which may be confluent with the discal plates laterally, is present between the furrow and collar. Pronotum separated from mesonotum by a deep sulcus which is medially interrupted by the apex of the anteriorly produced median ridge of the mesonotum.

Mesonotum wider and shorter than pronotum, comprising 2(1+1) nearly rectangular plates laterally, separated by a median, usually smooth, anteriorly pointing ridge which is posteriorly fused with a broad median elevation of the metanotum. Lateral lobes granulate, slightly reflexed, rendering mesopleural margins usually visible from above. Disk entirely smooth in most species but irregular excavations may occur sublaterally.

Metanotum longer and slightly wider than mesonotum, laterally well delimited from mesonotum by a prominent and deep sulcus which ends in a deep pit adjacent to median ridge. On the median ridge the meso- and metanotum is usually completely fused which no indication of sulcus or line of demarcation. Lateral lobes granulate, slightly elevated and reflexed. Disk smooth to irregularly excavated, separated from the wide median ridge by a wide, fairly shallow groove; posteriorly it rises sharply submedially to form a transverse ridge where it meets MTg 1. Metanotum laterally separated from MTg 1 by a clear sulcus but mediad this sulcus become less prominent, sometimes obliterated; boundary over total distance, however, marked by a bisinuate, lightly coloured, less sclerotized line.

MTg 1 and 2 together forming a transverse trapeziform plate that slopes posteriad. For about its lateral half Mtg 1 forms a narrow transverse bar, widening laterally, well delimited from MTg 2 by a deep sulcus. MTg 1 and 2 are completely fused medially and no line of demarcation is visible but sculpture may in some species give indication of border between them. MTg 2 sublaterally usually with 2(1+1) longitudinal ridges, confluent with sublateral carinae on abdominal tergal disk and medially a longitudinal bar may be present (in most species only discernable on anterior part of MTg 2). A smooth subrectangular or subtriangular area may be present on MTg 2 lateral of the sublateral ridges but it never possesses a deep pit.

Venter. Prosternum somewhat raised medially and this ridge is posteriorly produced laterad at level of procoxae to form 2(1+1) knobs. Collar may be present or absent ventrally of large lateral tubercles. Meso- and metasterna smooth, each with a median oval, finely rastrate , slightly depressed area.

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

Abdomen: Dorsum. Tergal disk (MTg 3-6) usually slightly longer than wide, moderately elevated along median line, highest on MTg 4; lateral margins slightly convex. Carinae which separate glabrous impressions variously developed, usually discernable. Surface between carinae and impressions areolate. DELTg 1-3 fused. Posterior angles of DELTg 2 to 7 increasingly protruding; all DELTg's densely tuberculate except for LGI's. MTg 7 of males raised medially for the reception of the pygophore; paratergites 8 of males short, conical, not reaching apex of pygophore. MTg 7 of females usually with a nodulate transverse ridge near posterior margin; anterior to this 2(1+1) subquadrangular elevations, which may be joined medially to form a single transverse subrectangular elevation, usually 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. Suboval, slightly depressed, finely rastrate areas medially present on sternites 1+2, 3-7. Intersegmental sutures 3/4, 4/5, 5/6 and 6/7 usually well developed, reaching lateral margins of body; 6/7 in females medially produced anteriad to accommodate genitalia. VLTg 3-6 delimited by longitudinal sulci. Spiracle 2 ventral, placed on a prominent tubercle about half the width of the VLTg from lateral margin, position of spiracles 3-5 varies, 6-7 always lateral and visible from above, 8 subterminal on paratergites.

Genitalia: Visible part of pygophore pyriform with a rugose surface, dorsally with 2(1+1) subtriangular elevations separated by a cleft which ends about at level of paratergites 8; ventral of this a short ridge is present. In dorsal view of part usually obscured by MTg 7, 2(1+1) subquadrate pseudophalic styli are present just posterior of the dorsal visible part of the parameres; anteromedially these styli are produced to form 2(1+1) finger-like extensions. Visible parts of parameres usually more or less transverse. Lateral sensory areas each bear a fringe a long hairs mesally and sparse short setae laterally. Female genitalia similar to those of most Carventinae.

Discussion: *Miteronotus* is closely related to *Silvacoris* but can be distinguished by having the meso- and metanotum fused on the median ridge; lacking the sublateral pits on MTg 2; lacking the

caudoventral pit on the male pygophore; having the dorsal visible part of the parameres more or less transversely placed; and by being more elongate and flatter in general facies, resulting in the tergal disk and dorsal laterotergites usually being longer than wide. It can be distinguished from *Dundocoris*, *Trichocarventus* and *Pondocoris* by the unsplit mesonotal median ridge and from *Adamanotus* by its unmodified legs, and metanotum reaching the lateral margin of the body. Four species belonging to *Miteronotus* are known, all from the evergreen coastal and montane forests of Kwazulu-Natal, the Eastern Cape Province and the Western Cape Province.

8.1.1 *Miteronotus labeosus* spec. nov., Figs 188-203, 235-236.

Length ♂ 4,1 - 4,6 mm; ♀ 4,9 - 5,7 mm.

Width ♂ 1,6 - 1,9 mm; ♀ 2,1 - 2,5 mm.

Diagnostic measurements are given in Tables 8.1 and 8.2. Apterous. Body coated with a greyish incrustation resulting that the general appearance of uncleaned specimens is rather uniform darkish grey. The following description is based on specimens with the incrustation removed.

Table 8.1. Measurements (in mm) of *Miteronotus labeosus* spec. nov. from Dhlinza forest.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range	AT#	N	Mean	SD	Range
Total	length	4.41	10	4.36	0.136	4.11-4.58	5.37	10	5.30	0.231	4.95-5.66
	width	1.78	10	1.76	0.062	1.61-1.85	2.34	10	2.33	0.104	2.15-2.50
Head	length	0.80	10	0.80	0.026	0.75-0.87	0.91	10	0.91	0.040	0.84-0.95
	width	0.80	10	0.78	0.025	0.73-0.83	0.86	10	0.87	0.032	0.81-0.93
Pronotum	length	0.49	10	0.51	0.024	0.46-0.57	0.59	10	0.58	0.031	0.53-0.63
	width	1.32	10	1.32	0.037	1.24-1.38	1.54	10	1.55	0.078	1.43-1.65
Tergal disk	length	1.24	10	1.25	0.040	1.15-1.31	1.64	10	1.62	0.094	1.49-1.77
	width	1.22	10	1.21	0.047	1.12-1.27	1.62	10	1.58	0.081	1.42-1.71
Antennal segments	I	0.38	10	0.37	0.017	0.34-0.40	0.40	10	0.42	0.019	0.39-0.46
	II	0.25	10	0.25	0.009	0.24-0.27	0.30	10	0.30	0.010	0.28-0.33
	III	0.28	10	0.29	0.015	0.25-0.30	0.34	10	0.35	0.019	0.31-0.37
	IV	0.25	10	0.25	0.012	0.23-0.27	0.29	10	0.28	0.011	0.25-0.31

* HT = holotype. # AT = allotype.

Head: Marginally longer (not including neck area) than its width across the eyes. Genae straight anteriorly, produced laterad at base at level of antenniferous lobes. Jugae small, triangular. Vertex with three irregularly nodose median ridges, the lateral two curving laterad at level of eyes and encircling the oval interocular callosities, the median ridge continues on clypeus as a row of irregularly spaced tubercles. A prominent subapical tubercle is usually absent. Antennae 1,48-1,68 times as long as width across eyes, first segment thickest and longest, slightly curved, and tapering toward base, extending beyond apex of genae by just more than half its length; second segment slightly curved basally, gradually thickened towards apex; third segment thinnest, straight, thickening slightly and

evenly towards apex, pedicellate; fourth segment fusiform, with short pedicel, conical apex pilose; relative lengths of segments 15:10,5:11,7:10 (differing slightly between population as well as between sexes). Elevated rim of rostral groove granulate, very wide and prominent especially at level of the slit-like atrium. Neck slightly constricted just behind head.

Table 8.2. Measurements (in mm) of *Miteronotus labeosus* spec. nov. from Karkloof forest.

STRUCTURE		MALES				FEMALES			
		N	Mean	SD	Range	N	Mean	SD	Range
Total	length	10	4.21	0.077	4.06-4.29	10	5.44	0.165	5.01-5.67
	width	10	1.63	0.045	1.54-1.70	10	2.40	0.070	2.08-2.61
Head	length	10	0.78	0.015	0.75-0.82	10	0.92	0.028	0.84-0.98
	width	10	0.75	0.010	0.73-0.77	10	0.84	0.015	0.80-0.88
Pronotum	length	10	0.49	0.029	0.43-0.55	10	0.58	0.020	0.53-0.64
	width	10	1.21	0.025	1.17-1.27	10	1.50	0.051	1.29-1.58
Tergal disk	length	10	1.23	0.021	1.19-1.28	10	1.72	0.049	1.58-1.80
	width	10	1.10	0.036	1.02-1.15	10	1.59	0.056	1.44-1.70
Antennal segments	I	10	0.39	0.013	0.37-0.41	10	0.44	0.013	0.41-0.48
	II	10	0.27	0.009	0.24-0.28	10	0.32	0.010	0.30-0.34
	III	10	0.29	0.010	0.27-0.31	10	0.35	0.011	0.33-0.37
	IV	10	0.26	0.008	0.24-0.28	10	0.30	0.008	0.28-0.31

Thorax: Dorsum. Pronotum about 2,55x as wide as long. Lateral lobes granulate with lateral margins converging anteriad, produced anteriad to level of anterior margin of collar. Disk smooth and shining but with somewhat uneven surface.

Mesonotal disk smooth and shining but usually with some irregular excavations; separated from median ridge by prominent furrows. Median ridge in males narrow anteriorly, widening strongly at level of posterior margin of the lateral lobes, in females wider and widening more evenly posteriad; in both sexes surface smooth and no longitudinal median suture or any sign of a median split is present.

Metanotal disk shining but irregularly excavated, delimited from wide median ridge by a shallow longitudinal depression. Median ridge with a shallow median longitudinal furrow in some populations; a transverse suture (usually incomplete) may also indicate its border with the mesonotal median ridge but often this is absent and the fusion complete (see discussion).

MTg 1 narrow, widening laterally, curving and tapering anterolaterally in an acute point that does not reach lateral margin of body. MTg 2 with sublateral longitudinal ridges prominent in females, less so in males; median longitudinal bar usually only discernable on anterior half of MTg 2 but often reaching posterior margin in males.

Venter. Collar complete.

Legs: As for genus.

Abdomen: Dorsum. Tergal disk 1,02-1,11 times longer than wide, moderately elevated along median line. Carinae which separate glabrous impressions clearly discernable but not prominent. Surface between carinae and impressions areolate, especially along margins of carinae.

Venter. Intersegmental suture 6/7 in males of the Karkloof population obliterate sublaterally for a short distance where sternites 6 and 7 are fused, complete in the other populations. Spiracle 2 ventral; 3 sublateral; placed about a spiracle width from lateral margin; 4 sublateral slightly less than a spiracle width from margin; 5-7 lateral and visible from above, 7 hardly visible from below, 8 subterminal on paratergite.

Genitalia: Pygophore (Figs 200-203) as for genus. Visible dorsal part of paramere (Figs 201, 203) sinuately transverse, being laterally sharply curved anteriad in the Ngoye population (Fig. 203). Removed parameres as in Figs 192-199.

Chromosome number: 2n(♂) = 26XY.

Habitat and distribution: Montane evergreen forests in Kwazulu-Natal. It has not yet been collected in the coastal forests. Their known distribution is shown in Fig. 183.

Etymology: Labeosus (L) = thick-lipped, referring to the prominent rim of the rostral groove.

Discussion: *Miteronotus labeosus* can be distinguished from the other known species of *Miteronotus* by its spiracle pattern, its first antennal segment extending beyond the apex of the genae by just more than half its length, by its chromosome number and, in most of the populations, by the prominent thickened rim of the rostral groove lateral to the position where the rostrum is attached to the head. Of the known species of *Miteronotus,* it is probably closest to *Miteronotus viginti* from which it can easily be distinguished by having spiracle 5 laterally placed and clearly visible from above, by its more prominent median thoracic ridge, by having antennal segment 2 longer than 4, and by its different chromosome number. Some remarkable and constant differences exist between the populations of different areas but I am not convinced that these justify subspecific status. The known populations of *Miteronotus labeosus* can be divided into three groups, corresponding to specific areas, which can readily be distinguished from each other, namely

1) the Ngoye populations occurring in Ngoye forest and Dhlinsa forest (type locality).
2) the Karkloof populations from Town Bush near Pietermaritzburg and Karkloof.
3) the Nkandla population from Nkandla forest.

The Karkloof populations are characterized by having the posteroexternal angles of DELTg 5, 6 and especially 7 much more produced than in the other populations (Fig. 189) (it is actually the VTLg's that are produced so that the suture between the DELTg and VLTg runs dorsally). These protrusions are present in both sexes although much more prominent in the males. In the males sternites 6 and 7 are fused sublaterally for a short distance in the region of the sublateral sulcus (Figs 235-236).

Other differences include the antenniferous spines that are usually more strongly developed in the Karkloof and Nkandla populations, resulting in the distance between the anterior margin of the eye and the anterolateral apex of the spine being markedly longer than the longitudinal diameter of the eye. In the Ngoye populations the antenniferous spine is weakly developed, often indistinguishable and the distance between the eye and the apex of the spine on the antenniferous lobe is usually only slightly longer than the longitudinal diameter of the eye.

The Nkandla population differs from the other by being larger and more slender (e.g. the tergal disk is about 1,13 times as long as wide), by a narrow median ridge and by having the rim of the rostral groove not as prominent as in the other populations.

The metanotal media[illegible] between individual populations. In the Shaws Wood farm population at Karkloof it is completely fused with the mesonotal ridge without any indication of a suture and there is also no indication of a median longitudinal furrow (Fig. 189) while some remnants of the intersegmental suture remain in all the other populations (very prominent in the Nkandla population) and a shallow median longitudinal furrow is present at least on the posterior half of the ridge (e.g. Figs 188, 191).

MATERIAL EXAMINED: **SOUTH AFRICA, Kwazulu-Natal.** ♂ holotype: Dhlinsa forest, Eshowe, 28°54′S 31°27′E, 12.iv.1980, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 217 paratypes as follows: 23♂♂ 8♀♀: Ngoye Forest Reserve, nr Empangeni, 28°50′S 31°43′E, 11-12.xii.1980, D.H. Jacobs (DHJS); 41♂♂ 41♀♀: Same data as holotype (DHJS, TMSA); 2♀♀: Nkandla forest, 28°44′S 31°08′E, 12.iv.1980, D.H. Jacobs (DHJS); 34♂♂ 38♀♀: Shaws Wood farm, Karkloof, 29°19′S 30°18′E, 1.ii.1983, D.H. Jacobs (DHJS); 13♂♂ 17♀♀: Town Bush, Pietermaritzburg, 29°33′S 30°20′E, 31.i.1983, D.H. Jacobs (DHJS).

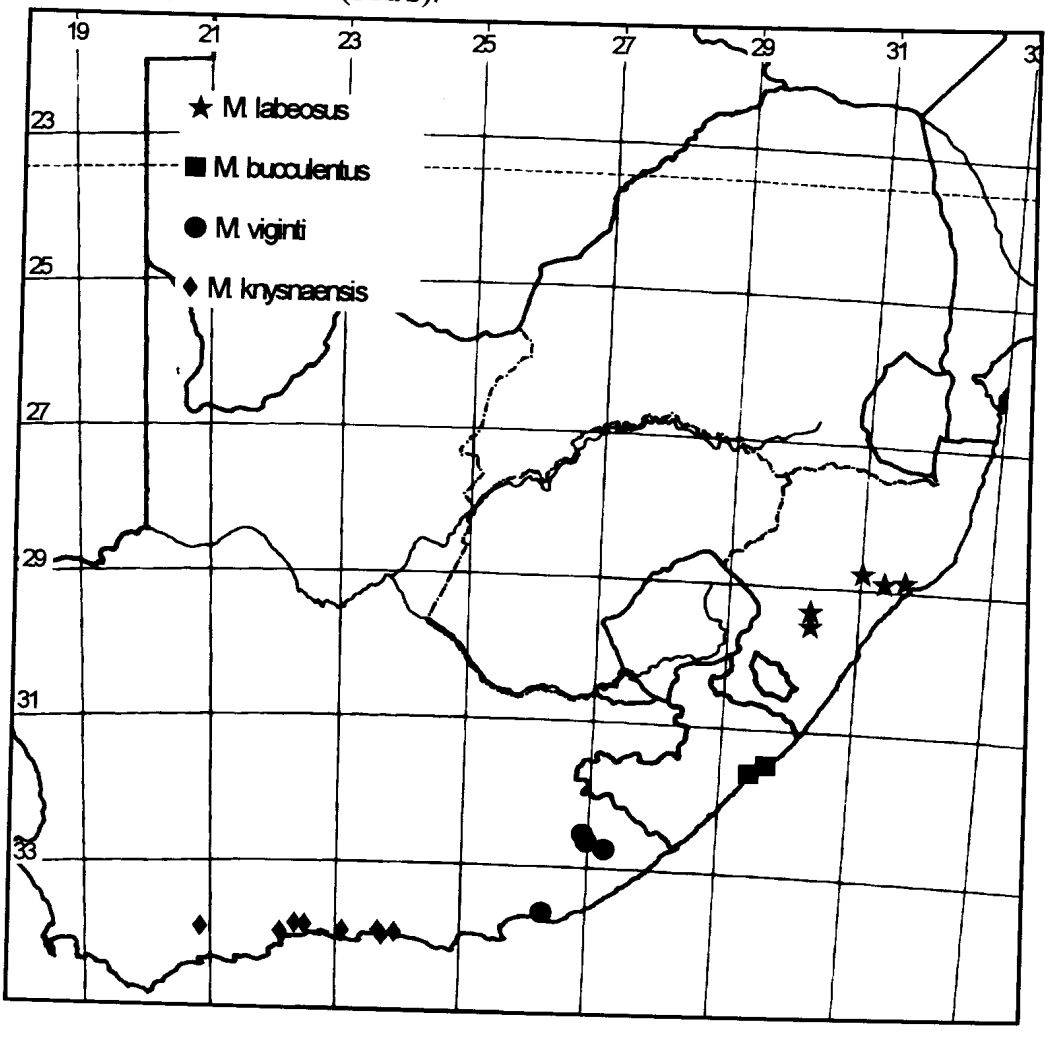


Figure 183. Distribution of *Miteronotus* species.

8.1.2 *Miteronotus viginti* spec. nov., Figs 204-211.

Length ♂ 3,82 - 4,66 mm; ♀ 4,50 - 5,27 mm.

Width ♂ 1,72 - 2,07 mm; ♀ 1,97 - 2,62 mm.

Diagnostic measurements are given in table 8.3.

Apterous, Body coated with a greyish incrustation, resulting in a general darkish appearance of uncleaned specimens. The following description is based on specimens with the incrustation removed

Head: Marginally longer (not including neck area) than its width across the eyes. Genae straight or slightly diverging anteriorly. Jugae small, triangular. Ridges on vertex as for previous species but subapical tubercle more prominent. Antennae 1,32-1,44 times as long as width across eyes, first segment thickest and longest, slightly curved and tapering towards base, extending beyond apex of genae by less than half of its length; second segment slightly curved basally, gradually thickening towards apex; third segment thinnest, straight, thickening slightly and evenly towards apex, pedicellate; fourth segment fusiform, sessile or with short pedicel, conical apex pilose; relative lengths of segments 15:10:13:11 (differing slightly between populations and sexes). Postocular tubercles prominent, often extending beyond level of outer margins of the eyes. Neck slightly constricted just behind the head.

Thorax: Dorsum. Pronotum 2,92-3,38 times as wide as long. Lateral lobes prominent, elevated, well delimited from disk, coarsely granulate; lateral margins straight or concave, converging anteriad; usually produced anteriad beyond level of collar. Disk smooth and shining with a somewhat uneven surface.

Mesonotal disk smooth and shining, usually with some irregular excavations posteriorly; disk separated from median ridge by prominent furrows. Median ridge in both sexes fairly narrow, at the most only slightly widening posteriad; surface smooth and no longitudinal suture or any sign of a median split discernable.

Metanotal disk smooth and shining anteriorly, usually exsculptate posteriorly, delimited from a rather narrow median ridge by a shallow longitudinal depression. Median ridge without a median longitudinal furrow, either completely fused and continuous with mesonotal ridge (e.g. Fig. 205) or delimited by a transverse (usually incomplete) suture (e.g. Fig 204).

MTg 1 narrow, widening laterally, slightly curving and tapering anterolaterally to end in an acute point that does not reach the lateral margin of the body. Laterally the sulcus between MTg 1 and MTg 2 is usually very narrow becoming much wider sublaterally before it completely disappear where they become fused. This results in 2(1+1) sublateral transverse elongate deep depressions on MTg 1+2. MTg 2 with 2(1+1) well developed sublateral ridges (just behind the above mentioned depressions) and usually a median bar, only visible on anterior part but sometimes not discernable.

Venter. Collar absent ventral of lateral tubercles or at most visible as a very narrow rim.

Legs: Trochanters not discernable.

Abdomen: Dorsum. Posteroexterior angles of only DELTg 6 and 7 moderately produced. Tergal disk 1,05-1,21 times as long as wide, only slightly elevated along median line. Carinae which separate glabrous impressions discernable but not prominent. Surface between carinae and impressions somewhat areolate especially along the margins of the carinae (however less than in previous species).

Table 8.3. Measurements (in mm) of *Miieronotus viginti* spec. nov.

	STRUCTURE		ISIDENGE FOREST				ALEXANDRIA FOREST				TOTAL			
			HT'	N	Mean	SD	Range‡	N	Mean	SD	Range‡	N	Mean	SD	Range®
MALES	Total	length	4.50	10	4.45	0.124	4.23-4.66	10	3.98	0.102	3.82-4.15	20	4.22	0.266	3.82-4.66
		width	2.00	10	1.97	0.082	1.82-2.07	10	1.87	0.060	1.76-1.96	20	1.92	0.087	1.72-2.07
	Head	length	0.85	10	0.84	0.022	0.79-0.87	10	0.78	0.024	0.74-0.82	20	0.81	0.040	0.74-0.87
		width	0.82	10	0.83	0.029	0.77-0.87	10	0.77	0.022	0.74-0.82	20	0.80	0.036	0.74-0.87
	Pronotum	length	0.50	10	0.47	0.025	0.42-0.52	10	0.39	0.020	0.35-0.43	20	0.43	0.044	0.35-0.52
		width	1.43	10	1.38	0.059	1.30-1.49	10	1.32	0.032	1.26-1.37	20	1.35	0.053	1.22-1.49
	Tergal disk	length	1.41	10	1.42	0.048	1.34-1.51	10	1.26	0.037	1.18-1.31	20	1.34	0.092	1.26-1.51
		width	1.24	10	1.22	0.057	1.10-1.30	10	1.20	0.038	1.10-1.25	20	1.21	0.048	1.10-1.30
	Antennal segments	I	0.35	10	0.36	0.015	0.34-0.39	10	0.32	0.011	0.29-0.34	20	0.34	0.026	0.29-0.35
		II	0.23	10	0.24	0.013	0.23-0.27	10	0.20	0.012	0.18-0.23	20	0.22	0.024	0.18-0.27
		III	0.30	10	0.30	0.020	0.26-0.33	10	0.27	0.010	0.25-0.28	20	0.28	0.022	0.25-0.33
		IV	0.25	10	0.26	0.010	0.24-0.28	10	0.23	0.009	0.21-0.25	20	0.25	0.018	0.21-0.28
			AT"	N	Mean	SD	Range‡	N	Mean	SD	Range‡	N	Mean	SD	Range®
FEMALES	Total	length	5.34	10	5.26	0.249	4.64-5.58	10	4.96	0.117	4.75-5.17	20	5.11	0.117	4.50-5.27
		width	2.46	10	2.42	0.156	2.05-2.62	10	2.33	0.090	2.13-2.45	20	2.37	0.132	1.97-2.62
	Head	length	0.92	10	0.93	0.038	0.83-0.99	10	0.88	0.014	0.85-0.91	20	0.90	0.038	0.83-0.99
		width	0.91	10	0.90	0.031	0.83-0.94	10	0.85	0.009	0.83-0.88	20	0.88	0.032	0.77-0.94
	Pronotum	length	0.54	10	0.54	0.048	0.41-0.59	10	0.47	0.017	0.43-0.51	20	0.50	0.051	0.41-0.59
		width	1.60	10	1.58	0.081	1.38-1.67	10	1.53	0.041	1.47-1.60	20	1.55	0.067	1.35-1.67
	Tergal disk	length	1.81	10	1.79	0.113	1.51-1.90	10	1.62	0.056	1.50-1.69	20	1.70	0.122	1.49-1.90
		width	1.48	10	1.48	0.100	1.25-1.60	10	1.46	0.049	1.37-1.56	20	1.47	0.078	1.23-1.60
	Antennal segments	I	0.40	10	0.39	0.014	0.36-0.42	10	0.35	0.009	0.33-0.37	20	0.37	0.024	0.33-0.42
		II	0.27	10	0.28	0.013	0.25-0.30	10	0.23	0.010	0.21-0.26	20	0.26	0.027	0.21-0.30
		III	0.35	10	0.34	0.024	0.28-0.38	10	0.31	0.014	0.28-0.34	20	0.33	0.027	0.28-0.38
		IV	0.29	10	0.29	0.008	0.27-0.31	10	0.26	0.010	0.23-0.28	20	0.27	0.020	0.23-0.31

' HT = holotype. " AT = allotype.
‡ May include measurements of specimens other than those used for statistical analysis.
® May include measurements of specimens from other localities.

Posterior nodulate transverse ridge on MTg 7 of females well developed with 2(1+1) prominent sublateral transverse elevations anterior to it.

Venter. Intersegmental suture 6/7 in males of most populations studied (not in the Alexandria population) obliterate for a short distance sublaterally (just mesally of the sublateral suture) where sternites 6 and 7 are fused. Spiracle 2 ventral; 3 & 4 sublateral, placed more than 1½ spiracle widths

from margin; 5 sublateral, less than a spiracle width from margin; 6 & 7 lateral and visible from above; 8 subterminal on paratergites.

Genitalia: Pygophore (Figs 210-211) as for genus. Dorsal visible part of parameres (Fig. 211) sinuately transverse, similar to that of previous species. Removed parameres as in Figs 206-209.

Chromosome number: 2n(♂) = 20XY.

Habitat and distribution: Montane and coastal evergreen forests of the Eastern Cape (Fig. 183).

Etymology: Viginti (L) = twenty referring to its chromosome number.

Discussion: *Miteronotus viginti* is characterized by having the notal median ridge thin and smooth without a median split or suture. It differs from *Miteronotus labeosus, M. bucculentus* and *M. knysnaensis* as discussed under those species.

As in *Miteronotus labeosus,* much variation exists between different populations. Especially the Alexandria forest population seems to differ quite markedly from the other populations, but these differences do not justify subspecific status. Specimens from Alexandria forest are generally smaller and less elongate resulting, inter alia, in the tergal disk being approximately 1,1 times as long as wide (1,2 times in other populations) and the pronotum being relatively wider. They also have the first antennal segment more slender and males lack the fusion of sternites 6 and 7.

MATERIAL EXAMINED: **SOUTH AFRICA, Eastern Cape**. ♂ holotype: Isidenge forest, nr. Stutterheim, 32°41′S 27°17′E, 14-17.xii.1981, D H Jacobs (TMSA); ♀ allotype: ditto (TMSA); 254 paratypes as follows: 28♂♂ 25♀♀: Aucland Forest Reserve, Hogsback, 32°36′S 26°56′E, 16.xii.1981, D.H. Jacobs (DHJS); 10♂♂ 23♀♀: Schwarzwald forest, nr. Hogsback, 32°39′S 27°00′E, 16.xii.1981, D.H. Jacobs (DHJS); 45♂♂ 62♀♀: Same data as holotype (DHJS, TMSA); 2♂♂ 4♀♀: ditto, 2.ii.1984 (DHJS); 3♀♀: S. Afr., Cape, Amatole, Isidenge Forest St., 32°41′S 27°15′E, 16.xi.1987, E-Y: 2518, Querc. & Eucal. fungi, leg. Endrödy-Younga (TMSA); 1♂ 1♀: ditto, E-Y: 2517, Quercus for. litter (TMSA); 1♂ 2♀♀: S. Afr., Ciskei, Amatole, Pirie forest, 32°43′S 27°17′E, 8.xii.1987, E-Y: 2561, sift. wet for. ditch, leg. Endrödy-Younga (TMSA); 3♂♂: ditto, E-Y: 2560, indig. forest litter (TMSA); 19♂♂ 21♀♀: Alexandria forest, nr. Alexandria, 33°43′S 26°22′E, 18.xii.1981, D. H. Jacobs (DHJS, TMSA), 3♀♀: ditto, 30.i.1984 (DHJS); 1♂: S. Afr., SE. Cape Prov., Alexandria For. St., 33°43′S 26°23′E, 6.xii.1987, E-Y: 2555, indig. forest litter, leg. Endrödy-Younga (TMSA).

8.1.3 *Miteronotus bucculentus* spec. nov., Figs 212-219, 233-234.

Length ♂ 3,47 - 3,95 mm; ♀ 4,28 - 4,97 mm.

Width ♂ 1,52 - 1,69 mm; ♀ 1,89 - 2,26 mm.

Diagnostic measurements are given in Table 8.4.

Apterous. Body coated with a greyish incrustation, resulting in a general darkish grey appearance of uncleaned specimens. The following description is based on specimens with the incrustation removed.

Table 8.4. Measurements (in mm) of *Miteronotus bucculentus* spec. nov. from Port St. Johns.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range$	AT#	N	Mean	SD	Range$
Total	length	3.81	10	3.74	0.144	3.47-3.95	4.38	10	4.52	0.209	4.28-4.97
	width	1.62	10	1.65	0.039	1.52-1.69	2.01	10	2.01	0.112	1.89-2.26
Head	length	0.76	10	0.74	0.027	0.68-0.79	0.80	10	0.81	0.030	0.76-0.87
	width	0.80	10	0.80	0.023	0.77-0.84	0.83	10	0.84	0.023	0.80-0.88
Pronotum	length	0.44	10	0.44	0.021	0.40-0.48	0.44	10	0.48	0.040	0.42-0.55
	width	1.22	10	1.26	0.032	1.19-1.34	1.47	10	1.43	0.070	1.32-1.55
Tergal disk	length	1.05	10	1.06	0.033	1.01-1.12	1.30	10	1.37	0.071	1.23-1.47
	width	1.03	10	1.02	0.032	0.95-1.07	1.27	10	1.33	0.066	1.22-1.44
Antennal segments	I	0.24	10	0.26	0.015	0.22-0.29	0.29	10	0.28	0.012	0.26-0.31
	II	0.16	10	0.18	0.010	0.16-0.20	0.20	10	0.21	0.009	0.19-0.23
	III	0.23	10	0.23	0.008	0.21-0.25	0.25	10	0.26	0.010	0.24-0.28
	IV	0.24	10	0.25	0.009	0.23-0.27	0.27	10	0.27	0.010	0.25-0.29

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.

Head: About 1,05 times as wide (across the eyes) as long (not including neck area). Genae straight, relatively broad, ending bluntly. Jugae small, triangular. Lateral ridges on vertex curving anterolaterad just anterior of interocular callosities, ending on antenniferous lobes; subapical tubercle not prominent. Antennae short, 1,15-1,22x as long as width across eyes; first segment sturdy, thickest and longest, markedly curved and strongly tapering towards base, extending beyond apex of genae by about one quarter of its length; second segment shortest, slightly curved basally and gradually thickening towards apex; third segment slender, straight, thickening slightly and evenly towards apex, pedicellate; fourth segment fusiform with a short pedicel, conical apex pilose; relative lengths of segments: 11:8:10:10,5. Postocular tubercles prominent, usually reaching nearly to level of the outer margins of the eyes. Neck slightly constricted just behind the head. Rostral groove of males broadly oval, whole area, except thickenings lateral to slit where rostrum leaves the head, areolate (Fig. 234). Rostral groove of females normal, area inside rim transversely striated.

Thorax: Dorsum. Pronotum about 2,9 times as wide as long. Lateral lobes strongly elevated, clearly separated from smooth disk, covered with prominent setiferous nodules (except for a oval glabrous area mesally). Setae, which is also present on lateral lobes of meso- and metanotum, about as long as the height of the nodules. Lateral margin of lateral lobes slightly convex, converging anteriad, produced anteriorly to level of the anterior margin of the collar.

Mesonotal disk smooth and shining with a somewhat uneven surface, delimited from median ridge by 2(1+1) submedian, anteriorly converging, furrows. Median ridge pointed anteriorly, broad posteriorly, smooth and shining without a median suture. Mesonotal lateral lobes also raised, coarsely nodulate.

Metanotal disk smooth and shining anteriorly, irregularly excavated posteriorly and with large punctures submesally adjacent to the median ridge. Median ridge fairly broad, sparsely punctate, these punctures may delimit it to some extent from mesonotal ridge. Lateral lobes slightly convex, subparallel, coarsely nodulate. Suture between meso- and metanotum ending submesally in 2(1+1) prominent falcate pits.

MTg 1 narrow, moderately widening laterally, smooth and shining but with some punctures sublaterally; one of these punctures seem to be larger and deeper than the rest, forming a small sublateral pit. MTg 1 and 2 delimited for lateral half by 2(1+1) prominent transverse sulci, fused mesally. MTg 2 with sublateral ridges well developed. Lateral of these ridges 2(1+1) smooth subquadrangular areas are present, mesally of them MTg 2 is irregularly punctate and excavate except for 2(1+1) median longitudinal ridges which may be fused anteriorly.

Venter. Collar absent ventral of lateral tubercles.

Legs: Trochanters usually not discernable, sometimes a very faint line may indicate their position.

Abdomen: Dorsum. Posteroexternal angles of only DELTg 6 and 7 slightly produced. Tergal disk about 1,03 times as long as wide, moderately elevated along median line. Carinae which separate glabrous impressions prominent, sparsely punctate. Surface between carinae and impressions fairly smooth but with large scattered punctures, especially on tergite 4. Posterior nodulate transverse ridge on MTg 7 of females prominent, convex, with a single prominent transverse elevation anterior to it.

Venter. Intersegmental suture 6/7 in males complete. Spiracle 2 ventral; 3 sublateral, about two spiracle widths from lateral margin, 4 & 5 sublateral, about 1½ spiracle widths from margin, 6 & 7 lateral and visible from above, 8 subterminal on paratergites.

Genitalia: Pygophore (Figs 218-219) as for genus. Dorsal visible part of parameres (Fig. 219) transverse. Removed parameres as in Figs 214-217.

Chromosome number: $2n(\sigma^{\prime}) = 27X_1X_2Y$.

Habitat and distribution: At present only known from the evergreen forests of the Port St. Johns area in the Eastern Cape (Fig. 183).

Etymology: Bucculentus (L) = big mouth referring to the large, broadly oval rostral groove of the males.

Discussion: *Miteronotus bucculentus* is a small, broadly oval species that can at once be distinguished from the other species of the genus by the peculiar rostral groove of the males and the prominent setiferous nodules on the notal lateral lobes which bear prominent and fairly long setae. It possesses a similar spiracle pattern to *M. viginti* but can easily be distinguished by the characters mentioned above, the more prominent and broader median notal ridge, by having antennal segment 4 longer than 3 and by its different chromosome number.

MATERIAL EXAMINED: **Eastern Cape**. ♂ holotype: Mount Thesiger Nature Reserve, Port St. Johns, 31°37′S 29°31′E, 4-5.xii.1981, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 55 paratypes as follows: 1♀: S. Afr., Transkei, Ntsubane forest, 31°27′S 29°44′E, 25.xi.1987, E-Y: 2537, fungi &

for. litter, leg. Endrödy-Younga (TMSA); 26♂♂ 25♀♀: Same data as holotype (DHJS, TMSA); 2♂♂ 1♀: nr. Port St. Johns, Transkei, 31°37′S 29°32′E, 3.xii.1981 D.H. Jacobs (DHJS).

8.1.4 *Miteronotus knysnaensis* spec. nov., Figs 220-231.

Length ♂ 3,49 - 4,34 mm; ♀ 4,38 - 5,16 mm.

Width ♂ 1,47 - 1,91 mm; ♀ 1,91 - 2,42 mm.

Diagnostic measurements are given in Table 8.5.

Apterous. Body coated with a greyish incrustation, resulting in a dark grey, nearly slate, appearance of uncleaned specimens. The following description is based on specimens with the incrustation removed.

Table 8.5. Measurements (in mm) of *Miteronotus knysnaensis* spec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range@	AT#	N	Mean	SD	Range@
Total	length	3.98	16	3.88	0.160	3.49-4.34	4.65	16	4.68	0.208	4.38-5.16
	width	1.77	16	1.73	0.088	1.47-1.91	2.14	16	2.12	0.109	1.91-2.42
Head	length$	0.71	16	0.69	0.024	0.64-0.80	0.80	16	0.78	0.029	0.73-0.83
	width	0.77	16	0.76	0.040	0.68-0.87	0.82	16	0.83	0.020	0.79-0.93
Pronotum	length	0.38	16	0.39	0.022	0.35-0.43	0.44	16	0.46	0.035	0.40-0.55
	width	1.13	16	1.17	0.093	0.99-1.31	1.24	16	1.31	0.071	1.21-1.44
Tergal disk	length	1.18	16	1.17	0.060	1.03-1.34	1.51	16	1.47	0.086	1.30-1.67
	width	1.13	16	1.15	0.046	0.99-1.27	1.45	16	1.40	0.075	1.25-1.62
Antennal segments	I	0.56	16	0.57	0.044	0.50-0.67	0.59	16	0.60	0.023	0.55-0.67
	II	0.20	16	0.20	0.014	0.16-0.23	0.23	16	0.21	0.015	0.17-0.24
	III	0.31	16	0.29	0.027	0.22-0.33	0.34	16	0.32	0.027	0.26-0.36
	IV	0.32	16	0.30	0.020	0.26-0.33	0.35	16	0.33	0.023	0.29-0.38

* HT = holotype. # AT = allotype.
@ May include measurements of specimens from other localities.
$ Because of much variation in the development of the genae, head length measurements were taken from base of head to tip of clypeus.
• Four individuals from each of the following localities: Witels forest, Collins Hoek forest, Diepwalle

Head: Wider (across eyes) as long (neck area and genae not included). Much variation exists in the development of the genae: 1.) they may be produced beyond the apex of the clypeus as 2(1+1) long, thin acute extensions that are either straight or converging (e.g. in Witels forest and Stormsriver Mouth populations - they may even touch anteriorly in some individuals) or diverging (e.g. in the Long forest population). 2.) they may be much shorter only just extending beyond apex of clypeus or in some specimens be slightly shorter than the clypeus (e.g. in the Diepwalle and George populations). Jugae small, triangular. Ridges on vertex as for *Miteronotus labeosus* but subapical tubercle prominent. Antennae 1,75-1,80 times as long as width of head across eyes; first segment by far the longest and thickest, tapering at base and slightly tapering apically; second segment short, slightly curved basally and thickening towards apex; third segment slender, straight, evenly thickening towards apex,

pedicellate; fourth segment oblong fusiform, conical apex pilose; relative lengths of segments: 28:10:15,5:16. The first antennal segment of the males of some populations (e.g. from Witels forest, Stormsriver mouth, Witteklip forest) bears a peculiar sculpture (Figs 228-230) while that from the most other populations is of the more conventional type (Figs 231-232). The significance of this difference or the function of these structures are not known at this stage. Postocular tubercles not reaching to level of outer margins of eyes.

Thorax: Dorsum. Pronotum 2,8-3 times as wide as long. Lateral lobes granulate, on same level and not clearly delimited from disk, lateral margins straight or slightly concave, converging anteriad and produced anteriorly beyond the level of the collar. Disk small, irregularly excavated but with glabrous patches medially.

Mesonotal disk smooth submedially adjacent to cleft that separates it from median ridge, irregularly excavated laterally. Lateral lobes not elevated, granulate, lateral margins straight, converging anteriad. Median ridge fairly narrow anteriorly, becoming broader posteriorly (more so in females), containing a median longitudinal suture that is usually only visible as lightly coloured, less sclerotised line but sometimes it forms a shallow impressed line. This suture ends posteriorly when it meets the transverse suture at the anterior margin of MTg 1.

Metanotal disk with variously developed smooth and irregularly excavated areas, delimited from median ridge by a shallow, irregularly excavated depression. Median ridge fairly wide, usually with some sparse punctures and an uneven surface, completely fused with mesonotal ridge, although area where uneven surface starts may indicate border between meso- and metanotum.

MTg 1 narrow, widening laterally and curving anterolaterally, separated from MTg 2 for lateral half of its width by 2(1+1) deep sulci, completely fused medially. MTg 2 with 2(1+1) well developed sublateral ridges and a median bar which is usually only discernable on anterior part, rest of surface usually fairly smooth.

Venter. Collar absent ventral of lateral tubercles.

Legs: Trochanters fused with femora but line of demarcation usually faintly discernable.

Abdomen: Dorsum. Tergal disk marginally longer than wide, only slightly elevated along median line. Carinae which separate glabrous impressions usually only faintly recognisable except on tergite 4 where the sublateral and often the median carinae is well developed anteriorly. Surface of largest part of tergal disk covered with oval or oblong punctures.

Venter. Intersegmental suture 6/7 of males complete. Spiracle 2 ventral; 3-7 lateral, visible from above, 8 subterminal on paratergites.

Genitalia: Pygophore (Figs 226-227) as for genus. Dorsal visible part of parameres as in Fig. 227 and removed parameres as in Figs 222-225.

Chromosome number: 2n(♂) = 32XY.

Habitat and distribution: Widespread and fairly common in the Tsitsikama evergreen forest in the Western and Eastern Cape.

Etymology: Named after Knysna, a town synonomous with the evergreen Tsitsikama forests.

Discussion: *Miteronotus knysnaensis* can readily be distinguished from all congeneric species by having spiracles 3-7 lateral and visible from above and by its very long first antennal segment which is longer than the second and third segments combined.

MATERIAL EXAMINED: **SOUTH AFRICA. Western Cape**. ♂ holotype: Diepwalle forest, Cape Province, 33°57′S 23°09′E, 19-21.xii.1977, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 327 paratypes as follows: 8♂♂ 19♀♀: Kop Forest, Cape Province, 33°52′S 23°08′E, 20.xii.1977, D.H. Jacobs (DHJS, TMSA); 1♀: Outenikwa Pass, S Afr., S. Cape Mt., 33°53′S 22°23′E, (TMSA); 2♂♂ 2♀♀: Helderfontein 1150 m, S Afr., S Cape Mt., 33°56′S 20°52′E, 7.iii.1979, E-Y: 1560, sift. forest litter, leg. Endrödy-Younga (TMSA); 7♂♂ 1♀: Boesmansbos, 1050m, S Afr., Langeberge, 33°56′S 20°53′E, 7.iii.1979, E-Y: 1560, sift. forest litter, leg. Endrödy-Younga (TMSA); 7♂♂ 1♀: Boesmansbos, 1050 m, S. Afr., Langeberge, 33°56′S 20°53′E, 7.iii.1979, E-Y: 1560, sifted forest lit., leg. Endrödy-Younga (TMSA); 7♂♂ 6♀♀: Collins Hook forest, Cape Province, 33°56′S 22°38′E, 22.xii.1979, D.H. Jacobs (DHJS); 1♂ 1♀: Knysna forest, S. Afr., S. Cape, 33°56′S 23°08′E, 19.xi.1973, E-Y: 272, sift. Podocarp. lit., leg. Endrödy-Younga (TMSA); 1♂ 1♀: S. Afr., S. Cape Prov., Tsitsikama, Lottering, 33°56′S 23°40′E, 12.xii.1977, E-Y: 1419, forest floor litter, leg. Endrödy-Younga (TMSA); 4♂♂ 23♀♀: Long forest, Cape Province, 33°57′S 22°11′E, 21.xii.1977, D.H. Jacobs (DHJS, TMSA); 22♂♂ 18♀♀: Same data as holotype (DHJS, TMSA); 2♀♀: ditto, 19-20.xii.1981 (DHJS); 11♂♂ 11♀♀: S. Afr., S. Cape, George, 33°58′S 22°28′E, 4.ix.1979, E-Y: 1632, sifted forest litter, leg. Endrödy-Younga (TMSA); 4♂♂ 1♀: ditto, E-Y: 1633, for. litter in gorge (TMSA); **Eastern Cape**. 5♂♂ 5♀♀: Elands forest, Cape Province, 33°58′S 23°47′E, 17.xii.1977, D. H. Jacobs (DHJS, TMSA); 10♂♂ 9♀♀: Witteklip forest, Cape Province, 33°58′S 23°51′E, 17.xii.1977, D.H. Jacobs (DHJS, TMSA); 1♀: Tsitsikama, Witelsbos, S. Afr., S. Cape Province., 33°58′S 24°02′E, 10.xii.1978, E-Y: 1529, sift. forest litter, leg. Endrödy-Younga (TMSA); 4♂ 8♀♀: Witels forest, Cape Province, 33°59′S 24°06′E, 15.xii.1977, D.H. Jacobs (DHJS); 12♂♂ 25♀♀: Stormsriver mouth, Cape Province, 34°01′S 23°54′E, 18.xii.1977, D.H. Jacobs (DHJS, TMSA); 12♂♂ 65♀♀: Witels forest, Cape Province, 34°03′S 24°08′E, 16.xii.1977, D.H. Jacobs (DHJS, TMSA); 1♂ 4♀♀: ditto, 19.xii.1981 (DHJS); 3♀♀: Tsitsikama F., Humansdorp D., humus, i.1961 (TMSA).

8.2 Cytogenetics of the genus Miteronotus

The locality and number of individuals of *Miteronotus* species that were cytogenetically studied are presented in Table 8.6. The course of meioses is of the regular Carventine type.

Table 8.6. Locality and numbers of individuals of *Miteronotus* species cytogenetically studied.

Locality	Co-ordinates	Date collected	No. of individuals cytogenetically studied
Miteronotus labeosus			
Ngoye forest, nr. Empangeni	28°50′S 31°43′E	11-12/xii/1980	7
Dhlinza forest, Eshowe	28°51′S 31°27′E	12/iv/1980	10
Karkloof, nr. Pietermaritzburg	29°19′S 30°18′E	1/ii/1983	10
Town Bush, Pietermaritzburg	29°33′S 30°20′E	31/i/1983	8
Miteronotus viginti			
Qacu Forest Res., nr. Stutterheim	32°25′S 27°28′E	17/xii/1981	1
Aucland Forest Reserve, Hogsback	32°36′S 26°56′E	16/xii/1981	6
Schwarzwald forest, nr. Hogsback	32°39′S 27°00′E	16/xii/1981	7
Isidenge forest, nr. Stutterheim	32°41′S 27°17′E	14-17/xii/1981	9
ditto	"	2/ii/1984	4
Alexandria forest, nr. Alexandria	33°43′S 26°22′E	18/xii/1981	5
Miteronotus bucculentus			
Mount Thesiger Nature Reserve, Port St. Johns, Eastern Cape	31°37′S 29°31′E	4-5/xii/1981	7
nr. Port St. Johns, Eastern Cape	31°37′S 29°32′E	3/xii/1981	3
Miteronotus knysnaensis			
Long forest, nr. Knysna	33°57′S 22°11′E	21/xii/1977	2
Diepwalle forest, nr. Knysna	33°57′S 23°09′E	19-21/xii/1977	4
ditto	"	19-20/xii/1981	10
Witels forest, Eastern Cape	33°59′S 24°06′E	15/xii/1977	7
ditto	"	19/xii/1981	4

8.2.1 *Miteronotus labeosus* (Figs 184, 237-240).

The chromosome number of *M. labeosus* is 2n(♂) = 26XY. The true and relative chromosome areas for *M. labeosus* of different localities are presented in Table 8.7 and an idiogram in Fig. 184. Autosomes A3-A12 form a more or less gradual size series. There is a slight step towards A2 which is moderately larger than A3 and a distinct step towards A1 while is much larger than the other autosomes. The X-chromosome is the largest chromosome in the complement while the Y-chromosome is on average of about the same size as autosome A2. There is a significant variation in the size of the

sex chromosomes between the different localities. For example: In the Karkloof individuals the Y-chromosome is distinctly smaller than in the other localities. There is also slight variation in autosome size between localities, but, taking A1 where reversal of order probably didn't take place as indicator, it doesn't seem to be significant.

Table 8.7. True and relative chromosome areas of *M. labeosus*.

True chromosome areas (μm²) and standard deviation.				
Chromosome	**Karkloof**	**Ngoye forest**	**Dhlinsa forest**	**TOTAL**
Individuals	2	2	1	5
Cells	11	10	2	23
A1	2.45(±0.49)	1.94(±0.37)	2.03(±0.19)	2.20(±0.48)
A2	1.84(±0.32)	1.49(±0.28)	1.48(±0.05)	1.65(±0.33)
A3	1.62(±0.27)	1.38(±0.23)	1.37(±0.02)	1.48(±0.27)
A4	1.54(±0.25)	1.27(±0.18)	1.35(±0.02)	1.41(±0.24)
A5	1.46(±0.22)	1.25(±0.19)	1.33(±0.02)	1.36(±0.22)
A6	1.42(±0.22)	1.21(±0.19)	1.18(±0.11)	1.31(±0.22)
A7	1.35(±0.23)	1.17(±0.19)	1.12(±0.07)	1.25(±0.22)
A8	1.31(±0.22)	1.14(±0.18)	1.07(±0.06)	1.22(±0.21)
A9	1.25(±0.23)	1.09(±0.19)	1.05(±0.06)	1.17(±0.22)
A10	1.16(±0.18)	1.05(±0.18)	0.97(±0.06)	1.09(±0.18)
A11	1.09(±0.19)	0.93(±0.16)	0.86(±0.02)	1.00(±0.19)
A12	0.98(±0.19)	0.82(±0.11)	0.83(±0.00)	0.90(±0.17)
X	2.47(±0.40)	2.48(±0.59)	2.05(±0.19)	2.44(±0.48)
Y	1.50(±0.39)	1.80(±0.28)	1.74(±0.19)	1.65(±0.35)
Autosomes	17.49(±2.89)	14.71(±2.38)	14.64(±0.44)	16.03(±2.85)
All chromosomes	21.45(±3.61)	18.98(±3.22)	18.43(±0.81)	20.12(±3.46)
Relative chromosome areas (% of total area of autosomes) and standard deviation.				
A1	14.00(±1.06)	13.19(±0.80)	13.88(±0.88)	13.64(±0.99)
A2	10.49(±0.51)	10.12(±0.56)	10.08(±0.02)	10.30(±0.53)
A3	9.29(±0.36)	9.08(±0.21)	9.40(±0.41)	9.21(±0.31)
A4	8.83(±0.50)	8.68(±0.26)	9.26(±0.39)	8.80(±0.42)
A5	8.39(±0.41)	8.52(±0.19)	9.06(±0.37)	8.51(±0.36)
A6	8.14(±0.27)	8.25(±0.22)	8.03(±0.51)	8.18(±0.26)
A7	7.74(±0.34)	7.93(±0.19)	7.65(±0.26)	7.81(±0.28)
A8	7.48(±0.28)	7.77(±0.21)	7.33(±0.17)	7.60(±0.28)
A9	7.16(±0.32)	7.43(±0.26)	7.17(±0.16)	7.28(±0.31)
A10	6.62(±0.30)	7.11(±0.25)	6.60(±0.60)	6.83(±0.38)
A11	6.24(±0.31)	6.29(±0.32)	6.85(±0.07)	6.23(±0.32)
A12	5.61(±0.38)	5.62(±0.41)	5.69(±0.15)	5.62(±0.37)
X	14.12(±0.72)	16.70(±1.58)	14.02(±0.85)	15.23(±1.74)
Y	8.51(±1.06)	12.24(±0.64)	11.87(±0.92))	10.42(±2.06)

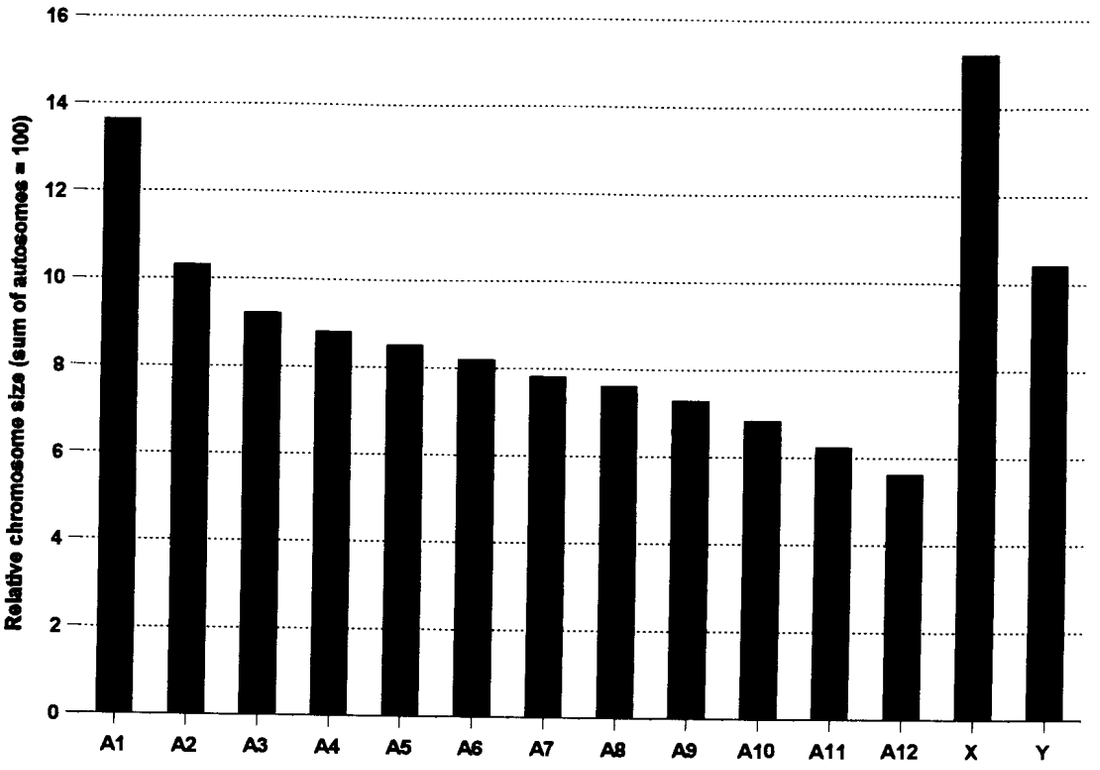


Figure 184. Idiogram of *Miteronotus labeosus*.

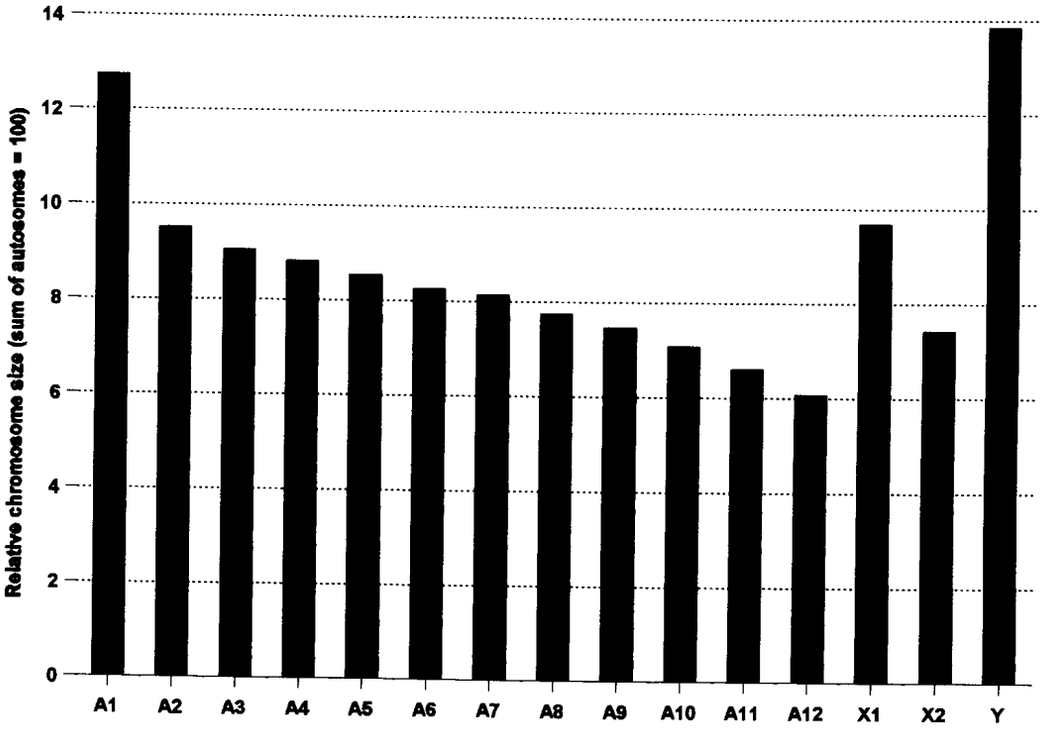


Figure 185. Idiogram of *Miteronotus bucculentus*.

8.2.2 *Miteronotus bucculentus* (Figs. 185, 251-253).

The chromosome number of *M. bucculentus* is 2n(♂) = $27X_1X_2Y$. The true and relative chromosome areas for *M. bucculentus* are presented in Table 8.8 and an idiogram in Fig. 185. The size distribution of the autosomes follows the same pattern as that of the previous species except that autosome A2 falls within the gradual series of A2-A12 but the sex chromosomes differ markedly. The sex chromosome system is presumably X_1X_2Y where the Y-chromosome is the largest chromosome in the complement while X_1 is of similar size as A2 and X_2 lies between A9 and A10 in size.

Table 8.8. True and relative chromosome areas of *M. bucculentus*.

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	4	4
Cells	15	15
A1	2.48(±0.40)	12.73(±0.70)
A2	1.85(±0.28)	9.50(±0.27)
A3	1.76(±0.26)	9.05(±0.32)
A4	1.72(±0.26)	8.82(±0.36)
A5	1.66(±0.26)	8.54(±0.40)
A6	1.61(±0.26)	8.26(±0.32)
A7	1.59(±0.26)	8.13(±0.32)
A8	1.51(±0.21)	7.76(±0.23)
A9	1.45(±0.20)	7.46(±0.22)
A10	1.38(±0.21)	7.08(±0.41)
A11	1.28(±0.20)	6.60(±0.51)
A12	1.18(±0.18)	6.07(±0.40)
X_1	1.89(±0.33)	9.68(±0.69)
X_2	1.44(±0.22)	7.42(±0.74)
Y	2.70(±0.42)	13.85(±0.75)
Autosomes	19.47(±2.76)	
All chromosomes	25.50(±3.62)	

8.2.3 *Miteronotus viginti* (Figs 186, 246-250).

The chromosome number of *M. viginti* is 2n(♂) = 20XY. The true and relative chromosome areas for this taxon from different localities are presented in Table 8.9 and an idiogram in Fig. 186. The autosomes form two gradual series: four autosomes (A1-A4) form one gradual series and is distinctly larger than the other five autosomes (A5-A9) which form the second gradual series. The X-chromosome is on average about as large as the second largest autosome while the Y-chromosome lies between autosomes A4 and A5 in size.

As in the case of *M. labeosus* the sex chromosomes exhibit much variation in size between localities and even between individuals of the same locality. For example: the relative sizes of the X-chromosome for six individuals from Isidenge forest are 17.93, 17.34, 15.64, 14.77, 13.06 and 12.66 respectively. The Y-chromosome in the individual from Schwarzwald forest (Fig. 250) is significantly smaller than that of individuals from the other localities.

Table 8.9. True and relative chromosome areas of *M. viginti*.

True chromosome areas (μm²) and standard deviation.				
Chromosome	**Isidenge forest**	**Schwarzwald forest**	**Aucland Forest Reserve**	**TOTAL**
Individuals	6	1	1	8
Cells	25	5	3	33
A1	2.67(±0.33)	3.00(±0.33)	2.89(±0.34)	2.74(±0.35)
A2	2.36(±0.29)	2.60(±0.11)	2.53(±0.34)	2.41(±0.28)
A3	2.22(±0.28)	2.44(±0.20)	2.38(±0.25)	2.27(±0.27)
A4	2.09(±0.30)	2.30(±0.17)	2.34(±0.26)	2.14(±0.29)
A5	1.60(±0.21)	1.81(±0.10)	1.90(±0.24)	1.66(±0.22)
A6	1.53(±0.23)	1.76(±0.12)	1.77(±0.24)	1.59(±0.23)
A7	1.44(±0.20)	1.62(±0.13)	1.69(±0.30)	1.49(±0.22)
A8	1.31(±0.19)	1.43(±0.10)	1.55(±0.19)	1.35(±0.19)
A9	1.19(±0.20)	1.34(±0.07)	1.41(±0.28)	1.23(±0.21)
X	2.50(±0.36)	2.14(±0.07)	2.60(±0.25)	2.46(±0.35)
Y	1.85(±0.20)	1.13(±0.06)	2.12(±0.43)	1.77(±0.35)
Autosomes	16.40(±2.10)	18.29(±0.66)	18.46(±2.42)	16.87(±2.11)
All chromosomes	20.76(±2.35)	21.56(±0.69)	23.18(±3.09)	21.10(±2.31)
Relative chromosome areas (% of total area of autosomes) and standard deviation.				
A1	16.31(±0.85)	16.38(±1.74)	15.70(±0.26)	16.27(±0.98)
A2	14.40(±0.64)	14.22(±0.61)	13.70(±0.47)	14.31(±0.64)
A3	13.55(±0.46)	13.31(±0.88)	12.90(±0.31)	13.45(±0.55)
A4	12.73(±0.68)	12.58(±0.72)	12.70(±0.24)	12.71(±0.65)
A5	9.74(±0.47)	9.88(±0.31)	10.30(±0.15)	9.81(±0.45)
A6	9.30(±0.51)	9.64(±0.37)	9.60(±0.17)	9.38(±0.48)
A7	8.75(±0.34)	8.84(±0.65)	9.13(±0.42)	8.80(±0.40)
A8	7.99(±0.44)	7.81(±0.55)	8.39(±0.26)	8.00(±0.45)
A9	7.23(±0.47)	7.34(±0.45)	7.58(±0.54)	7.28(±0.47)
X	15.39(±2.35)	11.69(±0.35)	14.11(±0.50)	14.71(±2.45)
Y	11.40(±1.33)	6.16(±0.46)	11.43(±1.09)	10.61(±2.25)

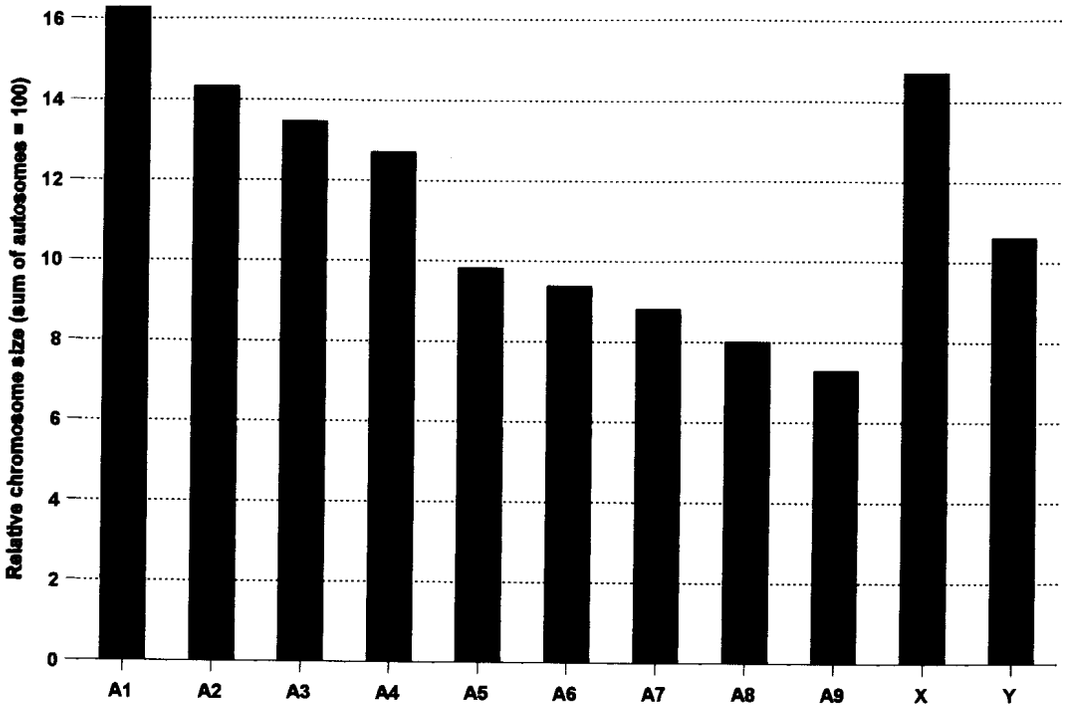


Figure 186. Idiogram of *Miteronotus viginti*.

8.2.4 ***Miteronotus knysnaensis*** (Figs 187, 241-245).

The chromosome number of *M. knysnaensis* is 2n = 32XY, the highest number thus far recorded in the Carventinae. The true and relative chromosome areas for *M. knysnaensis* are presented in Table 8.10 and an idiogram in Fig. 187. All the autosomes form a more or less gradual size series. Both sex chromosomes are much larger than any of the autosomes, the X-chromosome (on average) being about double the size of the largest autosome while the Y-chromosome is about 1.5x as large as the largest autosome. There is also a large difference in the size of the sex chromosomes (especially the X-chromosome) in the two individuals measured. The relative size of the X-chromosome of one individual is 24,02 (Figs 241-242) and of the other 18.27 (Figs 244-245).

8.2.5 Discussion.

The chromosome numbers of the species of *Miteronotus* are so widely divergent that it is difficult to deduct the relationships of the species from this cytogenetic data. The autosomal karyotypes of *M. bucculentus* and *M. labeosus* exhibit the same pattern and they are probably closely related. The multiple sex chromosome system (X_1X_2Y) in the former could have arisen by fragmentation of the X chromosome of a 26XY ancestor. Another possibility is that it could have arisen through chromatid autonomy when a 14XY protokaryotype underwent chromatid autonomy to form a $27X_1X_2Y$ or 26XY karyotype. The presence of a single large autosome in the karyotype of both these species indicates that

Table 8.10. True and relative chromosome areas of *M. knysnaensis*.

True chromosome areas (µm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Diepwalle forest	Diepwalle forest
Individuals	2	2
Cells	12	12
A1	1.88(±0.57)	9.38(±0.55)
A2	1.75(±0.55)	8.72(±0.40)
A3	1.66(±0.52)	8.28(±0.35)
A4	1.62(±0.49)	8.08(±0.33)
A5	1.56(±0.47)	7.81(±0.24)
A6	1.48(±0.40)	7.45(±0.37)
A7	1.38(±0.39)	6.95(±0.30)
A8	1.33(±0.38)	6.66(±0.19)
A9	1.27(±0.38)	6.32(±0.27)
A10	1.21(±0.35)	6.03(±0.22)
A11	1.14(±0.34)	5.68(±0.35)
A12	1.06(±0.28)	5.33(±0.37)
A13	0.99(±0.26)	4.96(±0.32)
A14	0.86(±0.23)	4.37(±0.48)
A15	0.79(±0.22)	3.97(±0.59)
X	4.33(±1.75)	21.14(±3.52)
Y	2.79(±0.60)	14.33(±1.80)
Autosomes	19.98(±5.74)	
All chromosomes	27.10(±7.95)	

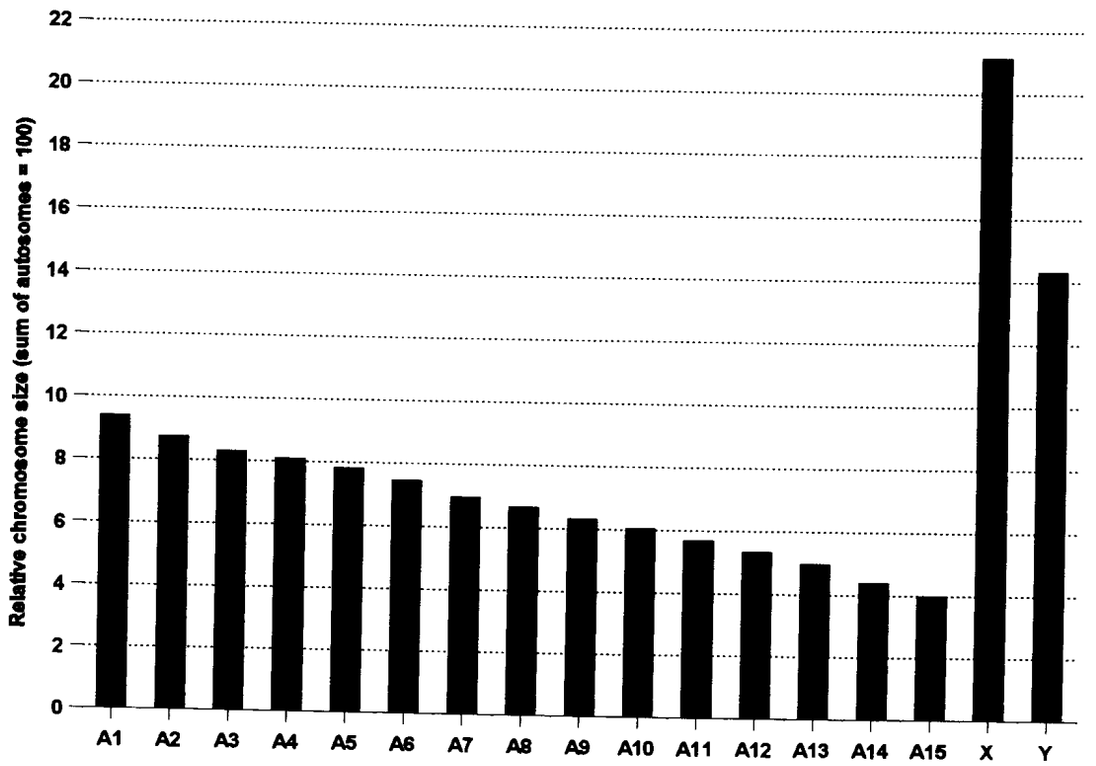


Figure 187. Idiogram of *Miteronotus knysnaensis*.

they are not the direct products of chromosome autonomy of a 14XY ancestor as one would then expect that each autosome would split up into two chromosomes of similar size. If chromatid autonomy indeed played a role in the origin of these karyotypes, at least another fission and a fusion event were necessary in order to be able to explain their origin.

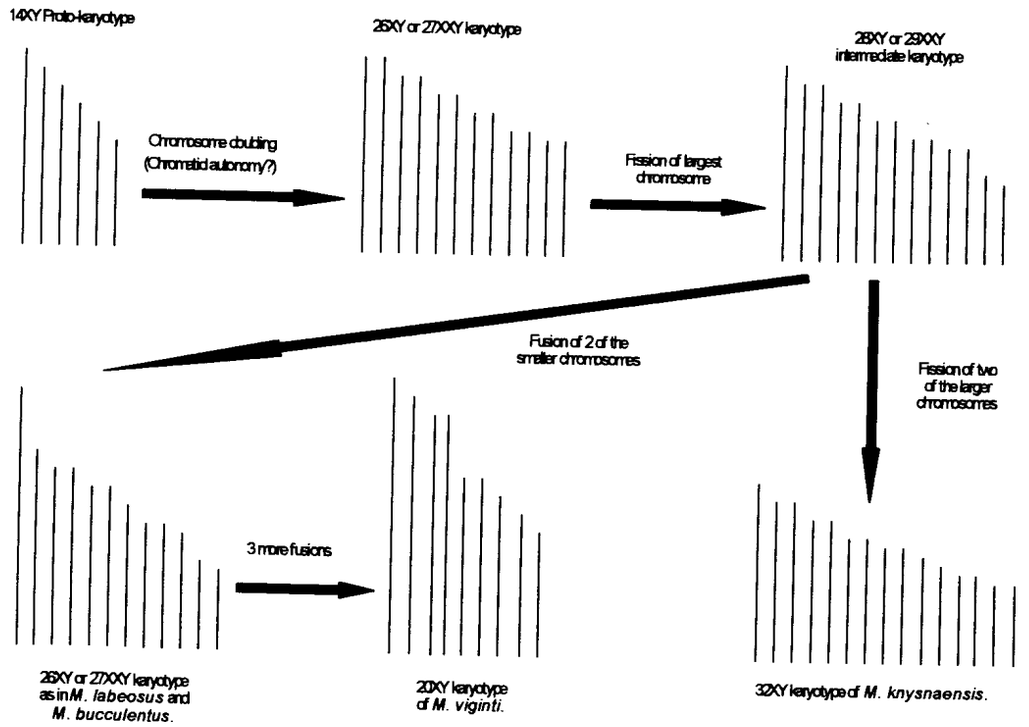
The other possibility to explain the origin of this karyotype is through multiple fissions (and perhaps some fusions) of the chromosomes of the 14XY protokaryotype.

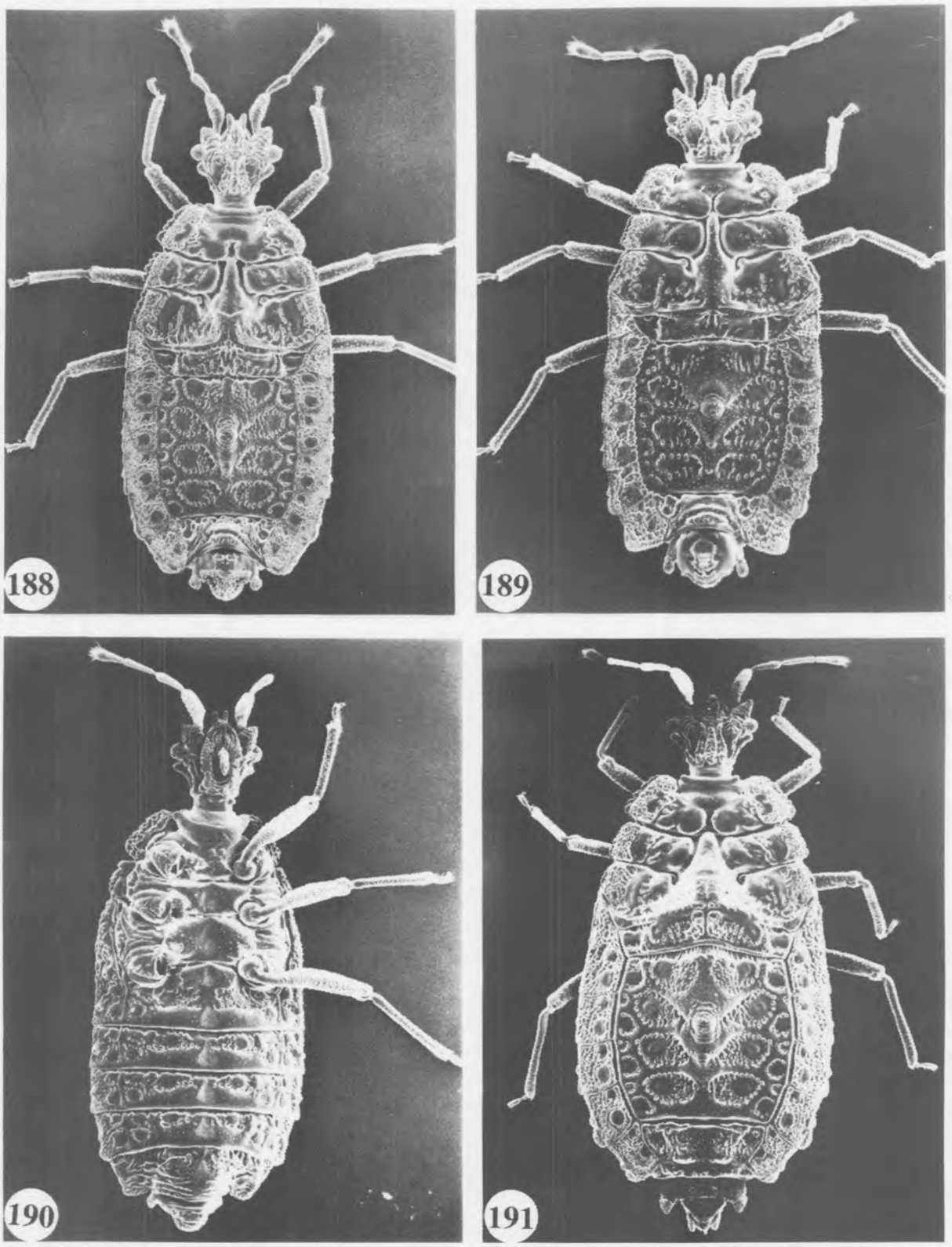
Notwithstanding the method of their origin, the similar pattern of these karyotypes almost certainly indicates a close relationship between the two species.

The karyotype of *M. viginti* shows four autosomes which are distinctly larger than the other five. If simple fragmentation of different chromosomes of a 14XY protokaryotype gave rise to this 20XY karyotype, one would expect three larger and six smaller autosomes. The fact that four large autosomes are present makes it more plausible that it originated from an 28XY karyotype, possibly the same one that was an intermediate step in the evolution of the karyotypes of *M. labeosus* and *M. bucculentus*.

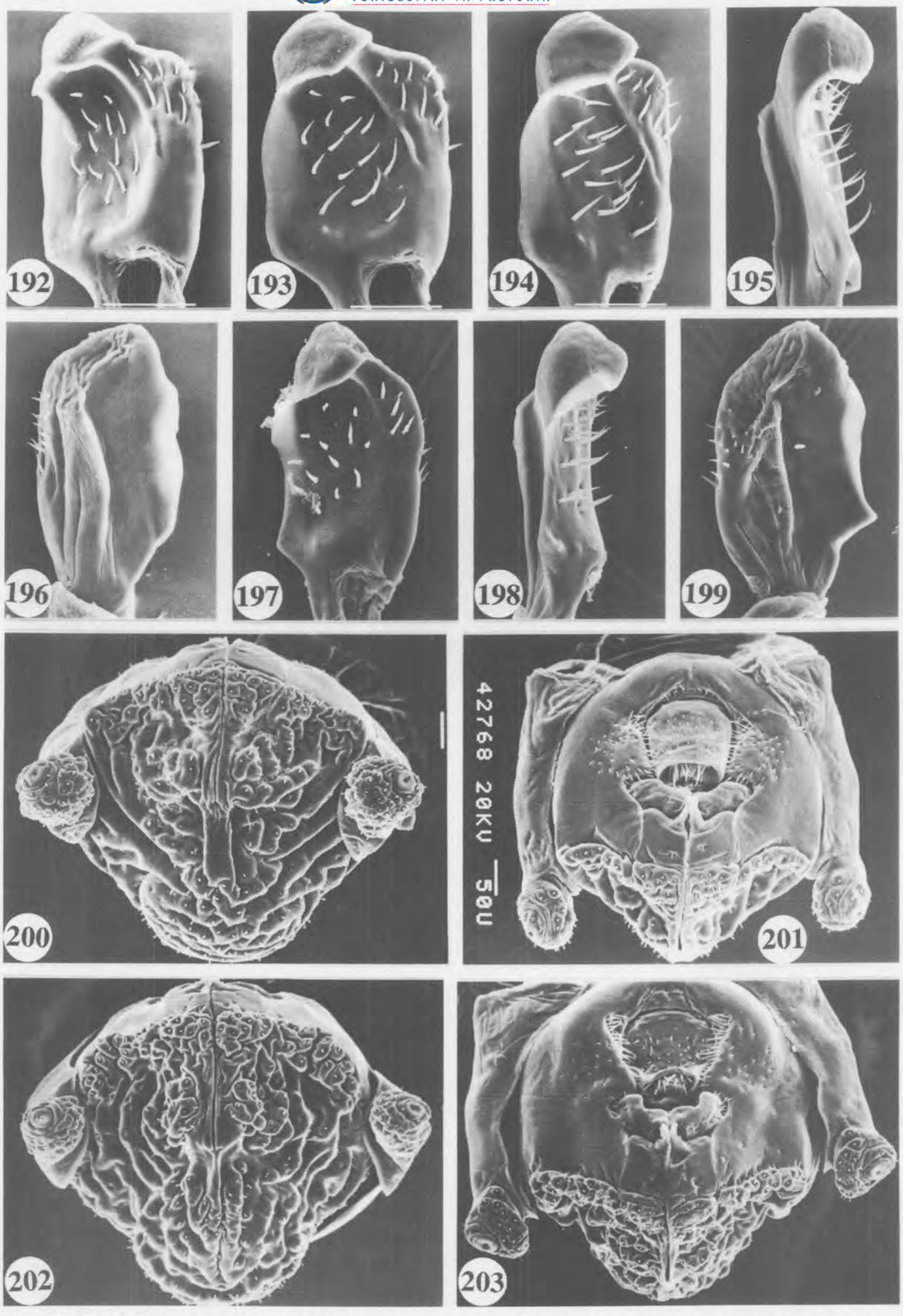
The 32XY karyotype of *M. knysnaensis* could have arisen by two fragmentation events from a 28XY intermediate karyotype.

The following scheme could explain the origin of the autosomal karyotypes of the four species discussed above:

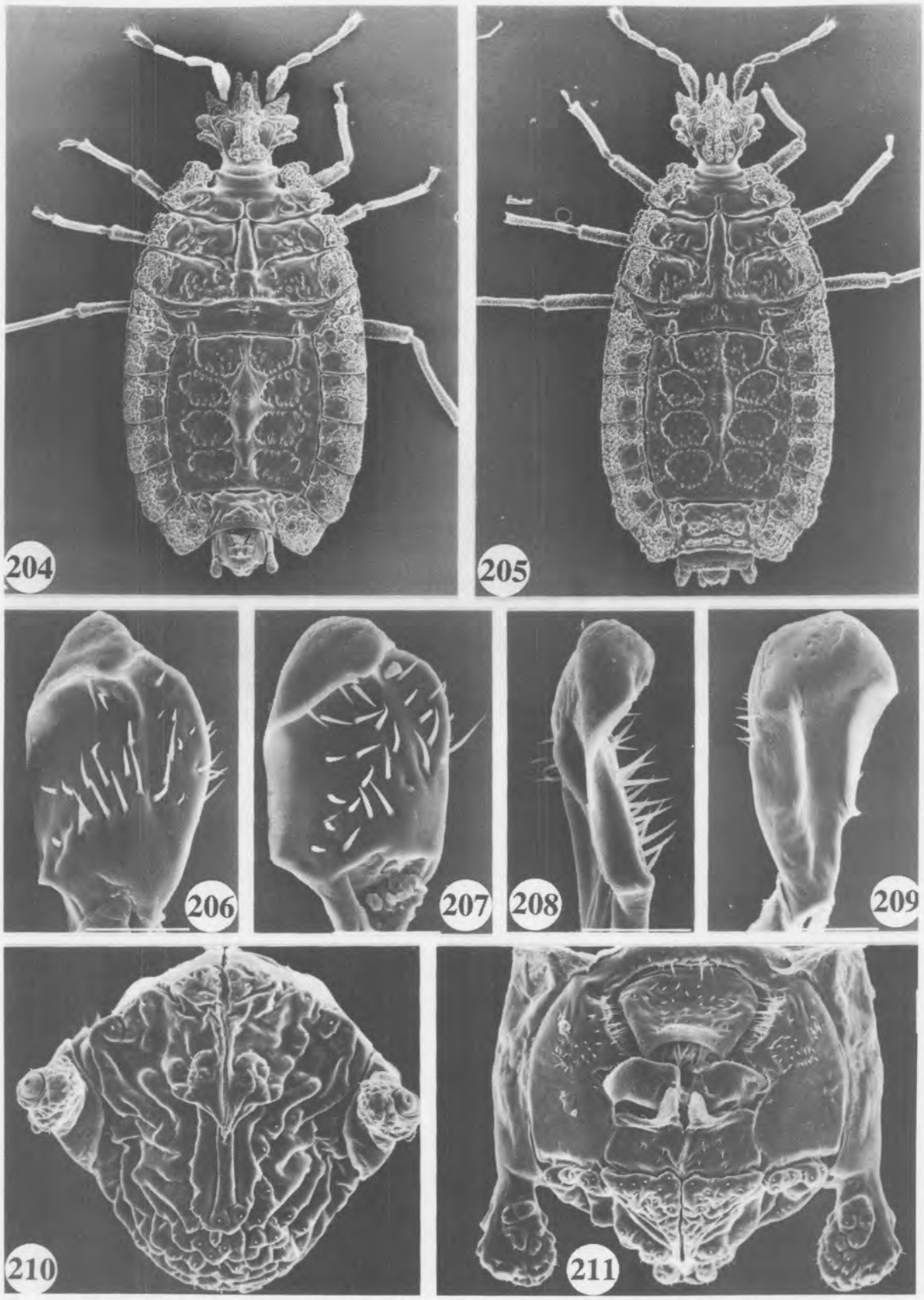




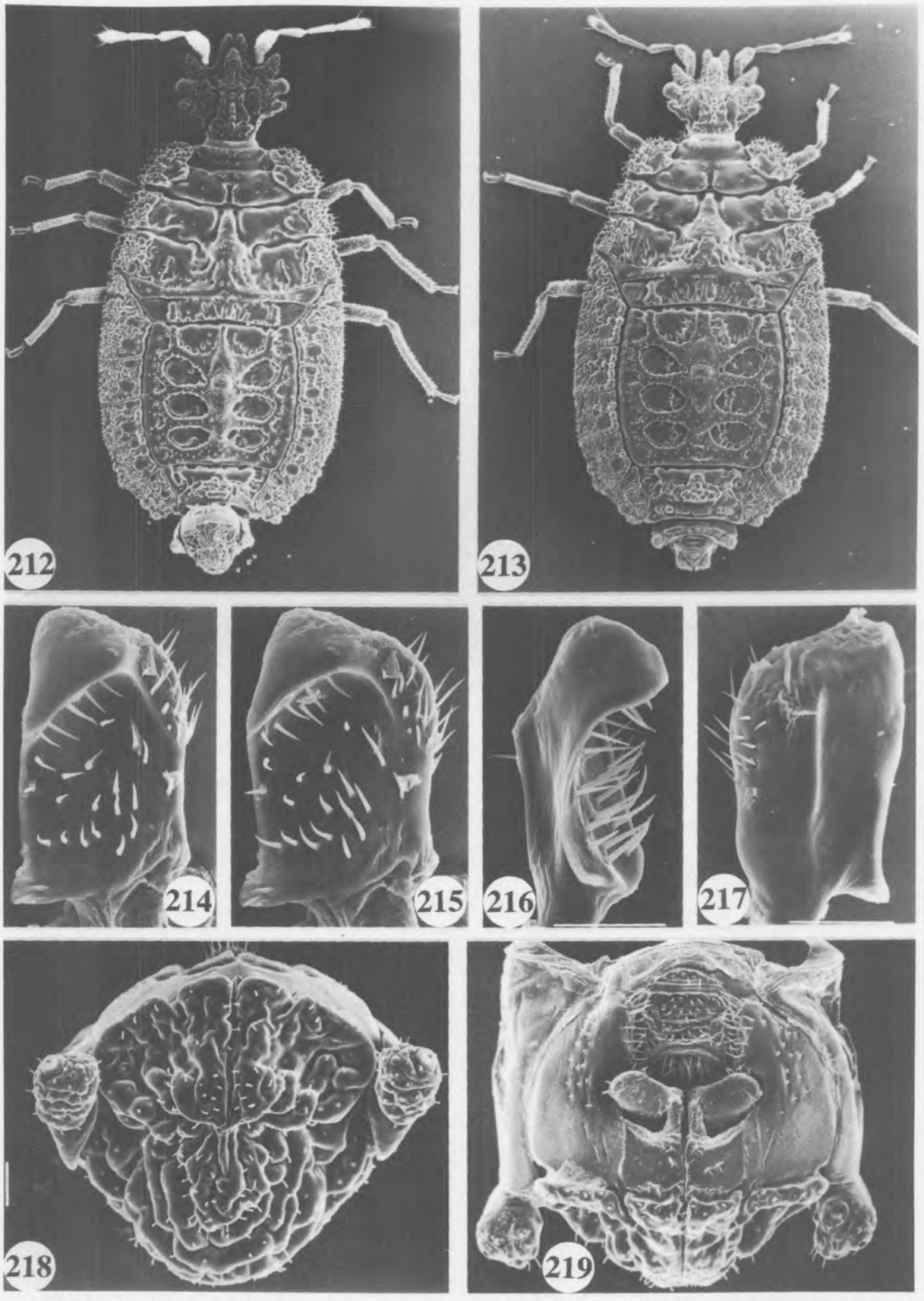
Figs 188-191. Scanning electron photomicrographs of *Miteronotus labeosus* **gen. et spec. nov.** 188. Dorsal aspect of male paratype from Ngoye forest. 189. Dorsal aspect of male paratype from Karkloof. 190. Ventral aspect of male paratype from Ngoye forest. 191. Dorsal aspect of female paratype from Ngoye forest.



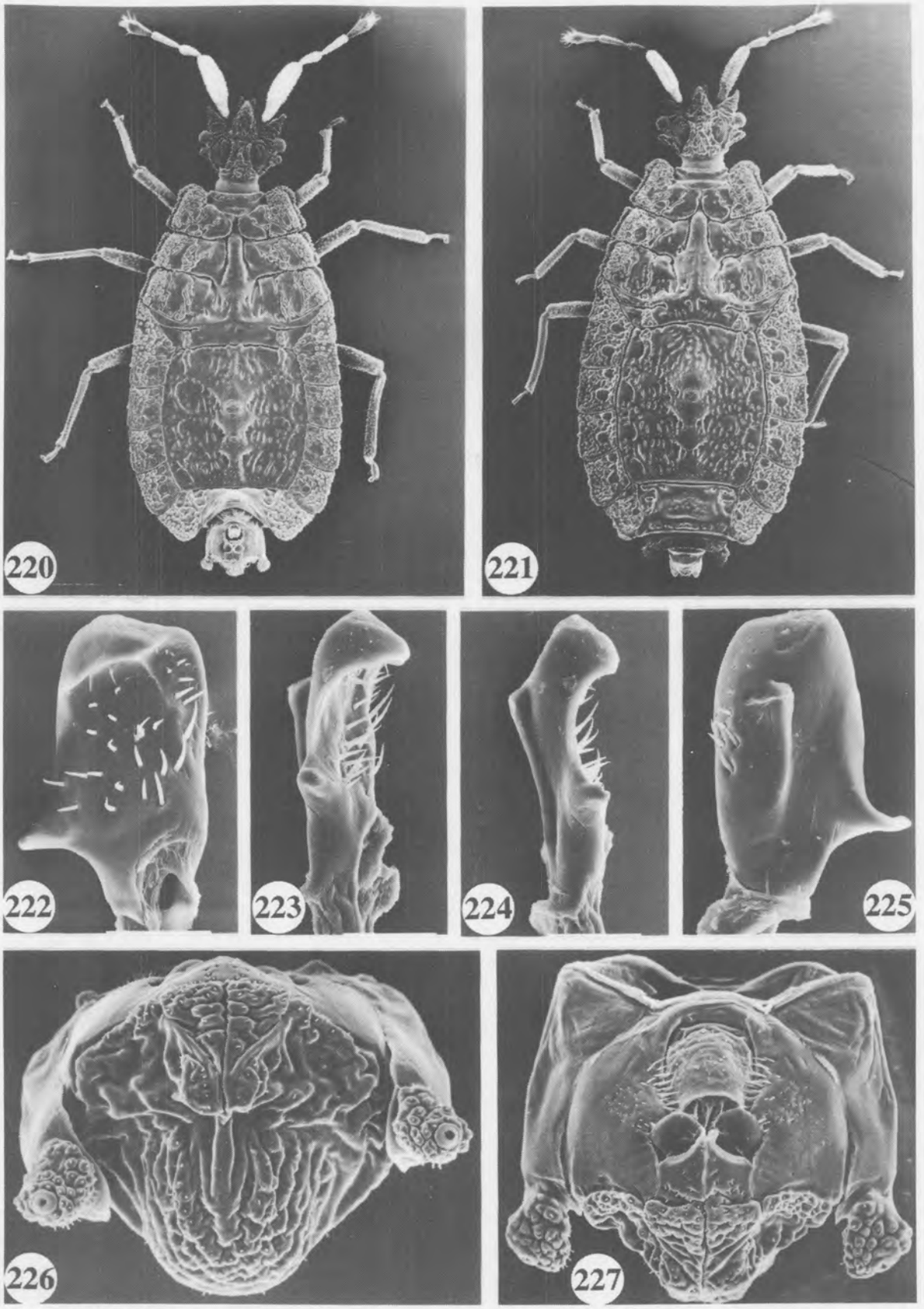
Figs 192-203. Scanning electron photomicrographs of *Miteronotus labeosus* **gen. et spec. nov.** 192-196. Different aspects of the left paramere of males from Ngoye forest (scale bar = 50 μm). 197-199. Different aspects of the left paramere of males from Karkloof. 200-201. Pygophore of male from Karkloof. 200. Caudal aspect (scale bar = 50 μm). 201. Dorsal aspect. 202-203. Pygophore of male from Ngoye forest. 202. Caudal aspect. 203. Dorsal aspect.



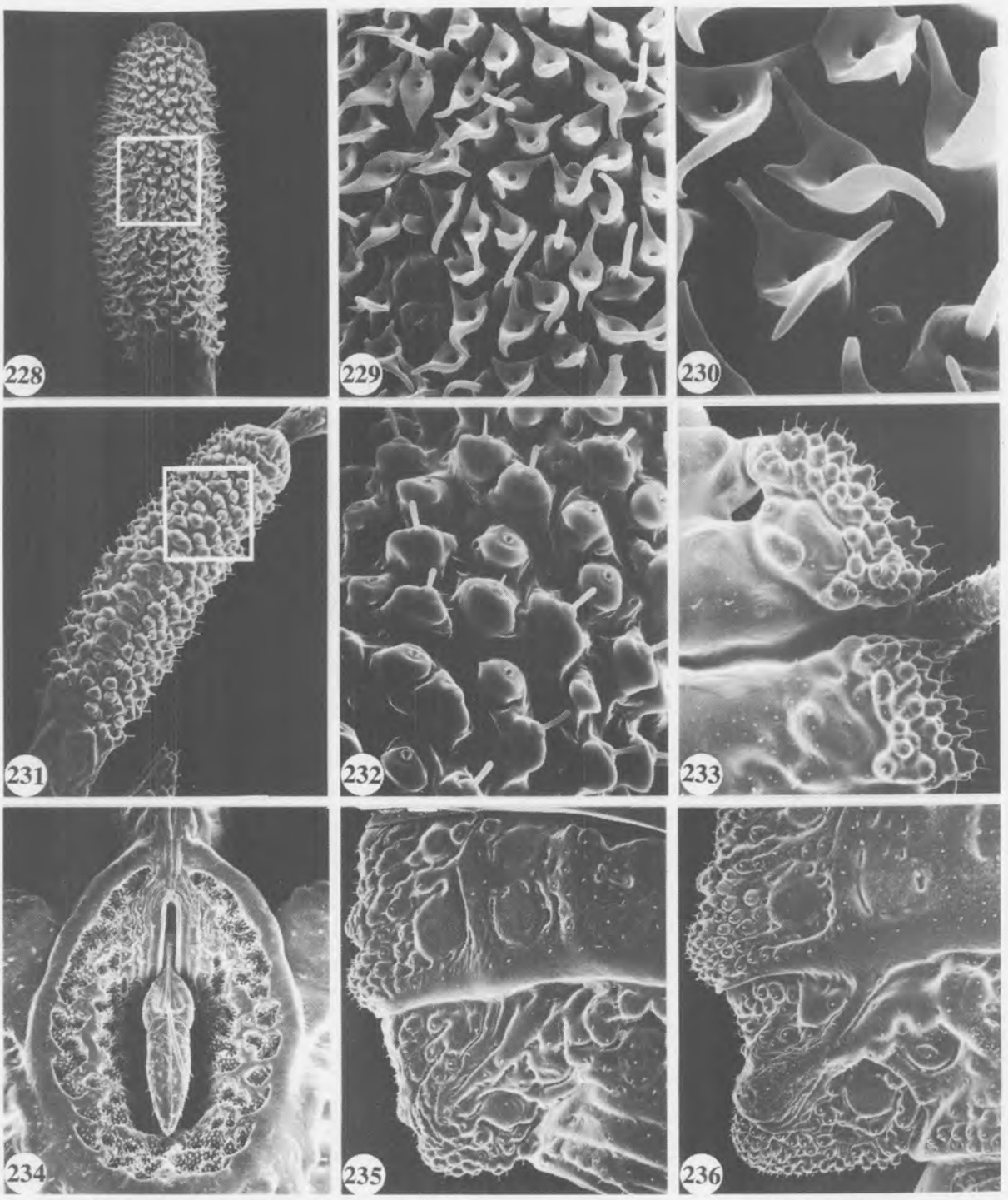
Figs 204-211. Scanning electron photomicrographs of *Miteronotus viginti* **gen. et spec. nov.** 204. Male paratype, dorsal aspect. 205. Female paratype, dorsal aspect. 206-209. Different aspects of the left paramere (scale bar = 50 μm). 210-211. Pygophore. 210. Caudal aspect. 211. Dorsal aspect (scale bar = 50 μm).



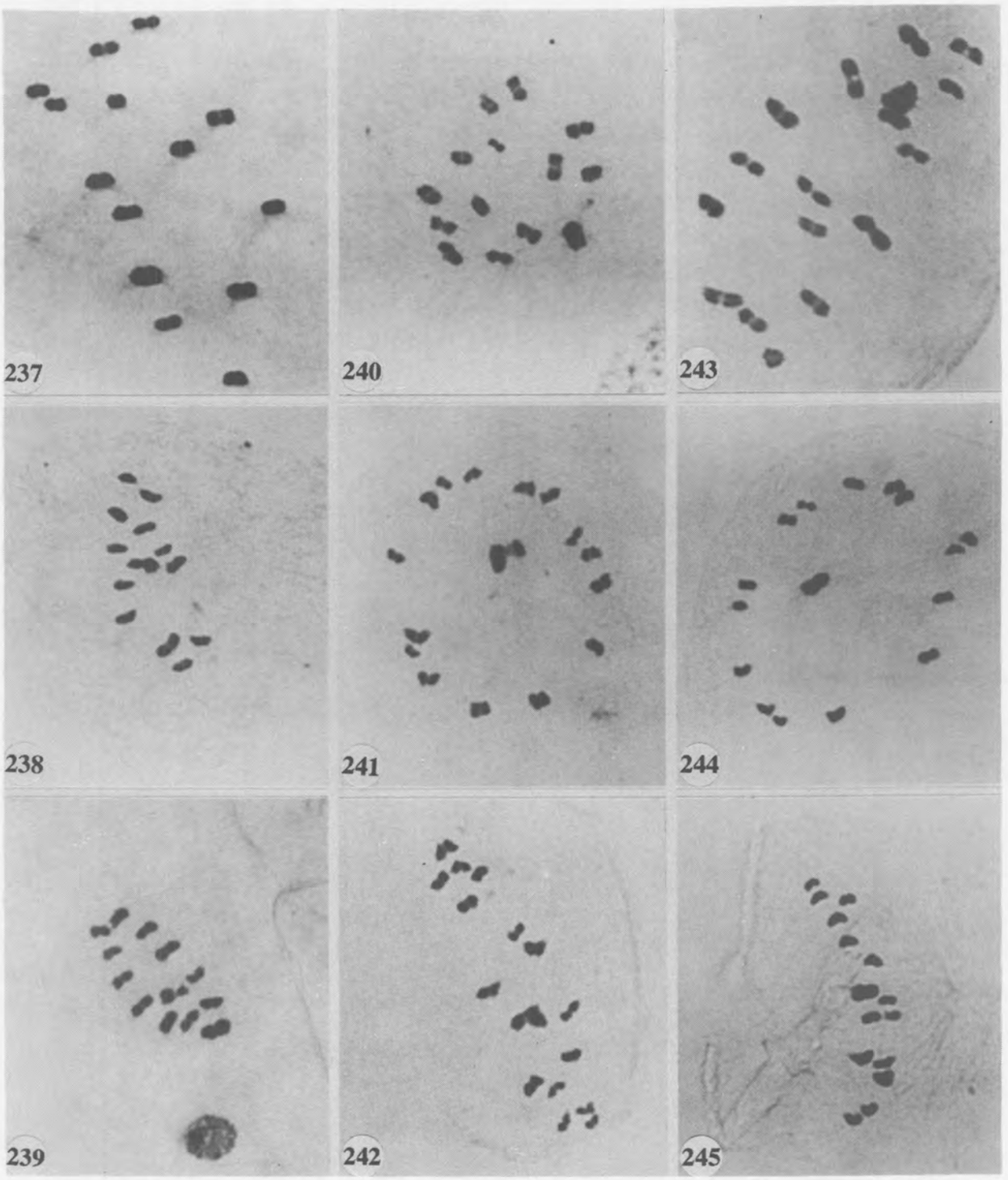
Figs 212-219. Scanning electron photomicrographs of *Miteronotus bucculentus* **gen. et spec. nov.** 212. Male paratype, dorsal aspect. 213. Female paratype, dorsal aspect. 214-217. Different aspects of the left paramere (scale bar = 50 μm). 218-219. Pygophore. 218. Caudal aspect (scale bar = 50 μm). 219. Dorsal aspect.



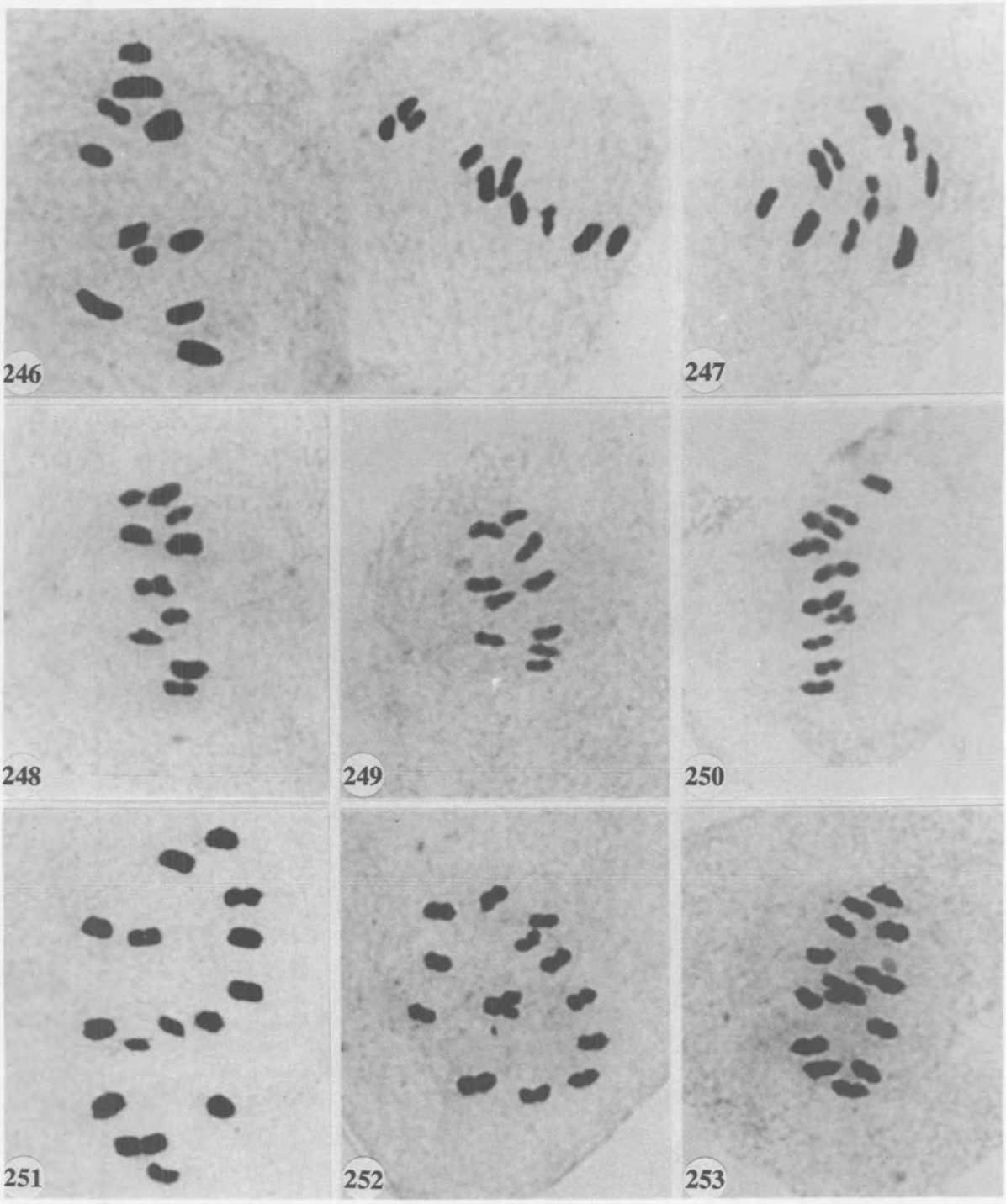
Figs 220-227. Scanning electron photomicrographs of *Miteronotus knysnaensis* **gen. et spec. nov.** 220. Male paratype, dorsal aspect. 221. Female paratype, dorsal aspect. 222-225. Different aspects of the left paramere (scale bar = 50 μm). 226-227. Pygophore. 226. Caudal aspect. 227. Dorsal aspect.



Figs 228-236. Scanning electron photomicrographs illustrating morphological features of *Miteronotus* **gen. nov.** species. 228-232. Sculpture of the first antennal segment of males of *M. knysnaensis* **spec. nov.** 228. First antennal segment of male from Witels forest. 229. Enlargement of indicated area of Fig. 228 showing its peculiar sculpture. 230. Same, showing detail of the sculpture. 231. First antennal segment of male from Kop forest. 232. Enlargement of indicated area of Fig. 230 showing its sculpture. 233. Lateral lobes of the pro- and mesothorax of *M. bucculentus* **spec. nov.** showing setiferous nodules bearing prominent, fairly long setae. 234. Ventral aspect of the head of a male of *M. bucculentus* **spec. nov.** showing the broadly oval, areolate rostral groove. 235-236. Ventral aspect of lateroposterior part of the abdomen of *M. labeosus* **spec. nov.** showing the fusion of ventrites 6 and 7. 235. Male from Ngoye forest. 236. Male from Karkloof.



Figs 237-245. Meiotic stages in *Miteronotus* species. 237-240. *M. labeosus*. 237-238. Specimen from Ngoye forest. 237. Metaphase I. 238. Metaphase II, note the relatively large Y-chromosome. 239-240. Specimen from Karkloof. 239. Metaphase II, note the relatively small Y-chromosome. 240. Metaphase I. 241-245. *M. knysnaensis*. 241-243. Specimen from Diepwalle forest. 241-242. Metaphase II, note the large size difference between the X- and Y-chromosomes. 243. Metaphase I. 244-245. Metaphase II in another specimen from the same locality. Note the small size difference between the X- and Y-chromosomes.



Figs 246-253. Meiotic stages in *Miteronotus* species. 246-250. *M. viginti*. 246-248. Specimens from Isidenge forest. 246. Metaphase I and Metaphase II. 247-248. Metaphase II. 249. Metaphase II in a specimen from Aucland Forest Reserve. 250. Metaphase II in a specimen from Schwarzwald forest. 251-253. *M. bucculentus*. 251. Metaphase I. 252-253. Metaphase II.

Chapter 9

GENUS *DUNDOCORIS* HOBERLANDT.

9.1 *Dundocoris*

Dundocoris was the first apterous carventine genus described from Africa. It was based on a single female from Dundo in Angola described as *Dundocoris vilhenai* by Hoberlandt (1952). Subsequently Hoberlandt also described *Dundocoris basilewskyi* from Ruanda (1956), *Dundocoris callani* and *Dundocoris latebrosus* from South Africa (1959) and *Dundocoris angolensis* also from Angola (1967). Kormilev (1961) described two more species from Natal (South Africa), namely *Dundocoris natalensis* and *Dundocoris stuckenbergi*. Heiss and Jacobs (1989) removed *latebrosus* from *Dundocoris* and erected the genus *Pondocoris* to accommodate it and they also described *Dundocoris nigromaculatus* from South Africa.

Hoberlandt mainly diagnosed the genus on account of

a) relative lengths of the antennae (all subequal)
b) position of the spiracles
c) fused trochanters

None of these characters proved to be reliable and much variation exist in the described species and also in the many undescribed species at hand. A redescription of the genus is thus appropriate.

Redescription:

Apterous. Body oval, incrustate, shining and granular beneath incrustation, in some species body colour in conjunction with incrustation form definite patterns. The following description is based on specimens with the incrustation removed.

Head: Wider across eyes than length (excluding neck area). Genae produced beyond apex of clypeus. Antenniferous lobes prominent, diverging anteriorly. Ocelli absent. Postocular tubercles variously developed, from indistinct to prominent, acute, extending beyond level of outer margins of eyes. Jugae small, triangular. Vertex with three irregularly nodose median ridges; the lateral two ending on jugae or curving laterad to follow the outline of the usually prominent oval interocular callosities; the median ridge extending nearly to the tip of the clypeus where it usually ends in a subapical tubercle. Antennae 4-segmented, longer than width of head, first segment always the thickest, slightly curved, tapering towards base and usually also towards apex, always extending beyond apex of genae; second segment always shorter and much thinner than segment one, slightly curved basally, gradually thickened towards apex; third segment slender, usually the longest and thinnest segment; pedicellate, slightly and evenly thickened towards apex; fourth segment fusiform, thicker than segments 2 and 3, conical apex pilose. Labium shorter than head, 3-segmented, only apical two segments visible

exteriorly, leaving the head through a split-like or elongate oval atrium. Labrum not discernable. Rostral groove well developed, closed posteriorly. Neck slightly constricted behind the head.

Thorax: Dorsum. Pronotum more than 2,5x as wide as long. Collar prominent with 2(1+1) large tubercles laterally and 2(1+1) smaller tubercles dorsolaterally. Pronotum constricted behind the collar. Lateral lobes granulate and usually slightly reflexed so that lobulate propleural margin is visible from above. Disk formed by 2(1+1) shining plates with uneven surface, medially separated by a longitudinal furrow, separated from collar by a depression and a transverse carina which is often also depressed or cleaved medially. Pronotum separated from mesonotum by a prominent transverse sulcus, posterior margin usually cut out medially for the reception of the mesonotal median ridge.

Mesonotum shorter and wider than pronotum, comprising 2(1+1) nearly rectangular plates separated by a median ridge. This ridge usually consist of 2(1+1) longitudinal elevations separated by a longitudinal median depression. In several species however, the two ridges fuse posteriorly to form a bar which may intersect the metanotum.

Metanotum medially shorter but laterally much longer than mesonotum, well delimited laterally from mesonotum by a sulcus which ends in a deep pit adjacent to the median ridge. Median ridge formed by 2(1+1) subrectangular or -triangular elevations which is separated medially by a longitudinal depression and often by the median, posteriorly extended part of the mesonotal ridge. Metanotal median ridge always separated from mesonotal median ridge by a transverse or posteromedially directed furrow. Lateral lobes granular, often not well delimited from disk. Disk with 2(1+1) glabrous comma-shaped elevations anteriorly and a transverse row of nodules on its posterior margin.

MTg 1 usually forming 2(1+1) transverse elevated parts of more or less constant width which are separated medially by a depression. MTg 1 and metanotum variously fused, from totally fused to separated along its total anterior margin by a thin suture (the latter in a few species where MTg I is very much elevated), it is usually fused medially but separated laterally by a suture.

MTg 2 slightly longer than MTg 1, separated from the latter by a thin transverse suture and being depressed relative to MTg 1. Surface of MTg 2 usually relatively smooth except for 2(1+1) longitudinal I- or L-shaped elevations adjacent to median groove and 2(1+1) sublateral ridges directly anterior to sublateral carinae on tergal disk.

Venter. Prosternum usually with an inverted T-shaped elevation. Collar variously developed ventrally of lateral tubercles. Meso- and metasterna smooth, each with a median finely rastrate, slightly depressed oval area.

Legs: Slender, covered with setiferous tubercles. Throchanters fused with femora, not 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. MTg 3-6 fused to form tergal disk which is variously elevated along median line, usually highest on MTg 4. Carinae separating glabrous impressions Y-shaped, variously developed: from well defined to fragmented in series of nodules to almost indiscernible. Sublateral glabrous impressions separated by the Y-shaped carinae that do not reach lateral margin. DELTg 1-3 fused but margin between DELTg 2 and 3 may be indicated by sculpture. DELTg 2-7 of females with a longitudinal sulcus that delimit a dorsal hem that is much less tuberculate than rest of the DELTg.

Dorsal hem darkly coloured on anterior half of each DELTg and light yellowish on posterior half giving it a typical checkered appearance. Posteroexterior angles of DELTg 3-7 and especially 5-7 increasingly protruding. MTg 7 of males raised medially for the reception of the pygophore; paratergites 8 of males short, conical, not reaching apex of pygophore. MTg 7 of females with a transverse ridge near posterior margin; paratergites 8 produced posteriorly as 2(1+1) semi-acute lobes that nearly reach the level of the apex of tergite 9.

Venter. Sternites 1-3 fused. Slightly depressed finely rastrate, oval 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 medially produced anteriad in females to accommodate genitalia. VLTg 3-6 delimited by longitudinal sulci. Ventral hem well developed in females on segments 2-4, variously developed on 5-7. Spiracle 2 ventral, 3-4 variously positioned, 5-7 lateral and visible from above, 8 subterminal on paratergites.

Genitalia: Visible part pygophore pyriform with a rugose surface, dorsally with 2(1+1) median subtriangular elevations separated by a cleft which ends about at level of paratergites 8, ventral of this a oval or elongate pit with carinate margins usually present. In dorsal view, of part usually obscured by MTg 7, 2(1+1) subquadrate "pseudophallic styli" are present just posterior of the visible dorsal parts of the parameres. Female genitalia similar to those of most Carventinae.

Discussion: *Dundocoris* is the most species rich genus of Afrotropical Carventinae. This, to my mind, is partly due to the fact that it has many plesiomorphic characters and is a "dumping ground" for species which does not show obvious apomorphic character states. The genus is very variable (e.g. species with nodulate carinae, species where the suture between the metathorax and MTg 1 is present along the total border, species where the mesonotal ridge is extended posteriorly and may reach MTg 1 or further back, variable spiracle patterns etc.) and it would not be impossible to fragment it into several genera. At this stage, however the relative importance of these characters is uncertain and much more study is necessary before the relationships between the species will be satisfactorily resolved.

Dundocoris is closely related to *Silvacoris* from which it can be distinguished by the presence of the dorsal and ventral hems, the Y-shaped carinae, which usually do not reach the lateral margins of the tergal disk, the non-granulate notal ridge and the different structure of MTg 1 and 2.

9.1.1 *Dundocoris nodulicarinus* spec. nov., Figs 274-293.

Length: ♂ 3,4 - 4,4 mm; ♀ 3,7 - 5,1 mm.

Width: ♂ 1,7 - 2,2 mm; ♀ 1,9 - 2,6 mm.

Diagnostic measurements are given in Tables 9.1-9.3.

Apterous. Body coated with a light yellowish incrustation resulting in a uniform brownish appearance of heavily coated specimens. Slightly incrustate specimens have the body light brownish except for collar, lateral part of MTg 2, the triangular anterior part of DELTg 1+2+3, the anterior halves of all other DELTg's the elevation on the middle of the tergal disk, the posterior part of MTg 7 and tergum 9(♀) or the pygophore (♂) which are dark brown to black. The following description is based on specimens with the incrustation removed.

Head: About 1,05x as wide (across eyes) as long (not including neck.) Genae straight or slightly diverging anteriorly. Postocular tubercles acute, laterally directed, usually reaching to level of outer margins of eyes. Subapical tubercle on clypeus well developed. Antennae about 1,7x as long as width across eyes, first segment tapering towards base and slightly towards apex, extending beyond apex of genae by about half its length; relative lengths of segments: 14:9,6:17:10 (differing slightly between subspecies and sexes).

Thorax: Dorsum. Pronotum about 3x as wide as long. Lateral lobes not well delimited from disk, coarsely granulate, forming a small anterolateral projecting lobe anteriorly. Disk irregularly excavated. Transverse ridge behind collar with a median depression.

Mesonotal median ridge with 2(1+1) parallel ridges, split over total length by a longitudinal suture, usually slightly curving laterad posteriorly and containing as a row of tubercles on posterior margin of mesonotum. Disk smooth anteriorly, adjacent to median ridge and sublaterally adjacent to lateral lobes; irregularly excavated posteriorly in middle. Lateral lobes coarsely granulate, margins straight, converging anteriorly.

Suture separating meso- and metanotum very shallow sublaterally, deeper submedially. Metanotal disk smooth anteriorly and laterally; a transverse row of tubercles indicate its posterior margin where it is completely fused with MTg 1. Lateral lobes coarsely granulate, margins straight or slightly concave. Median ridge with 2(1+1) suboval or subquadrangular elevations separated by a median depression.

MTg 1 completely fused with metanotum and even laterally no indication of a suture is present. MTg 1 slightly and evenly raised relative to metanotum except laterally where it is on a slightly lower level. MTg 1 with 2(1+1) posterolateral diverging elevations adjacent to median depression; 2(1+1) sublateral elevations, lateral of which the surface is relatively smooth while irregular elevations is present between them and the submedian elevations.

MTg 2 subequal in length to MTg 1, separated laterally from it by a suture, medially and submedially by a nearly vertical, abrupt incline as it is on a lower level; with 2(1+1) submedian and 2(1+1) sublateral longitudinal ridges, rest fairly smooth except for some irregular elevations just lateral of submedian ridges.

Venter and Legs: Collar fairly well developed ventral of lateral tubercles. Rest as for genus.

Abdomen: Dorsum. Tergal disk about 1,3x as wide as long in males and 1,13x in females; moderately elevated along median line. Carinae separating glabrous impressions nodulate, usually not reaching lateral margin of tergal disk. DELTg's of females
with well developed dorsal hem and typical checkered pattern. Posteroexterior angles of DELTg 5-7 increasingly protruding.

Venter. Ventral hem in females well developed on VELTg 1-4, less well and sometimes obliterated on 5-6 and usually indistinct on 7. Spiracles 2 ventral; 3-4 sublateral, 3 more than two spiracle widths from lateral margin in females and about 1½ in males, 4 just less than 2 spiracles widths from lateral margin in females and just more than 1 in males; 5-7 lateral and visible from above, 8 subterminal on paratergites.

Genitalia: Pygophore as in Figs 288-293. Removed parameres as in Figs 280-287.

Chromosome number: $2n(\sigma^{\prime}) = 14XY$, $9XY_1Y_2$ or $7XY_1Y_2$.

Habitat and distribution: Coastal and montane evergreen forests in southern Kwazulu-Natal and the Eastern Cape (Fig. 254)

Etymology: Nodulicarinus referring to the nodulate carinae on the tergal disk.

Discussion. *Dundocoris nodulicarinus* is closely related to *Dundocoris marieps* and *Dundocoris transvaalensis* with which it shares the nodulate carinae on the tergal disk, but can be distinguished from both by having no indication of a suture between the metanotum and MTg 1, by having the antennae more than 1,6x as long as width across eyes (less than 1,55x in other two species), by having spiracles 4 much further away from lateral margin, by having MTg 1 less elevated relative to metanotum, by having the longitudinal elevation on the mesonotal median ridge relatively shorter and broader and by its chromosome number. It can also be distinguished from *Dundocoris transvaalensis* by having the lateral margin of the pronotum concave and by having antennal segment 4 only slightly longer than 2 and segment 3 distinctly longer than 1. It can also be distinguished from *Dundocoris marieps* by never having the elevations of the mesonotal median ridge fused, having the tergal disk much wider than long, having antennal segment 2 and 3 relatively shorter and segment 1 not abruptly tapering towards apex.

MATERIAL EXAMINED: See under subspecies.

9.1.1.1 *Dundocoris nodulicarinus nodulicarinus* spec. et subspec. nov., Figs 274, 278, 282, 284, 288-289.

Diagnostic measurements are given in Table 9.1.

Table 9.1. Measurements (in mm) of *Dundocoris nodulicarinus nodulicarinus* spec. nov. from Mpesheni forest.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range	AT#	N	Mean	SD	Range
Total	length	4.05	3	4.07	0.036	4.04-4.11	4.78	2	4.90	0.168	4.77-5.02
	width	1.88	3	1.91	0.054	1.87-1.98	2.29	2	2.34	0.069	2.28-2.39
Head	length	0.78	3	0.76	0.025	0.73-0.79	0.84	2	0.83	0.019	0.81-0.85
	width	0.80	3	0.81	0.006	0.80-0.82	0.85	2	0.86	0.009	0.85-0.87
Pronotum	length	0.49	3	0.47	0.026	0.44-0.49	0.50	2	0.51	0.013	0.50-0.52
	width	1.40	3	1.41	0.018	1.39-1.43	1.52	2	1.55	0.039	1.52-1.58
Tergal disk	length	0.97	3	0.97	0.051	0.92-1.03	1.45	2	1.47	0.021	1.45-1.49
	width	1.24	3	1.27	0.043	1.23-1.33	1.62	2	1.65	0.042	1.61-1.68
Antennal segments	I	0.38	3	0.37	0.011	0.35-0.39	0.40	2	0.39	0.001	0.39-0.40
	II	0.26	3	0.26	0.004	0.25-0.27	0.28	2	0.28	0.009	0.27-0.29
	III	0.43	3	0.46	0.032	0.43-0.50	0.49	2	0.49	0.006	0.48-0.50
	IV	0.26	3	0.27	0.008	0.26-0.28	0.28	2	0.29	0.009	0.28-0.30

* HT = holotype. # AT = allotype.

I could not find any clear-cut and constant morphological differences between the three subspecies although there seem to be (on average) some slight morphometrical differences between them. The nominate subspecies seem to be marginally more elongate than the other two in being about 2,1x (versus 2x) as long as wide and it is also larger than *D. nodulicarinus septeni*.

Chromosome number: 2n(♂) = 14XY

Habitat and distribution: So far it has only been collected in montane evergreen forests in southern Kwazulu-Natal (Fig. 254).

Discussion: I have specifically chosen the 14XY cytotype as the nominate subspecies as the other two chromosome numbers are without doubt derived and the 14XY one probably represents the original chromosome number of the species.

MATERIAL EXAMINED: **SOUTH AFRICA**. **Kwazulu-Natal**. ♂ holotype: Mpesheni forest, nr. Kokstad, 30°38′S 29°40′E, 30.xi.1981, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 10 paratypes as follows: 5♂♂ 5♀♀: same data as holotype (DHJS, TMSA). I have also collected a single male at Lesser Stinkwood forest (30°33′S 29°43′E) that I used for cytogenetic studies.

9.1.1.2 *Dundocoris nodulicarinus novenus* spec. et subspec. nov., Figs. 276-277, 279, 281, 283, 287, 290-291.

Diagnostic measurements are given in Table 9.2.

Table 9.2. Measurements (in mm) of *Dundocoris nodulicarinus novenus* subspec. nov. from Isidenge forest.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range$	AT#	N	Mean	SD	Range$
Total	length	4.09	10	3.94	0.165	3.69-4.32	4.78	10	4.61	0.193	4.24-4.93
	width	1.94	10	1.91	0.092	1.74-2.15	2.48	10	2.38	0.105	2.19-2.57
Head	length	0.78	10	0.76	0.038	0.69-0.84	0.86	10	0.82	0.043	0.76-0.89
	width	0.80	10	0.80	0.029	0.73-0.85	0.88	10	0.85	0.032	0.81-0.93
Pronotum	length	0.47	10	0.45	0.027	0.39-0.52	0.51	10	0.48	0.032	0.43-0.53
	width	1.35	10	1.35	0.066	1.23-1.49	1.56	10	1.50	0.066	1.37-1.61
Tergal disk	length	1.01	10	1.00	0.054	0.89-1.11	1.45	10	1.42	0.061	1.28-1.55
	width	1.32	10	1.29	0.068	1.15-1.44	1.59	10	1.58	0.044	1.45-1.65
Antennal segments	I	0.37	10	0.37	0.011	0.34-0.39	0.42	10	0.40	0.016	0.37-0.43
	II	0.27	10	0.26	0.014	0.23-0.29	0.28	10	0.28	0.013	0.25-0.30
	III	0.48	10	0.46	0.027	0.41-0.53	0.53	10	0.50	0.034	0.43-0.56
	IV	0.28	10	0.27	0.011	0.24-0-29	0.30	10	0.29	0.011	0.27-0.31

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.

Dundocoris nodulicarinus novenus seems to be larger and its third antennal segment relatively longer than in *D. nodulicarinus septeni*.

Chromosome number: $2n(♂) = 9XY_1Y_2$.

Habitat and distribution: It has been collected in various inland and montane forests in the Eastern Cape (Fig. 254).

Etymology: Novenus (L) = nine each, referring to the chromosome number of the subspecies.

MATERIAL EXAMINED: **SOUTH AFRICA**. **Eastern Cape**. ♂ holotype: Isidenge forest, nr. Stutterheim, 32°40′S 27°17′E, 14-17.xii.1981, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 557 paratypes as follows: 17♂♂ 10♀♀: Qacu Forest Reserve, nr. Stutterheim, 32°25′S 27°18′E, 17.xii.1981, D.H. Jacobs (DHJS, TMSA); 1♂ 1♀ Schwarzwald forest, nr. Hogsback, 32°39′S 27°00′E, 16.xii.1981, D.H. Jacobs (DHJS); 316♂♂ 133♀♀: Same data as holotype (DHJS, TMSA); 20♂♂ 20♀♀: ditto, 26-31.i.1984 (DHJS, TMSA); 15♂♂ 15♀♀: S. Afr., Cape, Amatole, Isidenge, block A1, 32°41′S 27°16′E, 14.xi.1987, E-Y: 2511, indig. forest litter, leg. Endrödy-Younga (TMSA); 4♂♂ 2♀♀: S. Afr., Ciskei, Amatole, Pirie For., 32°43′S 27°17′E, 8.xii.1987, E-Y: 2560, indig. forest litter, leg. Endrödy-Younga (TMSA); 1♀: ditto, E-Y: 2564, beating, indig. for. (TMSA); 1♂1♀: ditto, E-Y: 2561, sift. wet for. ditch (TMSA).

9.1.1.3 *Dundocoris nodulicarinus septeni* spec. & subspec. nov., Figs 275, 285-286, 292-293.

Diagnostic measurements are given in Table 9.3.

Table 9.3. Measurements (in mm) of *Dundocoris nodulicarinus septeni* subspec. nov. from Alexandria forest.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range	AT#	N	Mean	SD	Range
Total	length	3.72	10	3.76	0.163	3.47-4.01	4.48	10	4.38	0.264	3.75-4.82
	width	1.83	10	1.89	0.079	1.70-2.00	2.23	10	2.27	0.144	1.94-2.48
Head	length	0.71	10	0.72	0.036	0.65-0.79	0.80	10	0.79	0.053	0.68-0.90
	width	0.77	10	0.76	0.031	0.71-0.83	0.82	10	0.83	0.047	0.73-0.92
Pronotum	length	0.41	10	0.43	0.029	0.38-0.49	0.47	10	0.47	0.038	0.37-0.52
	width	1.34	10	1.36	0.055	1.24-1.44	1.41	10	1.47	0.081	1.30-1.58
Tergal disk	length	0.95	10	0.98	0.031	0.91-1.02	1.32	10	1.34	0.083	1.13-1.46
	width	1.23	10	1.29	0.047	1.19-1.36	1.55	10	1.54	0.071	1.37-1.63
Antennal segments	I	0.37	10	0.36	0.022	0.33-0.39	0.39	10	0.39	0.025	0.33-0.43
	II	0.26	10	0.25	0.016	0.22-0.27	0.28	10	0.27	0.019	0.23-0.30
	III	0.45	9	0.44	0.032	0.39-0.50	0.46	10	0.46	0.040	0.39-0.52
	IV	0.28	9	0.26	0.008	0.25-0.28	0.27	10	0.28	0.013	0.25-0.30

* HT = holotype. # AT = allotype.

Chromosome number: $2n(♂) = 7XY_1Y_2$.

Habitat and distribution: So far it has only been collected in the Alexandria forest nr. Alexandria (Fig. 254).

Etymology: Septeni (L) = seven each, referring to the chromosome number of the subspecies.

MATERIAL EXAMINED: **SOUTH AFRICA. Eastern Cape.** ♂ holotype: Alexandria forest, nr. Grahamstown, 33°43′S 26°24′E, 30.i.1984, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 40 paratypes as follows: 17♂♂ 17♀♀: Same data as holotype (DHJS, TMSA); 1♂: Alexandria forest, 33°43′S 26°22′E, 18.xii.1981, D.H. Jacobs (DHJS); 3♂♂ 2♀♀: S. Afr., SE. Cape Prov., Alexandria For. St., 33°43′S 26°23′E, 6.xii.1987, E-Y: 2555, indig. forest litter, leg. Endrödy-Younga (TMSA).

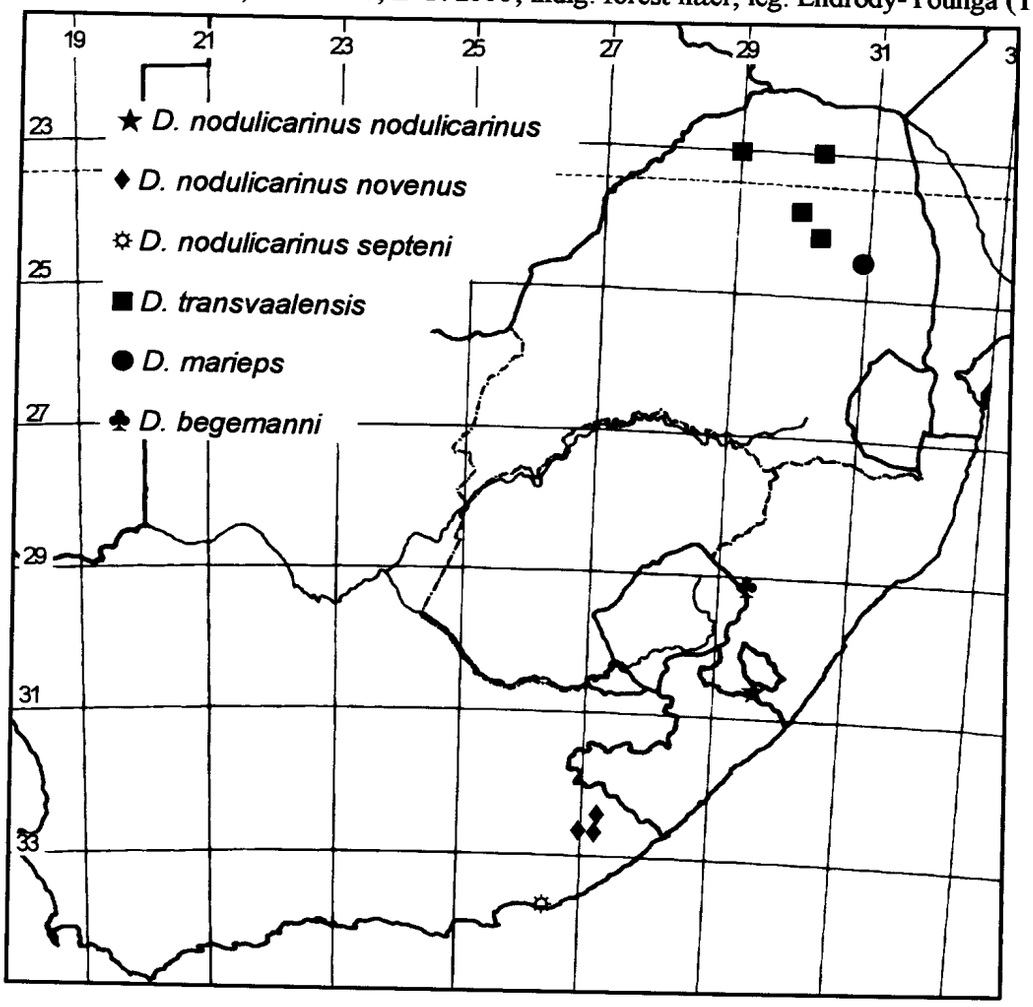


Figure 254. Distribution of *Dundocoris* species and subspecies.

9.1.2 *Dundocoris transvaalensis* spec. nov., Figs 294-301.

Length: ♂ 3,2 - 3,7 mm; ♀ 3,6 - 4,5 mm.
WIdth: ♂ 1,5 - 1,9 mm; ♀ 1,6 - 2,2 mm.
Diagnostic measurements are given in Table 9.4.

Table 9.4. Measurements (in mm) of *Dundocoris transvaalensis* spec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	♂N	Mean	SD	Range$	AT#	♂N	Mean	SD	Range$
Total	length	3.34	15	3.42	0.123	3.24-3.64	3.91	10	3.98	0.123	3.60-4.45
	width	1.62	15	1.67	0.061	1.58-1.82	1.95	10	1.99	0.081	1.69-2.17
Head	length	0.66	15	0.67	0.018	0.63-0.70	0.72	10	0.71	0.022	0.66-0.76
	width	0.72	15	0.74	0.025	0.69-0.79	0.78	10	0.79	0.031	0.74-0.87
Pronotum	length	0.37	15	0.37	0.017	0.34-0.41	0.40	10	0.39	0.016	0.35-0.43
	width	1.16	15	1.18	0.045	1.12-1.26	1.30	10	1.28	0.055	1.14-1.38
Tergal disk	length	0.85	15	0.88	0.033	0.82-0.93	1.20	10	1.17	0.051	1.00-1.36
	width	1.08	15	1.13	0.047	1.04-1.23	1.34	10	1.32	0.068	1.12-1.44
Antennal segments	I	0.30	15	0.31	0.009	0.29-0.35	0.32	10	0.33	0.011	0.29-0.36
	II	0.20	15	0.20	0.010	0.18-0.23	0.21	10	0.21	0.011	0.18-0.23
	III	0.31	15	0.32	0.014	0.29-0.35	0.33	10	0.33	0.018	0.29-0.38
	IV	0.24	15	0.25	0.013	0.23-0.27	0.26	10	0.26	0.008	0.23-0.27

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.
♦ 2♂♂ 2♀♀ from Balloon forest, 1♂ 1♀ from Woodbush forest, 7♂♂ 7♀♀ from Entabeni forest and 5♂♂ from Blouberg Mountain.

Apterous. Body coated with light yellowish incrustation. In specimens not heavily incrustate the notum including MTg 1 usually light, yellowish; most of abdominal terga is somewhat darker, light to dark brown, but usually MTg 2, the anterior triangular part of DELTg 1+2+3, the scent gland protuberance on the tergal disk and in females the dorsal part of the genitalia segment and posterior part of MTg 7 is dark brownish to black, strongly contrasting with the rest of the body. The following description is based on specimens with the incrustation removed.

Head: About 1,1x as wide (across eyes) as long (not including neck). Genae usually straight. Antenniferous lobes prominent. Postocular lobes variously developed, usually acute, directed laterally, reaching to the level of the outer margins of the eyes or slightly beyond. Subapical tubercle on clypeus usually well developed. Antennae about 1,45x as long as width across eyes, first segment tapering towards base and slightly towards apex, extending beyond apex of genae by about one third of its length; relative lengths of segments: 12,5:8:12,5:10.

Thorax: Dorsum. Pronotum about 3,2x as wide as long. Lateral lobes not well delimited from disk; coarsely granulate; lateral margins straight, anteriorly converging; anterolateral angels rounded. Disk irregularly excavated. Transverse ridge behind collar with a median depression.

Median ridge of mesonotum narrow, comprising 2(1+1) longitudinal parallel ridges which are always split in males over total length by a suture, mostly in females also but fused posteriorly in few specimens; ridges usually gradually widening on posterior half. Disk smooth anteriorly, adjacent to median ridge and laterally adjacent to lateral lobes; tuberculate posteromedially, with a transverse

bisinuate row of tubercles on posterior margin which may be confluent with posterolateral extreme of median ridge. Lateral lobes coarsely granulate. Meso/metanotal suture well developed.

Mesonotal disk with a smooth comma-shaped area anterolaterally, tuberculate laterally where it is indistinct from tuberculate lateral lobes, and posteromedially where a transverse row of tubercles is present on posterior margin. Median ridge with 2(1+1) suboval or subquadrangular elevations separated by a median depression in which a central longitudinal bar is often present.

MTg 1 elevated relative to metanotum, laterally separated by a suture which is usually quite well developed but indistinct in some specimens. MTg 1 with 2(1+1) transverse elevations medially, well developed on posterior margin, transforming to irregular nodules anterolaterally, lateral third fairly smooth. These elevations are medially always separated by a depression, some with a indication of a median bar.

MTg 2 subequal in length to MTg 1, on a lower level than it and separated from it by a vertical abrupt decline as well as a suture laterally, with 2(1+1) submedian and 2(1+1) sublateral longitudinal ridges, rest fairly smooth except for some irregularly tubercles just lateral of submedian ridge.

Venter and legs: Collar fairly well developed ventral of lateral tubercles. Rest as for genus.

Abdomen: Dorsum. Tergal disk about 1,3x as wide as long in males and 1,13x in females; moderately elevated along median line but often with the hump on MTg 3 and 4 well developed and abruptly raised. Carinae separating glabrous impressions nodulate, usually very weakly developed or obliterated against lateral margin of tergal disk. Dorsal hem in females usually not distinguishable, sometimes vaguely recognizable, checked pattern of DELTg's present but often of low contrast. Posteroexterior angles of DELTg 5-7 increasingly protruding.

Venter. Ventral hem in females usually recognisable on VELTg 1-3, variously developed on 4-6. Spiracle 2 ventral; 3-4 sublateral, 3 about a spiracle width from lateral margin in females and about ½ - ¾ spiracle widths in males, 4 about half a spiracle width or less from lateral margin in females and ¼ or less in males, often marginally visible from above; 5-7 lateral and visible from above; 8 subterminal on paratergites.

Genitalia: Pygophore as in Figs 300-301. Removed parameres as in Figs 296-299.

Chromosome number: The chromosome number could not unambiguously determined as no metaphase cells were present on the cytogenetical preparations. From the diffuse/diplotene stage it seems that the chromosome number is either 2n(♂) = 26XY or 28XY.

Habitat and distribution: Montane evergreen forests in the Northern Province. This species occur over a wide area in the Northern Province, even in small isolated patches of forest for example Blouberg which is a relative dry evergreen forest (Fig 254).

Etymology: From Transvaal, the former name of the province of South Africa where the species occurs.

Discussion: *Dundocoris transvaalensis* is closely related to *Dundocoris marieps* and *Dundocoris nodulicarinus*. From the former it differs in being smaller, having the lateral margin of the pronotum straight and not concave and the anterolateral angle rounded, by having antennal segment one only slightly and evenly tapering towards apex and segments 1 and 3 relatively shorter, by having the elevations on the mesonotal ridge never fused posteriorly in males (and seldom in females) and by the

different position of spiracles 3 and 4 in females. From the latter it differs as discussed under that species.

MATERIAL EXAMINED: **SOUTH AFRICA. Northern Province.** ♂ holotype: Entabeni forest, nr. Louis Trichardt, 23°00′S 30°16′E, 7-9.v.1978, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 94 paratypes as follows: 1♂ 2♀♀: S. Afr., N. Transvaal, Soutpansberg, Entabeni, 22°28′S 30°15′E, 15.iii.1973, E-Y: 58, sifted compost, leg. Endrödy-Younga (TMSA); 37♂♂ 31♀♀: Same data as holotype (DHJS, TMSA); 7♂♂ 3♀♀: Blouberg mountain, 30 km west Vivo, 23°05′S 29°01′E, 4-5.v.1978, D.H. Jacobs (DHJS, TMSA); 1♂ 2♀♀: Debegeni falls, nr. Tzaneen, 10.ix.1979, D.H. Jacobs (DHJS); 1♂ 1♀: Woodbush forest, Transvaal, 23°50′S 30°00′E, 9.v.1978, D.H. Jacobs (DHJS); 4♂♂ 4♀♀: Balloon forest, Transvaal, 24°11′S 30°19′E, 8-9.x.1977 (DHJS, TMSA).

9.1.3 *Dundocoris marieps* spec. nov., Figs 302-309.

Length: ♂ 3,7 - 4,1 mm; ♀ 4,2 - 4,7 mm.
Width: ♂ 1,7 - 2,1 mm; ♀ 2,0 - 2,4 mm.
Diagnostic measurements are given in Table 9.5.

Table 9.5. Measurements (in mm) of *Dundocoris marieps* spec. nov. from Mariepskop forest.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range$	AT#	N	Mean	SD	Range$
Total	length	3.89	10	3.86	0.110	3.70-4.08	4.56	10	4.52	0.097	4.20-4.65
	width	1.81	10	1.82	0.064	1.74-2.01	2.25	10	2.21	0.069	2.04-2.36
Head	length	0.71	10	0.71	0.018	0.67-0.76	0.80	10	0.76	0.024	0.71-0.81
	width	0.82	10	0.84	0.019	0.81-0.87	0.92	10	0.89	0.033	0.81-0.95
Pronotum	length	0.43	10	0.43	0.014	0.40-0.46	0.46	10	0.45	0.018	0.42-0.50
	width	1.41	10	1.39	0.032	1.31-1.47	1.51	10	1.49	0.044	1.33-1.59
Tergal disk	length	1.04	10	1.02	0.033	0.94-1.08	1.38	10	1.39	0.040	1.29-1.46
	width	1.24	10	1.21	0.045	1.14-1.33	1.44	10	1.43	0.057	1.31-1.53
Antennal segments	I	0.38	10	0.38	0.017	0.35-0.40	0.40	10	0.40	0.007	0.38-0.42
	II	0.21	10	0.22	0.010	0.19-0.24	0.22	10	0.22	0.008	0.20-0.23
	III	0.41	10	0.41	0.019	0.38-0.44	0.43	10	0.42	0.011	0.40-0.44
	IV	0.27	10	0.28	0.013	0.25-0.28	0.29	10	0.28	0.011	0.26-0.30

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.

Apterous. Body coated with a light yellowish brown incrustation resulting in an uniform brownish appearance of heavily coated specimens. Less heavily incrustate specimens with a pattern

similar to the previous species. The following description is based on specimens with the incrustation removed.

Head: About 1,17x as wide (across eyes) as long (not including neck). Genae straight or slightly diverging anteriorly, usually only extending beyond apex of clypeus for a short distance. Antenniferous lobes prominent, lateral margins only slightly diverging. Postocular lobes small, usually not reaching to level of outer margins of eyes.

Subapical tubercle on clypeus usually well developed. Antennae about 1,5x as long as width across eyes, first segment extending beyond apex of genae by just less than half its length, tapering towards base and abruptly towards apex just distal to the curve in the segment, resulting that the inner margin is usually concave; relative lengths of segments: 14:8:15:10, differing slightly between sexes.

Thorax: Dorsum. Pronotum about 3,25x as wide as long. Lateral lobes coarsely granulate, lateral margins prominently concave, anterolateral angle acutely angularly projected, posterolateral angles acutely angular. Disk irregularly excavated. Transverse ridge behind collar with a slight median depression.

Median ridge of mesonotum strongly elevated, comprising 2(1+1) parallel ridges which are usually fused posteriorly (sometimes over the greater part of its length in males), forming a posteriad pointing wedge which usually partly separate the elevations on the metanotal median ridge and extends posteriorly to the anterior margin of MTg 1 as a very narrow longitudinal bar in the median depression. Disk and lateral lobes as in previous species.

Metanotum as in *Dundocoris transvaalensis* except that the median depression is very narrow.

MTg 1 medially and submedially fairly strongly elevated relative to metanotum, laterally separated by a suture. Further as in *D. transvaalensis* except that the two ridges usually meet anteromesally.

MTg 2 subequal in length or longer (especially in females) than MTg 1, very depressed relative to the latter and separated from it by the abrupt vertical decline and a suture laterally; with 2(1+1) submedian and 2(1+1) sublateral longitudinal ridges, the latter very prominent; rest fairly smooth except for some tubercles just laterad of submedian ridges.

Venter and legs: Collar weakly developed ventral of lateral tubercles. Rest as for genus.

Abdomen: Dorsum. Tergal disk about 1,2x as wide as long in males and 1,02x in females, moderately elevated along median line except for the hump on MTg 3 and 4 which is abruptly and strongly elevated. Carinae separating glabrous impressions nodulate, although some variation exist in that the sublateral carinae and those posteriorly on segments 4, 5 and 6 are sometimes entire or have stretches where they are entire; carinae on segment 3 are always nodulate and the median carina in front of the hump is also always nodulate with some nodulations adjacent to it on both sides. Dorsal hem in females well developed displaying the typical checkered colour pattern. Posteroexterior angles of DELTg 5-7 increasingly protruding.

Venter. Ventral hem in females well developed. Spiracle 2 ventral; 3-4 sublateral, 3 about 1 - 1½ spiracle widths from lateral margin in females and 1 or just less in males, 4 about ½ - 1 spiracle widths from lateral margin in females and about ¼ width in males, sometimes marginally visible from above; 5-7 lateral and visible from above; 8 subterminal on paratergites.

Genitalia: Pygophore as in Figs 308-309. Removed parameres as in Figs 304-307.

Chromosome number: 2n(♂) = 28XY.

Habitat and distribution: Probably confined to the montane evergreen forest at Mariepskop in Mpumalanga (Fig 254).

Etymology: From Mariepskop, the type locality of the species. Although the recommended latinisation of the name derived from this locality is "mariepskopensis", I decided on the name "marieps" in accordance with its use in other species unique to this forest, for example the butterfly *Charaxes marieps*.

Discussion: At first I considered to describe *Dundocoris marieps* as a subspecies of *Dundocoris transvaalensis* as some of the differences may probably be explained by allometry. However, after careful consideration of all the differences between these taxa I am convinced that it justifies specific status. Mariepskop is also renowned for its unique fauna and flora and this is yet another example thereof.

MATERIAL EXAMINED: **SOUTH AFRICA**. **Mpumalanga**. ♂ holotype: Mariepskop forest, nr. Hoedspruit, 24°33′S 30°54′E, 4.x.1981, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 80 paratypes as follows: 34♂♂ 37♀♀: Same data as holotype (DHJS, TMSA); 1♂ 4♀♀: S Afr., E. Transvaal, Mariepskop, 24°35′S 30°50′E, 5.v.1981, leg. Endrödy-Younga (TMSA); 2♂♂ 2♀♀: Mariepskop, Transvaal, Humus, viii 1960 (TMSA).

9.1.4 *Dundocoris begemanni* spec. nov., Figs 310-317.

Length: ♂ 3,6 - 3,8 mm; ♀ 4,0 - 4,7 mm.
Width: ♂ 1,6 - 1,8 mm; ♀ 1,8 - 2,2 mm.
Diagnostic measurements are given in Table 9.6.

Table 9.6. Measurements (in mm) of *Dundocoris begemanni* spec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range	AT#	N	Mean	SD	Range
Total	length	3.74	2	3.71	0.045	3.67-3.75	4.33	6	4.29	0.202	4.07-4.64
	width	1.71	2	1.69	0.023	1.67-1.71	1.98	6	1.93	0.103	1.82-2.11
Head	length	0.68	2	0.67	0.012	0.66-0.68	0.73	6	0.72	0.026	0.69-0.77
	width	0.72	2	0.71	0.011	0.70-0.72	0.75	6	0.76	0.013	0.74-0.79
Pronotum	length	0.39	2	0.39	0.005	0.38-0.40	0.43	6	0.42	0.027	0.38-0.46
	width	1.21	2	1.21	0.001	1.21-1.22	1.32	6	1.31	0.049	1.24-1.38
Tergal disk	length	1.01	2	1.02	0.020	1.00-1.04	1.43	6	1.37	0.073	1.28-1.46
	width	1.11	2	1.09	0.019	1.07-1.11	1.21	6	1.25	0.095	1.13-1.41
Antennal segments	I	0.37	2	0.35	0.015	0.34-0.37	0.37	6	0.37	0.012	0.34-0.39
	II	0.23	2	0.22	0.013	0.20-0.23	0.23	6	0.22	0.017	0.19-0.24
	III	0.33	2	0.33	0.003	0.33-0.34	0.34	6	0.33	0.012	0.31-0.35
	IV	0.26	2	0.25	0.004	0.25-0.26	0.27	10	0.26	0.012	0.24-0.27

* HT = holotype. # AT = allotype.

Apterous. Body coated with light yellowish brown incrustation. In specimens at hand the thoracic dorsum is lighter than the abdomen where the tergal disk is darkish brown except for the midline anterior and posterior to the central elevation which is light reddish brown. The following description is based on specimens with the incrustation removed.

Head: About 1,05x as wide (across eyes) as long (excluding neck). Genae straight. Antenniferous lobes prominent, diverging anteriorly. Postocular lobes usually well developed, reaching to level of outer margins of eyes or little beyond. Subapical tubercle on clypeus present. Antennae about 1,6x as long as width across eyes, first segment extending beyond apex of genae by about half its length; relative lengths of segments 14:8,5:13:10.

Thorax: Dorsum. Pronotum about 3,1x as wide as long. Lateral lobes elevated, coarsely granulate, lateral margin slightly concave, anterolateral lobes angularly rounded. Disk irregularly excavated.

Mesonotum with median ridge only slightly elevated, comprising 2(1+1) narrow, parallel elevations separated medially by a prominent furrow. Disk smooth on anterior margin, mesally adjacent to median ridge and laterally adjacent to lateral lobes; tuberculate posteromedially, with a bisinuate transverse row of tubercles on posterior margin. Lateral lobes coarsely granulate, slightly reflexed.

Metanotal disk with 2(1+1) smooth comma-shaped areas anterolaterally, tuberculate laterally where it is indistinct from tuberculate lateral lobes; a transverse row of tubercles is present on its posterior border. Median ridge with 2(1+1) elongate suboval elevations separated by a median depression with a elongate bar-like slight elevation in the centre, the latter usually reaching posteriorly to the posterior margin of MTg 1.

MTg 1 comprising 2(1+1) transverse ridges with smooth but uneven surface, only moderately elevated relative to metanotum; medially separated by a depression with the above mentioned bar-like elevation in its centre. MTg 1 separated anterolaterally from metanotum by a suture and posterolaterally from MTg 2 by a well developed suture.

MTg 2 longer than MTg 1 (especially in females), surface smooth and shining except for 2(1+1) submedian and 2(1+1) sublateral well developed longitudinal ridges; a few small tubercles may be present just lateral of submedian ridges.

Venter and legs: As for genus.

Abdomen: Dorsum. Tergal disk about 1,07x as wide as long in males but about 1,1x as long as wide in females, very flat and only elevated at central hump. Carinae separating glabrous impressions nodulate, weakly developed or obliterated against lateral margin of tergal disk; sublateral carina on MTg 3 usually more elevated and prominent than others and often not nodulate. Dorsal hem of females indistinct and checkered pattern of DELTg's at most vaguely recognizable. Postero-exterior angles of DELTg 3-5 not protruding, that of 6-7 only very slightly.

Venter. Ventral hem in females indistinct. Spiracle 2 ventral; 3-4 sublateral, 3 nearly 2 spiracle widths from lateral margin in females and about 1 spiracle width in males, 4 more than 1 spiracle width from lateral margin in females and about half a spiracle width in males; 5-7 lateral and visible from above; 8 subterminal on paratergites.

Genitalia: Pygophore as in Figs 316-317. Removed parameres as in Figs 312-315.

Chromosome number: 2n(♂) = 26XY.

Habitat and distribution: The specimens have been collected in a small piece (much less than a square kilometre) of indigenous evergreen forest near Injasuti in the Giants Castle National Park in the Kwazulu-Natal Drakensberg mountains (Fig. 254).

Etymology: I dedicate this species to my friend and fellow entomologist Deon Begemann who has accompanied me on various field trips and other adventurous outings.

Discussion: *Dundocoris begemanni* is related to the previous three species but can be distinguished from them by being more elongate oval in general body form with DELTg 5-7 much less protruding and the tergal disk more elongate, it is also much more dorsoventrally compressed with the tergal disk only slightly elevated along the median line. It is probably closest related to *Dundocoris transvaalensis* from which it can (apart from the above-mentioned) be distinguished by having antennal segment 1 extending beyond the genae by about half its length and being decidedly longer than segment 3.

MATERIAL EXAMINED: **SOUTH AFRICA**. **Kwazulu-Natal**. ♂ holotype: nr. Injasuti, Giants Castle Reserve, 29°06'S 29°29'E, 3.ii.1983, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 4♂♂ 8♀♀ paratypes with the same data as the holotype.

9.1.5 *Dundocoris stuckenbergi* Kormilev 1961, Figs 318-333.

Redescription:

Length: ♂ 4,0 - 4,9 mm; ♀ 5,0 - 6,0 mm.

Width: ♂ 1,8 - 2,3 mm; ♀ 2,4 - 3,1 mm.

Diagnostic measurements are given in Tables 9.7 and 9.8.

Apterous. Male oval, female ovate. Body coated with a yellowish incrustation resulting in a chestnut brown appearance. The following description is based on specimens with the incrustation removed.

Head: Marginally wider (across eyes) as long (neck not included). Genae usually slightly diverging anteriorly. Antenniferous lobes prominent, slightly diverging anteriorly. Postocular tubercles small, not reaching to level of outer margins of eyes. Subapical tubercle on clypeus usually well developed. Antennae about 2x as long as width across eyes, first segment long, extending beyond apex of genae by about ⅔ its length, relative lengths of segments: 17:9,7:21,5:10.

Thorax: Dorsum. Pronotum about 3x as wide as long. Lateral lobes not well delimited from disk, densely granulate laterally, lateral margin distinctly concave, strongly diverging posteriorly, anterolateral angles projected anteriorly to collar. Disk irregularly excavated, with 2(1+1) variable smooth areas adjacent to median furrow. Transverse ridge behind collar usually with a slight depression.

Mesonotal median ridge comprising 2(1+1) parallel longitudinal ridges, separated medially by a longitudinal suture except at extreme posterior where they are usually confluent, forming a median

wedge between the elevations of metanotal median ridge, reaching the anterior margin of MTg 1. Disk smooth anteromedially and laterally, further irregularly excavated and with a row of tubercles on its posterior border which often link up with the median ridge. Lateral lobes coarsely granulate, lateral margins straight or very slightly concave.

Metanotal median ridge comprising 2(1+1) suboval elevations well separated by the posterior extension of the mesonotal median ridge. Disk with 2(1+1) sub comma-shaped glabrous areas anteriorly and a transverse row of tubercles on its posterior margin where it is completely fused to MTg 1. Lateral lobes coarsely granulate, lateral margins straight or very slightly concave.

MTg 1 elevated relative to metanotum for median half, rest on same level - comprising 2(1+1) curving ridges running posteriorly and laterally along posterior margin, with uneven surface, separated medially by a prominent furrow; rest of MTg 1 with irregular depressions and elevations.

MTg 2 subequal in length to MTg 1, separated from it by being on a lower level and a suture laterally, surface fairly smooth except for 2(1+1) submedian longitudinal elevations separated by a median furrow and 2(1+1) sublateral longitudinal elevations. The area between these elevations on more or less the same height and elevations often posteriorly confluent with these areas.

Venter and legs: As for genus.

Abdomen: Dorsum. Tergal disk about 1,22x as wide as long in males and 1,08x in females; very moderately elevated along median line. Carinae separating glabrous impressions entire, usually prominent, Y-shaped and not reaching lateral border of tergal disk. Dorsal hem of DELTg 2-7 very well developed in females and even present (although much narrower) in males. Posteroexterior angles of DELTg 4-7 increasingly protruding.

Venter. Ventral hem in females present on all VELTg's. Spiracle 2 ventral, 3 nearly lateral, usually less than a quarter spiracle width from lateral margin but sometimes further in females, usually but not always visible from above; 4-7 lateral and visible from above; 8 subterminal on paratergites.

Genitalia: Pygophore as in Figs 324-325, 332-333. Removed parameres as in Figs 320-323, 328-331.

Chromosome number: 2n(♂) = 26XY or 28XY. The 28XY subspecies (ngomensis) possesses much larger sex chromosome than the 26XY nominate subspecies indicating extensive karyotypic evolution other than fusion or fission of chromosomes.

Habitat and distribution: Montane evergreen forests in Kwazulu-Natal (Fig. 255).

Discussion: *Dundocoris stuckenbergi* can be distinguished from all other species by the combination of its long and slender antennae which are more than 1,95x as long as width across eyes and its spiracle pattern where spiracle 3 is usually visible from above and 4 is always visible from above. *Dundocoris nigromaculatus* also possesses long slender antennae but spiracles 3 and 4 are sublateral, more than one spiracle width from lateral margin and never visible from above; furthermore it is larger, antennal segment 1 is relatively shorter and segment 2 is longer than 4.

Except for the specimens belonging to the two subspecies I also collected a male and female at Dhlinza forest. The male was used to make a cytogenetic preparation. The female is smaller than the other specimens and it possibly represent another subspecies. The chromosome number of the male is 2n = 28XY and its karyotype is very similar to that of *D. stuckenbergi ngomensis*, except that the sex

chromosomes are markedly smaller. I shall refrain from describing it as a subspecies until I have more specimens for comparison and cytogenetic analysis.

9.1.5.1 *Dundocoris stuckenbergi stuckenbergi* Kormilev 1961, Figs 318-325.

Length: ♂ 4,0 - 4,6 mm; ♀ 5,3 - 5,5 mm.
Width: ♂ 1,8 - 2,2 mm; ♀ 2,7 - 2,8 mm.
Diagnostic measurements are given in Table 9.7.

Table 9.7. Measurements (in mm) of *Dundocoris stuckenbergi stuckenbergi* Kormilev.

STRUCTURE		MALES					FEMALES			
		HT*	N*	Mean	SD	Range	N*	Mean	SD	Range
Total	length	4.08	4	4.33	0.240	4.08-4.58	2	5.42	0.058	5.37-5.46
	width	1.90	4	2.02	0.168	1.85-2.20	2	2.73	0.045	2.70-2.77
Head	length	0.79	4	0.79	0.039	0.74-0.84	2	0.87	0.012	0.86-0.89
	width	0.83	4	0.85	0.031	0.81-0.89	2	0.88	0.014	0.87-0.90
Pronotum	length	0.44	4	0.48	0.043	0.43-0.52	2	0.55	0.029	0.53-0.58
	width	1.35	4	1.44	0.094	1.35-1.54	2	1.62	0.053	1.58-1.67
Tergal disk	length	1.07	4	1.13	0.071	1.06-1.21	2	1.64	0.017	1.63-1.66
	width	1.31	4	1.39	0.078	1.31-1.47	2	1.76	0.037	1.73-1.79
Antennal segments	I	0.49	4	0.51	0.026	0.48-0.55	2	0.55	0.022	0.53-0.57
	II	0.29	4	0.30	0.013	0.28-0.33	2	0.33	0.010	0.32-0.34
	III	0.66	4	0.67	0.026	0.64-0.71	2	0.69	0.007	0.68-0.70
	IV	0.30	4	0.31	0.008	0.30-0.33	2	0.29	0.001	0.29-0.30

* HT = holotype.
* All ♂♂ and 1 ♀ from Town Bush, 1 ♀ from Shaws Wood farm.

Chromosome number: 2n(♂) = 26XY.

Habitat and distribution: Montane evergreen forests in the Karkloof area in Kwazulu-Natal (Fig. 255).

This subspecies is morphological indistinguishable from the next one and the only constant difference seem to be the different chromosome number and karyotype.

MATERIAL EXAMINED: **SOUTH AFRICA. Kwazulu-Natal.** ♂ holotype: Town Bush, Pietermaritzburg, 2.ix.1960, B. & P. Stuckenberg (NMSA); 5♂♂ 2♀♀: ditto, 29°33'S 30°20'E, 31.i.1983 D.H. Jacobs (DHJS); 1♂: ditto, Humus, x.1960, Z.A 22 (no collector given) (TMSA); 1♀: Shaws Wood farm, Karkloof, 29°19'S 30°18'E, 31.i.1983, D.H. Jacobs (DHJS).

9.1.5.2 *Dundocoris stuckenbergi ngomensis* subspec. nov., Figs 326-333.

Length: ♂ 4,0 - 4,9 mm; ♀ 5,0 - 6,0 mm.

Width: ♂ 1,8 - 2,3 mm; ♀ 2,4 - 3,1 mm.

Diagnostic measurements are given in Table 9.8.

Table 9.8. Measurements (in mm) of *Dundocoris stuckenbergi ngomensis* subspec. nov. from Ngome forest.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range$	AT#	N	Mean	SD	Range$
Total	length	4.47	10	4.53	0.148	4.05-4.88	5.48	10	5.55	0.294	5.05-5.94
	width	2.09	10	2.12	0.059	1.87-2.23	2.71	10	2.74	0.165	2.46-3.05
Head	length	0.88	10	0.86	0.031	0.77-0.91	0.96	10	0.95	0.035	0.87-0.99
	width	0.90	10	0.88	0.030	0.83-0.94	0.97	10	0.97	0.027	0.89-1.01
Pronotum	length	0.50	10	0.52	0.032	0.42-0.59	0.60	10	0.58	0.030	0.51-0.64
	width	1.49	10	1.54	0.042	1.32-1.49	1.69	10	1.73	0.087	1.51-1.84
Tergal disk	length	1.14	10	1.16	0.046	1.07-1.15	1.57	10	1.63	0.096	1.47-1.79
	width	1.39	10	1.42	0.037	1.29-1.49	1.74	10	1.78	0.085	1.61-1.90
Antennal segments	I	0.55	10	0.53	0.025	0.49-0.56	0.56	10	0.57	0.018	0.52-0.60
	II	0.32	10	0.31	0.021	0.28-0.34	0.32	10	0.31	0.011	0.29-0.33
	III	0.72	10	0.68	0.051	0.59-0.77	0.71	10	0.70	0.031	0.65-0.76
	IV	0.32	10	0.31	0.016	0.29-0.36	0.31	10	0.33	0.017	0.30-0.36

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.

Chromosome number: 2n(♂) = 28XY.

Habitat and distribution: Thus far only collected in the Ngome forest near Louwsburg (Fig. 255).

MATERIAL EXAMINED: **SOUTH AFRICA. Kwazulu-Natal.** ♂ holotype: Ngome forest station, nr. Louwsburg, 27°49′S 31°25′E, 20-24.i.1983, D,H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 71♂♂ 34♀♀ paratypes: ditto (DHJS, TMSA).

9.1.6 *Dundocoris nigromaculatus* Heiss & Jacobs, Figs 334-341.

Length: ♂ 4,2 - 5,3 mm; ♀ 5,2 - 6,8 mm.

Width: ♂ 2,0 - 2,7 mm; ♀ 2,8 - 3,5 mm.

Diagnostic measurements are given in Table 9.9.

Table 9.9. Measurements (in mm) of *Dundocoris nigromaculatus* Heiss & Jacobs.

STRUCTURE		MALES				FEMALES			
		♂N	Mean	SD	Range[$]	♀N	Mean	SD	Range[$]
Total	length	10	4.83	0.316	4.23-5.26	10	6.00	0.425	5.26-6.75
	width	10	2.38	0.126	2.08-2.63	10	3.14	0.216	2.82-3.45
Head	length	10	0.92	0.046	0.81-1.02	10	1.02	0.049	0.92-1.11
	width	10	0.93	0.034	0.85-0.98	10	1.02	0.048	0.94-1.08
Pronotum	length	10	0.60	0.030	0.52-0.65	10	0.66	0.034	0.60-0.76
	width	10	1.65	0.082	1.43-1.77	10	1.86	0.083	1.70-2.09
Tergal disk	length	10	1.29	0.077	1.11-1.40	10	1.87	0.123	1.67-2.10
	width	10	1.57	0.084	1.41-1.71	10	2.00	0.128	1.78-2.18
Antennal segments	I	10	0.47	0.028	0.42-0.50	10	0.52	0.026	0.45-0.54
	II	10	0.33	0.015	0.29-0.36	10	0.36	0.019	0.32-0.39
	III	10	0.71	0.039	0.59-0.78	10	0.74	0.063	0.64-0.84
	IV	10	0.31	0.011	0.28-0.34	10	0.33	0.020	0.30-0.37

[*] HT = holotype. [#] AT = allotype.
[$] May include measurements of specimens other than those used for statistical analysis.
[•] 4♂♂ 5♀♀ from Ngoye forest, 3♂♂ 3♀♀ from Dhlinza forest and 3♂♂ 2♀♀ from Umlalazi nature reserve.

Male. Body oval, shining and granular beneath incrustation. Colour yellowish-brown, black are the anterolateral angles of DELTg 2-7, a spot at middle of the elevation of tergal disk, the pygophore in male, MTg 7 and 8 medially and tergite 9 in female. Lateral margins of body finely granulate, the granules bearing small, stiff erect bristles.

Head: Length including neck/width across eyes 1.02/0.96; anterior process of genae straight with blunt apices, reaching 1/2 of antennal segment 1. Clypeus with a prominent tubercle anterodorsally Antenniferous spines slightly diverging anteriorly, apices acute. Eyes small, globose. Postocular tubercles small and acute, reaching outer border of eyes, posterior margin converging to constricted neck. Vertex with three rows of longitudinal carinae, depressed laterad before eyes. Antennae 2.08x as long as width across eyes, lengths of segments 1-4=0.5:0.387:0.775:0.34; first segment thickest, tapering towards base and apex; second thinner, enlarged posteriorly, third is the longest and twice as long as second, thin, slightly enlarged at apex; fourth fusiform with pilose conical apex. Rostrum short, not reaching posterior margin of head, arising from a slit-like atrium. Rostral groove wide and closed posteriorly, its lateral margins granulate.

Thorax. Pronotum length/width across posterior lobes 0.625/1.75, with a thick, ring-like collar which bears 2(1+1) small round tubercles dorsolaterally and 2(1+1) large, projecting tubercles laterally on a lower level. Lateral lobes slightly upturned, surface densely granular, incised before collar. Anterolateral angles projecting over collar. Posterolateral lobes rounded, projecting, lateral margins

granulate and concave. Disk separated from collar by a deep sulcus and a transversal carina, with a longitudinal groove widening at base. Surface rugose. Posterior margin convex.

Mesonotum wider than pronotum, width across posterior lobe 2.25 mm. Subtriangular median elevation with a longitudinal sulcus anteriorly, producing posteriorly into a thin ridge which reaches anterior margin of MTg 2. Lateral lobes with 2(1+1) smooth oblique plates adjacent to median ridge, then rugose, lateral margins slightly reflexed, granulate and converging anteriorly.

Metanotum longer and wider than mesonotum, width across posterior lobe 2.5, with 2(1+1) elevated oval sclerites laterad of projecting metanotal ridge; fused with bisinuate MTg 1 which has the shape of 2(1+1) curved, elevated transversal ridges. Lateral lobes with 2(1+1) smooth round plates with a row of distinct granules posteriorly, then rugose, lateral margins reflexed and converging anteriorly, constricted posteriorly.

MTg 2 depressed, separated from MTg 1 anterolaterally by a thin suture, with 2(1+1) L-shaped elevations laterad of median groove and 2(1+1) short ridges on posterolateral angles.

Abdomen. Tergal plate with deep glabrous impressions, the submedian ones separated by Y-shaped carinae which do not reach lateral margin of tergal disk, roundedly elevated along median line with highest point on posteriorly producing MTg 3. Around scent glands surface transversely striate. DELTg 1-3 fused, reaching anteriorly to posterolateral angle of metanotum. Posteroexterior angles of DELTg 2-7 with small but increasing rounded lobes, formed by the reflexed ventral laterotergites. Surface of DELTg's rugose.

MTg 7 in male raised medially, with a feeble transverse ridge before posterior margin and 2(1+1) prominent tubercles anterolaterally. Pygophore pyriform with rugose surface (Figs 340-341), paratergites 8 slender, not reaching apex of pygophore. Parameres as Figs 336-339.

MTg 7 in female with a transverse granular carina posteriorly, paratergites 8 produced posteriorly, not reaching apex of tricuspidate tergite 9.

Ventral side: Pro-, meso- and metasternum separated by a sulcus, with 2(1+1) lateral projections which are contiguous with coxae. Sternites 1-3 fused. Spiracles 2 ventral, far from lateral margin, 3 and 4 ventral and close to margin, 5-7 lateral and visible from above, 8 subterminal.

Legs: slender, trochanters fused with femora, parempodia and pseudopulvilli present.

Chromosome number: 2n(♂) = 20XY.

Habitat and distribution: Coastal and Montane evergreen forests in northern Kwazulu-Natal (Fig. 255).

Etymology: Nigromaculatus = 'black spot' referring to the black coloration of the central hump of the tergal disk.

Discussion: *D. nigromaculatus* can be distinguished from all other species by a combination of its long antennae (more than 2x as long as width across eyes), its large size and antennal segment 2 being distinctly longer than segment 4. It is related to *D. stuckenbergi* and *D. flavilineatus* from which it can be distinguished as discussed under those species respectively.

MATERIAL EXAMINED: Holotype ♂: South Africa, Kwazulu-Natal, St. Lucia 25. x.81 leg. Klapperich (BMNH); 192 paratypes as follows: 2♂♂ 2♀♀: collected with holotype (EHIA); 6♂♂ 3♀♀: Kwazulu-

Natal, Umlalazi Nat. Reserve nr. Mtunzini, 28°58'E, viii.85 (EHIA); 14♂♂ 6♀♀: ditto. 21-23.viii.1985, (DHJS); 9♂♂ 5♀♀: Kwazulu-Natal, Ngoye Forest, 28°50'S 31°43'E (EHIA); 68♂♂ 20♀♀: ditto, ll-12.xii.1980, (DHJS); 10♂♂ 8♀♀: ditto, 22.viii.1985 (DHJS); 12♂♂ 8♀♀: Kwazulu-Natal, Dhlinza Forest, nr. Eshowe, 24°54'S 31°27'E (EHIA); 8♂♂ 8♀♀: ditto, 21.viii.1985 (DHJS); 3♀♀: ditto, 12.iv.1980 (DHJS).

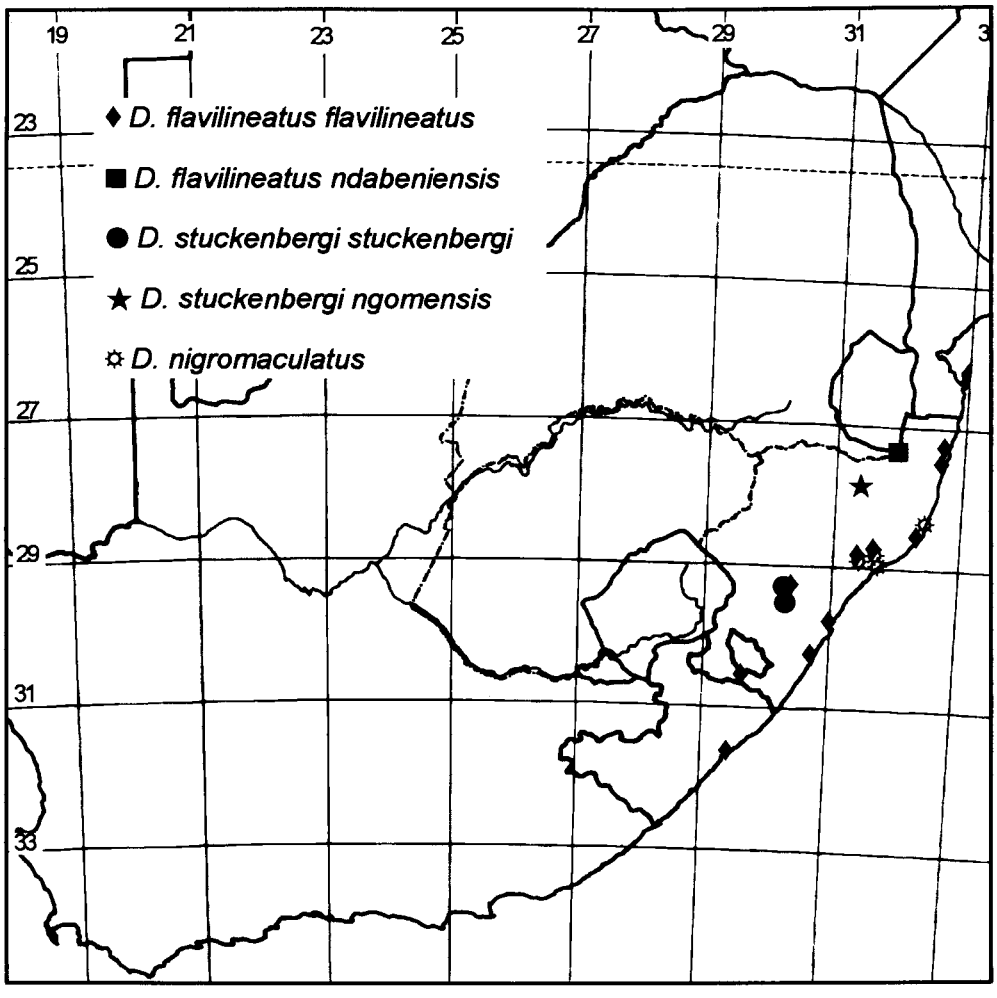


Figure 255. Distribution of *Dundocoris* species and subspecies.

9.1.7 *Dundocoris flavilineatus* spec. nov., Figs 342-357.

Length: ♂ 4,2 - 5,7 mm; ♀ 5,7 - 7,2 mm.

Width: ♂ 1,9 - 2,9 mm; ♀ 2,7 - 3,8 mm.

Diagnostic measurements are given in Tables 9.10 and 9.11.

Apterous. Broadly oval. Body coated with a whitish incrustation forming a characteristic colour pattern in specimens not heavily coated (presumably younger specimens). Thorax, including MTg 1 white but with 2(1+1) sub-comma-shaped glabrous non-incrustate chestnut-brown areas on mesonotum, 2(1+1) comma-shaped ones on metanotum and a few small ones on pronotum; MTg 2 white medially but dark brown or chestnut brown and non-incrustate laterally, visible as 2(1+1) sinuate

transverse dark bands; tergal disk with non-incrustate yellowish-white or yellowish brown median band with the central part of the hump often brownish (but not black as in previous species), lateral of this with white incrustation except for callosities which are brown and non-incrustate; DELTg's with white incrustation (except for callosities medially) but dorsal hem in females non-incrustate and with typical checkered pattern; MTg 7 white anteriorly, brown posteriorly; head, collar and genitalia mostly brown. The following description is based on specimens with the incrustation removed.

Head: As wide (across eyes) as long (neck not included). Genae usually straight. Antenniferous lobes prominent, diverging anteriorly. Postocular tubercles small, not reaching level of outer margins of the eyes. Subapical tubercle on clypeus well developed. Antennae about 1,6x as long as width across eyes, first segment extending beyond apex of genae by less than half its length, relative lengths of segments: 13,5:8,5:19:10.

Thorax: Dorsum. Pronotum about 3,1x as wide as long. Lateral lobes densely granulated, rectangularly projected anteriorly to level of anterior margin of collar, posterolateral angles strongly projected laterally, lateral margin strongly concave, strongly converging anteriorly. Disk irregularly excavated with 2(1+1) variable smooth areas adjacent to median furrow. Transverse ridge behind collar with prominent median depression.

Mesonotal median ridge comprising 2(1+1) parallel, fairly narrow, longitudinal ridges, separated medially by a longitudinal furrow except at extreme posterior where they are usually confluent forming a median bar between the elevations of the metanotal median ridge, often extending posteriorly to the posterior margin of MTg 1 or beyond, even to the posterior margin of MTg 2. Disk with narrow smooth areas, anteromedially, anteriorly and sublaterally, rest irregularly excavated and with a row of tubercles on its posterior border which often link up with the median ridge. Lateral lobes granulated, reflexed with posterolateral angles produced laterally.

Metanotal median ridge comprising 2(1+1) suboval elevations, well separated by the posterior extension of the mesonotal median ridge. Disk with 2(1+1) prominent comma-shape glabrous areas anteriorly and a transverse row of tubercles on its posterior margin where it is fused to MTg 1; rest irregularly granulated. Lateral lobes granulated, lateral margins straight, converging anteriorly.

MTg 1 with 2(1+1) transverse curving ridges on its posterior margin and 2(1+1) roundish sublateral elevations anterior to ridge; rest fairly smooth but some irregular nodulations may be present. Ridges medially well separated by a depression.

MTg 2 subequal in length to MTg 1, separated from it laterally by a suture and submedially by being on a lower level, medially completely fused, often with a bar-like slight elevation confluent with posterior extension of mesonotal ridge. Surface of MTg 2 fairly smooth except for 2(1+1) submedian longitudinal elevations (always well separated by a median depression) and 2(1+1) sublateral elevations.

Venter and legs: As for genus.

Abdomen: Dorsum. Tergal disk about 1,22x as wide as long in males and 1,05x in females; only slightly elevated along median line which is, even in the specimens with the incrustation removed, of lighter coloration than rest of tergal disk. Carinae usually entire but knobbly adjacent to the longitudinal median elevation, in some specimens the transverse carinae are broken up into irregular nodules. Irregular nodules are usually present on MTg 3 between median elevation and glabrous

impression and often on some of the other MTg's as well. Dorsal hem in females prominent on all DELTg's and in males also present on DELTg 1-4. Checkered pattern of DELTg's present, but not as prominent as in *Dundocoris nigromaculatus*. Posteroexterior angles of DELTg 5-7 increasingly protruding.

Venter. Ventral hem in females well developed, sometimes recognizable in males on VELTg 2-4. Spiracle 2 ventral, 3-4 sublateral, 3 more than 2 spiracle widths from lateral margin in both sexes (mediad to margin of ventral hem in females), 4 about 1½ spiracle widths from lateral margin in males and about 2 spiracle widths in females, on margin of ventral hem, 5-7 lateral and visible from above, 8 subterminal on paratergites.

Genitalia: Pygophore as in Figs 346-349. Removed parameres as in Figs 350-357.

Chromosome number: 2n(♂) = 28XY or $27X_1X_2Y$.

Habitat and distribution: Montane and coastal evergreen forests in Kwazulu-Natal (Fig. 255).

Etymology: Flavilineatus = longitudinal yellow stripe, referring to the yellowish colour of the median line of the tergal disk.

Discussion: In size and general appearance *Dundocoris flavilineatus* is similar to *Dundocoris nigromaculatus* but it can be distinguished by the lack of the black spot and the presence of a yellow band on the tergal disk; by antennal segment 2 being relatively shorter; by its different chromosome number and the relatively wider and stronger anteriorly converging lateral margins of the prothorax. From other *Dundocoris* species its large size immediately sets it apart except perhaps from *Dundocoris stuckenbergi* from which it can immediately be distinguished by spiracles 3 and 4 being sublateral, remote from lateral margin of body, by its shorter first antennal segment and by its broadly oval body form.

Two subspecies are recognized at this stage, one widespread in Kwazulu-Natal and Eastern Cape with a chromosome number of 2n(♂) = 28XY and the other apparently restricted to the Ndabeni forests near Josini with a 2n(♂) = $27X_1X_2Y$.

MATERIAL EXAMINED: See under the subspecies.

9.1.7.1 *Dundocoris flavilineatus flavilineatus* spec. and subspec. nov., Figs 342-344, 346-347, 350-354.

Length: ♂ 4,2 - 5,6 mm; ♀ 5,7 - 6,5 mm.
Width: ♂ 1,9 - 2,8 mm; ♀ 2,7 - 3,4 mm.
Diagnostic measurements are given in Table 9.10.

Table 9.10. Measurements (in mm) of *Dundocoris flavilineatus flavilineatus* spec. & subspec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	♂N	Mean	SD	Range§	AT#	♀N	Mean	SD	Range§
Total	length	5.27	12	4.92	0.316	4.22-5.60	6.22	12	6.14	0.279	5.71-6.49
	width	2.65	12	2.38	0.200	1.90-2.80	3.34	12	3.11	0.216	2.73-3.39
Head	length	1.01	12	0.93	0.059	0.82-1.04	1.15	12	1.05	0.056	0.97-1.15
	width	1.00	12	0.92	0.050	0.83-1.03	1.07	12	1.03	0.042	0.97-1.11
Pronotum	length	0.63	12	0.56	0.046	0.47-0.67	0.72	12	0.64	0.037	0.58-0.72
	width	1.91	12	1.73	0.125	1.44-1.98	2.13	12	1.93	0.091	1.79-2.13
Tergal disk	length	1.39	12	1.27	0.094	1.05-1.48	1.94	12	1.88	0.123	1.66-2.08
	width	1.71	12	1.57	0.117	1.29-1.82	2.13	12	1.97	0.104	1.78-2.13
Antennal segments	I	0.44	12	0.40	0.022	0.35-0.47	0.49	12	0.44	0.030	0.39-0.49
	II	0.29	12	0.26	0.023	0.21-0.29	0.31	12	0.28	0.020	0.23-0.31
	III	0.70	12	0.57	0.059	0.48-0.70	0.73	12	0.63	0.063	0.53-0.73
	IV	0.33	12	0.30	0.021	0.26-0.33	0.35	12	0.32	0.014	0.30-0.35

* HT = holotype. # AT = allotype.
§ May include measurements of specimens other than those used for statistical analysis.
♦ 4♂♂ 3♀♀ from Ngoye forest, 4♂♂ 4♀♀ from Manzengwenya, 4♂♂ from Scottburgh, 4♀♀ from Ehlatini farm and 1♀ from Shaws Wood farm.

The nominate subspecies occurs widespread in Kwazulu-Natal and Eastern Cape and has a chromosome number of 2n(♂) = 28XY.

MATERIAL EXAMINED: **SOUTH AFRICA. Kwazulu-Natal.** ♂ holotype: Ngoye forest reserve, nr Empangeni, 28°50′S 31°43′E, 11-12.xii.1980, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 135 paratypes as follows: 1♂ 7♀♀: Manzengwenya, Kwazulu, 27°16′S 32°46′E, 3-7.xii.1980, D.H. Jacobs (DHJS, TMSA); 18♂♂ 4♀♀: nr. Manzengwenya, Kwazulu, 27°18′S 32°45′E, 6.xii.1980, D.H. Jacobs (DHJS, TMSA); 2♂♂ 1♀: Sordwana Bay, Natal, 27°32′S 32°40′E, 23.vii.1977, D.H Jacobs (DHJS); 3♀♀: ditto, 4.ix.1978 (DHJS); 1♀: Nhlabane forest nr. St. Lucia, 2832 CB, 3.ii.1991, M. Vogt (DHJS); 3♂♂ 3♀♀: nr. Maphelana, Natal, 28°26′S 32°25′E, 10.xii.1980, D.H. Jacobs (DHJS); 33♂♂ 8♀♀: Same data as holotype (DHJS, TMSA); 13♂♂ 4♀♀: Dhlinza forest, Eshowe, 24°54′S 31°27′E, 12.iv.1980, D.H. Jacobs (DHJS, TMSA); 2♂♂: ditto, 21.viii.1985, (DHJS); 1♂ 4♀♀: Shaws Wood farm, Karkloof, 29°19′S 30°18′E, 1.ii.1983, D.H. Jacobs (DHJS); 4♀♀: Ehlatini farm, Karkloof, 29°19′S 30°17′E, 1.ii.1983, D.H. Jacobs (DHJS, TMSA); 1♀: Umhlanga Rocks Nature Reserve, nr. Durban 29°42′S 31°06′E, 11.ix.1991, D.H. Jacobs (DHJS); 1♂ 2♀♀: nr. Durban, 29°45′S 31°04′E, 4.iv.1980, D.H. Jacobs (DHJS); 10♂♂ 3♀♀: nr. Scottburgh, 30°15′S 30°46′E, 25.i.1983, D.H. Jacobs (DHJS, TMSA); 1♂: Lesser Stinkwood forest, nr. Kokstad, 30°33′S 29°43′E, 29.xi.1981, D.H. Jacobs

(DHJS); 3♂♂ 1♀: Mpsheni forest nr. Kokstad, 30°38′S 29°40′E, 30.xi.1981, D.H. Jacobs (DHJS). **Eastern Cape**. 1♀: Mount Thesiger Nature Reserve, Port St. Johns, 31°37′S 29°31′E, 4-5.xii.1981 D.H. Jacobs (DHJS).

9.1.7.2 *Dundocoris flavilineatus ndabeniensis* subspec. nov., Figs 345, 348-349, 355-357.

Length: ♂ 5,6 mm; ♀ 6,7 - 7,2 mm.
Width: ♂ 2,8 mm; ♀ 3,1 - 3,8 mm.
Diagnostic measurements are given in Table 9.11.

Table 9.11. Measurements (in mm) of *Dundocoris flavilineatus ndabeniensis* subspec. nov. from Ndabeni forest.

STRUCTURE		MALE	FEMALES				
		HT*	AT#	N	Mean	SD	Range
Total	length	5.61	6.91	10	6.96	0.151	6.72-7.13
	width	2.79	3.34	10	3.41	0.185	3.18-3.74
Head	length	1.02	1.13	10	1.15	0.031	1.10-1.19
	width	1.03	1.15	10	1.16	0.026	1.12-1.20
Pronotum	length	0.64	0.71	10	0.72	0.020	0.69-0.76
	width	1.98	2.26	10	2.29	0.050	2.22-2.39
Tergal disk	length	1.43	2.10	10	2.10	0.043	2.04-2.18
	width	1.79	2.28	10	2.27	0.070	2.17-2.39
Antennal segments	I	0.44	0.48	10	0.48	0.016	0.45-0.50
	II	0.29	0.32	10	0.31	0.008	0.29-0.33
	III	0.68	0.63	10	0.68	0.037	0.63-0.75
	IV	0.33	0.36	10	0.35	0.007	0.34-0.37

* HT = holotype. # AT = allotype.

Apart from being larger than the nominate subspecies and the different chromosome number of $2n(♂) = 27X_1X_2Y$, there seem to be no clear-cut morphological differences between them. This subspecies is probably restricted to the Ndabeni forests near Josini.

Etymology: From Ndabeni, the type locality.

MATERIAL EXAMINED: **SOUTH AFRICA. Kwazulu-Natal**. ♂ holotype: Ndabeni forest, nr. Josini, 27°22′S 32°00′E, 24.i.1983, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 1♂ 12♀♀ paratypes: ditto. (DHJS, TMSA).

9.1.8 *Dundocoris schoemani* spec. nov., Figs 358-374.

Length: ♂ 3,5 - 4,2 mm; ♀ 4,0 - 5,1 mm.

Width: ♂ 1,7 - 2,0 mm; ♀ 1,9 - 2,6 mm.

Diagnostic measurements are given in Tables 9.12 and 9.13.

Apterous. Male oval, female subovate. Body coated with a yellowish incrustation resulting in a overall brownish appearance of the insect, the thorax usually lighter than the abdomen. The following description is based on specimens with the incrustation removed:

Head: Slightly wider (across eyes) as long (neck not included). Genae straight or slightly diverging anteriorly. Antenniferous lobes prominent, slightly diverging anteriorly. Postocular tubercles small, usually not reaching the level of the outer margins of the eyes. Subapical tubercle on clypeus prominent. Antennae about 1,8x as long as width across eyes, first segment extending beyond apex of genae by about half its length, third segment long and slender, relative lengths of segments: 15,5:10:21:11 (differing slightly between the subspecies).

Thorax: Dorsum. Pronotum about 3x as wide as long. Lateral lobes not well delimited from disk, densely granulated, laterally projected anteriorly to level of anterior margin of collar or beyond; lateral margin slightly concave, diverging posteriorly. Disk irregularly excavated. Transverse ridge behind collar usually with a median depression.

Mesonotal median ridge comprising 2(1+1) parallel, fairly broad, posteriorly widening, longitudinal ridges, separated medially by a prominent and fairly wide longitudinal furrow, ridges never converging posteriorly. Disk smooth anteromedially, anteriorly and sublaterally adjacent to lateral lobes; irregularly excavated posteriorly in middle and one or two tubercles may occur posteromedially where the may link up with the median ridge. Lateral lobes densely granulate, lateral margins straight or slightly rounded.

Metanotal median ridge comprising 2(1+1) subquadrangular elevations, separated by a median depression. Disk with 2(1+1) roughly comma-shaped glabrous areas anteriorly and a transverse row of tubercles on its posterior margin where it is completely fused with MTg 1; rest with some irregular nodules and excavations. Lateral lobes granulate, lateral margins straight, slightly converging anteriorly.

MTg 1 with 2(1+1) transverse ridges on its posterior margin, dilating medially where they occupy the total length of MTg 1 and are separated by only a slight depression; rest with irregular surface and nodulations.

MTg 2 medially shorter than MTg 1 in males, subequal in females, separated from the latter by a suture and being abruptly depressed over its total width. The 2(1+1) submedian 2(1+1) sublateral longitudinal elevations are sometimes connected by a transverse elevation on the posterior margin in front of which some irregular nodules may occur.

Venter and legs: As for genus.

Abdomen: Dorsum. Tergal disk about 1,29x as wide as long in males and 1,18x in females; moderately elevated along median line. Carinae separating glabrous impressions Y-shaped, usually

entire but margins often uneven and median carina on MTg 3 sometimes broken up in irregular nodules. Nodules usually present between median carina and glabrous impressions especially on MTg 3, 5 and 6. Dorsal hem in females present on all DELTg's, usually not or only vaguely discernable in males. Posteroexterior angles of DELTg 5-7 increasingly protruding.

Venter. Ventral hem in females present on all VELTg's but usually not prominent. Spiracle 2 ventral, 3 lateral or very nearly so and visible from above, 4-7 lateral and visible from above, 8 subterminal on paratergites.

Genitalia: Pygophore as in Figs 365-366, 373-374. Dorsal view of unremoved parameres (Figs 366, 374) shows that the median part is well elevated in relation to the rest. This elevated part is also evident in the removed parameres (Figs 361-364, 369-372).

Chromosome number: 2n(♂) = 26XY.

Habitat and distribution: Evergreen montane and coastal forests in the Eastern Cape.

Etymology: I have pleasure in dedicating this species to my friend and fellow entomologist, Dr. A.S. Schoeman who has been of great assistance to me in difficult circumstances.

Discussion: *Dundocoris schoemani* is set apart from all other species by the combination of its spiracle pattern where spiracle 3 is always visible from above, its relatively long 3rd antennal segment which is about 1,36x as long as segment 1 and more than twice as long as segment 2, and its mesonotal median ridge where the longitudinal elevations never converge or meet posteriorly.

It shares the same spiracle pattern with *Dundocoris stuckenbergi* but can immediately be distinguished by its relatively shorter antennae (less than 1,9x as long as width across eyes) and shorter antennal segment 1 (extending beyond apex of genae by just about half its length), and its mesonotal median ridge as discussed above.

Dundocoris schoemani is closely related to *Dundocoris scholtzi* from which it can be distinguished by the lateral position of spiracle 3, and by having antennal segment 3 more than 1,3x as long as segment 1 (less than 1,1x in the latter), MTg 1 which is medially longer than MTg 2 in males and the mesonotal ridge as discussed above.

Two subspecies are currently recognized, mainly on account of different karyotypes.

9.1.8.1 *Dundocoris schoemani schoemani* spec. et subspec. nov., Figs 359-366.

Length: ♂ 3,7 - 4,2 mm; ♀ 4,4 - 5,1 mm.
Width: ♂ 1,7 - 2,0 mm; ♀ 1,9 - 2,6 mm.
Diagnostic measurements are given in Table 9.12.

Table 9.12. Measurements (in mm) of *Dundocoris schoemani schoemani* spec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	♂N	Mean	SD	Range$	AT#	♀N	Mean	SD	Range$
Total	length	3.97	10	3.98	0.110	3.78-4.13	4.76	10	4.75	0.183	4.47-5.07
	width	1.80	10	1.84	0.062	1.73-1.93	2.27	10	2.30	0.130	1.99-2.53
Head	length	0.71	10	0.71	0.016	0.68-0.73	0.80	10	0.78	0.022	0.74-0.82
	width	0.77	10	0.76	0.019	0.72-0.79	0.84	10	0.82	0.029	0.77-0.87
Pronotum	length	0.49	10	0.48	0.020	0.43-0.50	0.52	10	0.52	0.040	0.45-0.59
	width	1.39	10	1.38	0.041	1.28-1.44	1.48	10	1.51	0.067	1.38-1.61
Tergal disk	length	0.97	10	0.99	0.033	0.94-1.04	1.33	10	1.32	0.062	1.21-1.44
	width	1.24	10	1.25	0.032	1.19-1.30	1.46	10	1.52	0.058	1.43-1.64
Antennal segments	I	0.39	10	0.38	0.010	0.36-0.42	0.41	10	0.41	0.009	0.39-0.43
	II	0.25	10	0.25	0.007	0.22-0.26	0.25	10	0.26	0.012	0.24-0.29
	III	0.50	10	0.53	0.024	0.49-0.59	0.56	10	0.57	0.028	0.52-0.61
	IV	0.26	10	0.27	0.009	0.25-0.29	0.29	10	0.28	0.008	0.27-0.30

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.
♦ 3♂♂ 3♀♀ from Kambi Forest Reserve, 3♂♂ 3♀♀ from Ku-Manina forest and 4♂♂ 4♀♀ from Baziya forest.

Chromosome number: 2n(♂) = 26XY.

The nominate subspecies is very similar to *D. schoemani dwesaensis* and the only reliable differences seem to be the different karyotype. In the former all the autosomes form a gradual size series while the largest autosome of *D. schoemani dwesaensis* is distinctly larger than the next largest one (compare Figs 267 and 268). On average *D. schoemani dwesaensis* is smaller and little stouter than *D. schoemani schoemani* resulting in a more transverse tergal disk (1,32x as wide as long in males and 1,20x in females versus 1,27x and 1,15x respectively). There is also on average a slight difference in the relative length of the antennal segments (15,3:10:20,8:11,5 in *D. schoemani dwesaensis* and 15,5:10:21,4:10,8 in *D. schoemani schoemani*). It is, however, often impossible to classify individuals on account of these small differences and for example, the specimens from Ntsubane forest and Silaka forest are intermediate in some of these characters. They are included in the nominate subspecies but it may prove to be a mistake when their karyotype becomes known.

Habitat and distribution: So far the nominate subspecies has mainly been collected in montane evergreen forests of the Eastern Cape.

MATERIAL EXAMINED: **Eastern Cape**. ♂ holotype: Baziya forest, nr. Umtata, 31°34′S 28°25′E, 8-9.xii.1981, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 152 paratypes as follows: 2♂♂ 2♀♀: S. Afr. Transkei, Ntsubane forest, 31°27′S 29°44′E, 25.xi.1987, E-Y:2537, fungi & for. litter, leg.

8.xii.1981, D.H. Jacobs (DHJS, TMSA); 1♀: S. Afr. Transkei, Silaka Forest Reserve, 31°33′S 29°30′E, 24.xi.1987; E-Y:2533 indig forest litter, leg. Endrödy-Young (TMSA); 16♂♂ 18♀♀: Kumanina forest, nr. Umtata, 31°34′S 28°09′E, 9.xii.1981, D.H. Jacobs (DHJS, TMSA); 33♂♂ 26♀♀: Same data as holotype (DHJS, TMSA); 1♂ 2♀♀: Nquaba forest, nr. Umtata, 31°36′S 28°07′E, 9.xii.1981, D.H. Jacobs (DHJS).

9.1.8.2 *Dundocoris schoemani dwesaensis* spec. et subspec. nov., Figs 367-374.

Length: ♂ 3,5 - 3,9 mm; ♀ 4,0 - 4,7 mm.
Width: ♂ 1,7 - 1,9 mm; ♀ 1,9 - 2,3 mm.
Diagnostic measurements are given in Table 9.13.

Table 9.13. Measurements (in mm) of *Dundocoris schoemani dwesaensis* spec. & subspec. nov. from Dwesa forest.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range	AT#	N	Mean	SD	Range
Total	length	3.65	5	3.65	0.132	3.51-3.87	4.48	9	4.39	0.187	4.03-4.69
	width	1.79	5	1.78	0.060	1.72-1.88	2.25	9	2.18	0.096	1.95-2.28
Head	length	0.69	5	0.67	0.018	0.64-0.69	0.74	9	0.74	0.029	0.69-0.79
	width	0.72	5	0.72	0.010	0.70-0.73	0.78	9	0.78	0.025	0.73-0.82
Pronotum	length	0.40	5	0.40	0.019	0.36-0.42	0.46	9	0.46	0.025	0.41-0.50
	width	1.27	5	1.26	0.020	1.23-1.29	1.41	9	1.41	0.040	1.35-1.47
Tergal disk	length	0.90	5	0.92	0.049	0.84-0.98	1.20	9	1.22	0.048	1.13-1.32
	width	1.21	5	1.21	0.044	1.13-1.27	1.45	9	1.47	0.055	1.40-1.58
Antennal segments	I	0.34	5	0.34	0.006	0.33-0.35	0.37	9	0.36	0.013	0.34-0.39
	II	0.23	5	0.22	0.010	0.20-0.23	0.23	9	0.24	0.007	0.22-0.25
	III	0.48	5	0.46	0.021	0.43-0.49	0.51	9	0.50	0.021	0.44-0.53
	IV	0.27	5	0.27	0.006	0.25-0.28	0.27	9	0.27	0.011	0.25-0.28

* HT = holotype. # AT = allotype.

Chromosome number: 2n(♂) = 26XY.

Differences with the nominate subspecies were discussed under the latter. The specimens from Mpame forest are included in this species on account of the proximity of the locations and the fact that both are coastal forests. The chromosome number or karyotype which has not yet been determined, may, however, prove otherwise.

Habitat and distribution: Coastal forests in the Eastern Cape.

MATERIAL EXAMINED: **Eastern Cape**. ♂ holotype: Dwesa forest Transkei, 32°18′S 28°50′E, 10-13.xii.1981 D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 25 paratypes as follows: 1♂ 3♀♀:

Mpame forest, Transkei, 32°05'S 29°02'E, 12.xii.1981, D.H. Jacobs (DHJS, TMSA); 9♂♂ 12♀♀: Same data as holotype (DHJS, TMSA).

9.1.9 *Dundocoris scholtzi* spec. nov., Figs 375-382.

Length: ♂ 3,3 - 4,0 mm; ♀ 3,9 - 4,7 mm.
Width: ♂ 1,5 - 1,9 mm; ♀ 1,9 - 2,3 mm.
Diagnostic measurements are given in Table 9.14.

Table 9.14. Measurements (in mm) of *Dundocoris scholtzi* spec. nov. from Ngome forest.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range$	AT#	N	Mean	SD	Range$
Total	length	3.78	10	3.68	0.134	3.37-3.94	4.36	10	4.35	0.128	3.93-4.62
	width	1.66	10	1.67	0.081	1.56-1.83	2.14	10	2.16	0.079	1.91-2.29
Head	length	0.73	10	0.72	0.015	0.69-0.75	0.78	10	0.79	0.018	0.74-0.82
	width	0.79	10	0.77	0.019	0.74-0.82	0.85	10	0.82	0.033	0.77-0.88
Pronotum	length	0.44	10	0.43	0.017	0.36-0.48	0.43	10	0.46	0.018	0.41-0.50
	width	1.34	10	1.30	0.056	1.22-1.40	1.42	10	1.42	0.047	1.26-1.51
Tergal disk	length	0.94	10	0.90	0.046	0.82-1.00	1.32	10	1.28	0.061	1.16-1.38
	width	1.15	10	1.13	0.068	1.04-1.24	1.39	10	1.40	0.060	1.21-1.52
Antennal segments	I	0.40	10	0.39	0.011	0.37-0.42	0.41	10	0.41	0.016	0.37-0.43
	II	0.24	10	0.24	0.010	0.21-0.26	0.25	10	0.25	0.015	0.23-0.29
	III	0.40	10	0.40	0.021	0.37-0.44	0.41	10	0.42	0.028	0.38-0.48
	IV	0.27	10	0.28	0.010	0.26-0.31	0.28	10	0.29	0.013	0.26-0.32

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.

Apterous. Male oval, female more ovate. Body coated with a whitish to brownish incrustation. Heavily incrustate specimens uniformly dark brown, slightly incrustate specimens with thorax lighter than abdomen and checkered pattern on margin of female abdomen prominent.

The following description is based on specimens with the incrustation removed:

Head: About 1,05x as wide (across eyes) as long (neck not included). Genae straight or slightly diverging anteriorly. Antenniferous lobes prominent, diverging anteriorly. Postocular lobes small, seldom reaching to level of outer margins of eyes. Subapical tubercle on clypeus present. Antennae about 1,68x as long as width across eyes; first segment long and slender, extending beyond apex of genae by more than half its length; relative lengths of segments: 16:10:17:11,5.

Thorax: Dorsum. Pronotum about 3,05x as wide as long. Lateral lobes not well delimited from disk, granulate lateral margins slightly concave, anterolateral angles usually produced to little

beyond the level of the anterior margin of the collar, posterolateral angles angularly produced laterally. Disk irregularly excavated. Transverse ridge behind collar usually with a slight median depression.

Mesonotal median ridge narrow, comprising 2(1+1) long, narrow, parallel longitudinal ridges separated medially by a longitudinal furrow; ridges often converging and confluent at extreme posterior where it then slightly wedge in between the elevations of the metanotal median ridge. Disk smooth anteriorly, anteromedially and anterolaterally; rest irregularly excavated with a bisinuate transverse row of irregular tubercles on posterior margin, usually merging with posterior extremity of median ridges. Lateral lobes densely granulate, lateral margins straight, converging anteriorly.

Metanotal median ridge comprising 2(1+1) suboval elevations, well separated by a median depression. Disk with 2(1+1) irregular smooth areas, often comma-shaped, further with irregular nodules and excavations and a transverse row of nodules on its posterior margin. Lateral lobes densely granulate, lateral margins straight.

MTg 1 fairly strongly elevated relative to metanotum for median half, rest more or less on same level, comprising 2(1+1) transverse ridges separated medially by a prominent depression, in males the ridge has an uneven surface anterolaterally while it is more even with only a sublateral transverse depression in females. MTg 1 is laterally separated from the metanotum by a suture which is more prominent in females.

MTg 2 subequal or slightly longer than MTg 1, abruptly depressed relative to MTg 1 except at median depression, laterally separated by a suture; with 2(1+1) submedian and 2(1+1) sublateral longitudinal ridges, rest fairly smooth except for some irregular tubercles just laterad of submedian ridges.

Venter and legs: As for genus.

Abdomen: Dorsum. Tergal disk about 1,26x as wide as long in males and 1,09x in females, moderately elevated along median line. Carinae separating glabrous impressions entire, prominent, Y-shaped and not reaching lateral border of tergal disk. Dorsal hem well developed in females. Posteroexterior angles of DELTg 5-7 slightly but increasingly protruding.

Venter. Ventral hem present in females but not prominent. Spiracle 2 ventral; 3-4 sublateral, 3 slightly more than a spiracle width from lateral margin in females, less than half a spiracle width in males, not visible from above in both sexes, 4 about half a spiracle width from lateral margin in females and not visible from above, lateral or nearly so in males and usually visible from above; 5-7 lateral and visible from above; 8 subterminal on paratergites. VELTg 7 of males with a transverse, strongly elevated, bulbous elevation running anteromesad from under the spiracle to near the anterior margin in line with the sublateral glabrous impressions of the previous segment.

Genitalia: Pygophore as in Figs 381-382. Removed parameres as in Figs 377-380.

Chromosome number: 2n(♂) = 26XY.

Habitat and distribution: At present only known from the montane evergreen forests in the Ngome wilderness area where it is very common.

Etymology: I dedicate this species to Prof C.H. Scholtz, head of the Department of Zoology and Entomology of the University of Pretoria for his moral and financial support of my research.

Discussion: *Dundocoris* [illegible] is characterized by a combination of its long antennal segment 1 (which is more than half as long as width across eyes and surpasses the genae by more than half its length), spiracle 4 of the males which is usually visible from above and the mesonotal median ridge where the longitudinal elevations converge and often merge at posterior extreme.

Dundocoris scholtzi is related to *Dundocoris schoemani* (refer to latter species for differences) and *Dundocoris fuscus* from which it differs in its median ridge (see discussion above), spiracle 4 of males which is not visible from above, the 2(1+1) bulbous elevations on VELTg 7 of males, and the slightly different shape of MTg 1, especially in females.

MATERIAL EXAMINED: **SOUTH AFRICA. Kwazulu-Natal.** ♂ holotype: Ngome forest station, nr. Louwsburg, 27°49'S 31°25'E, 20-24.i.1983, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 450♂♂ 393♀♀ paratypes: Same data as holotype (DHJS, TMSA).

9.1.10 *Dundocoris fuscus* spec. nov., Figs 383-391.

Length: ♂ 3,4 - 4,0 mm; ♀ 4,1 - 4,7 mm.

Width: ♂ 1,5 - 2,0 mm; ♀ 2,0 - 2,4 mm.

Diagnostic measurements are give in Table 9.15.

Table 9.15. Measurements (in mm) of *Dundocoris fuscus* spec. nov.

	STRUCTURE		MARIEPSKOP FOREST					OTHER@			
			HT*	N	Mean	SD	Range	N	Mean	SD	Range
MALES	Total	length	3.67	10	3.67	0.090	3.53-3.80	5	3.62	0.187	3.44-3.94
		width	1.71	10	1.72	0.068	1.56-1.81	5	1.80	0.115	1.69-2.00
	Head	length	0.67	10	0.68	0.019	0.64-0.70	5	0.70	0.014	0.67-0.72
		width	0.74	10	0.75	0.018	0.73-0.78	5	0.76	0.027	0.73-0.81
	Pronotum	length	0.43	10	0.43	0.018	0.40-0.46	5	0.44	0.014	0.42-0.46
		width	1.24	10	1.24	0.038	1.16-1.32	5	1.33	0.048	1.27-1.39
	Tergal disk	length	0.93	10	0.93	0.030	0.89-0.98	5	0.92	0.057	0.87-1.02
		width	1.13	10	1.15	0.040	1.11-1.24	5	1.21	0.074	1.15-1.34
	Antennal segments	I	0.36	10	0.36	0.011	0.33-0.38	5	0.36	0.021	0.34-0.40
		II	0.23	10	0.22	0.010	0.20-0.24	5	0.24	0.008	0.22-0.25
		III	0.37	10	0.37	0.020	0.34-0.42	5	0.39	0.012	0.37-0.40
		IV	0.25	10	0.25	0.010	0.23-0.28	5	0.26	0.011	0.25-0.28
			AT #	N	Mean	SD	Range	N	Mean	SD	Range
FEMALES	Total	length	4.49	10	4.43	0.160	4.16-4.62	3	4.49	0.052	4.43-4.54
		width	2.19	10	2.23	0.101	2.06-2.35	3	2.31	0.037	2.27-2.35
	Head	length	0.76	10	0.75	0.017	0.70-0.78	3	0.77	0.002	0.77-0.78
		width	0.83	10	0.81	0.026	0.77-0.85	3	0.83	0.006	0.82-0.84
	Pronotum	length	0.45	10	0.47	0.024	0.43-0.52	3	0.50	0.009	0.49-0.51
		width	1.37	10	1.41	0.081	1.27-1.54	3	1.50	0.011	1.48-1.52
	Tergal disk	length	1.38	10	1.33	0.065	1,20-1.43	3	1.35	0.015	1.33-1.37
		width	1.51	10	1.46	0.078	1.34-1.59	3	1.49	0.022	1.46-1.51
	Antennal segments	I	0.40	10	0.38	0.014	0.35-0.41	3	0.40	0.004	0.39-0.41
		II	0.26	10	0.24	0.011	0.22-0.27	3	0.27	0.008	0.25-0.28
		III	0.42	10	0.40	0.016	0.37-0.42	3	0.42	0.009	0.41-0.44
		IV	0.27	10	0.26	0.010	0.24-0.29	3	0.28	0.005	0.27-0.29

* HT = holotype. # AT = allotype.
@ 3♂♂ 3♀♀ from Grootkloof, 1♂ from Nelshoogte and 1♂ from Bridal Veil Falls.

Apterous. Male oval, female ovate. Body coated with a yellowish or brownish incrustation. Heavily incrustate specimens uniformly dark brown, slightly incrustate specimens with thorax lighter than abdomen and checked pattern on females abdominal margins visible.

The following description is based on specimens with the incrustation removed.

Head: About 1,09x as wide (across eyes) as long (neck not included). Genae straight, extending beyond apex of clypeus for only a short distance. Antenniferous lobes prominent, diverging anteriorly. Postocular lobes variable, usually not reaching level of outer margins of eyes. Subapical tubercle on clypeus present. Antennae 1,6 - 1,65x as long as width across eyes; first segment long, extending beyond apex of genae by about half its length, relative lengths of segments: 15,5:10:16:10,8.

Thorax: Dorsum. Pronotum about 3x as wide as long. Lateral lobes not well delimited from disk, irregularly granulate, lateral margins concave, anterolateral angles produced slightly beyond level of anterior margins of collar, posterolateral angles produced laterally. Disk irregularly excavated. Transverse ridge behind collar with a slight median depression.

Mesonotal median ridge narrow, longitudinal elevations parallel or slightly diverging posteriorly, narrow but usually widening posteriorly, always separated by a prominent, fairly wide median furrow along their total length. Disk with irregular smooth patches anteriorly, medially and laterally, rest irregularly excavated and with irregular nodules, especially along posterior margin where they may link up with the elevations of the median ridge. Lateral lobes coarsely granulate, lateral margins straight, converging anteriorly.

Metanotal median ridge comprising 2(1+1) suboval or subquadrangular elevations, well separated by a median depression. Disk with 2(1+1) more or less comma-shaped smooth areas, rest with irregular nodules and excavations and an irregular transverse row of nodules on its posterior margin. Lateral lobes granulate, lateral margins straight.

MTg 1 moderately elevated relative to metanotum for median half, remainder on approximately the same level; comprising 2(1+1) transverse ridges always separated medially by a prominent and usually fairly wide depression; medially the ridge occupy the total length of MTg 1 but narrows laterally and occupy the posterior half of MTg 1 for about three fifths of its width to where it is partially fused to 2(1+1) sublateral elevations (in line with sublateral elevations of MTg 2); lateral of this it continues as a sinuate bar-like thickening of the posterior and lateral margin of MTg 1; surface anterior to ridge uneven. MTg 1 fused with metanotum but a suture may be vaguely discernable laterally.

MTg 2 usually slightly longer than MTg 1, laterally separated from it by a well developed suture, submedially by the abrupt decline of the ridge on MTg 1 but they are usually fused at the median depression and separated only by a moderate decline. MTg 2 with 2(1+1) submedian ridges which are often L-shaped and 2(1+1) sublateral longitudinal ridges, rest fairly smooth.

Venter and legs: As for genus.

Abdomen: Dorsum. Tergal disk about 1,25x as wide as long in males and 1,1x in females, moderately elevated along median line. Carinae separating glabrous impressions entire, prominent, Y-shaped and not reaching lateral border of tergal disk. Dorsal hem well developed in females. Posteroexterior angles of DELTg 4 - 7 increasingly protruding, especially in males.

Venter. Ventral hem present in females. Spiracle 2 ventral; 3 sublateral, usually about half a spiracle width from lateral margin and sometimes visible from above; 4-7 lateral and visible from above; 8 subterminal on paratergites.

Genitalia: Pygophore as in Figs 390-391. Removed parameres as in Figs 386-389.

Chromosome number: 2n(♂) = 28XY.

Habitat and distribution: Montane evergreen forests in Mpumalanga and Swaziland.

Etymology: fuscus (L) = dark brown, referring to the general colour of specimens.

Discussion: *Dundocoris fuscus* can be distinguished from all other species by a combination of its fairly long first antennal segment (extending beyond apex of genae by about half its length), long third antennal segment (that is distinctly longer than segment one), spiracle 4 which is visible from above in both sexes and the mesonotal median ridge where the longitudinal elevations are separated by a prominent furrow over its total length and never merge at posterior extreme.

It differs from *Dundocoris scholtzi* as discussed under that species.

MATERIAL EXAMINED: **SOUTH AFRICA**. **Mpumalanga**. ♂ holotype: Mariepskop forest, nr. Hoedspruit, Tvl, 24°33′S 30°54′E, 6.x.1981, Liebenberg & Jacobs (TMSA); ♀ allotype: ditto (TMSA); 131 paratypes as follows: 14♂♂ 12♀♀: Same data as holotype (DHJS, TMSA); 1♀: S. Afr., E. Transvaal, Blyderivier Canyon 24°35′S 30°49′E, 5.v.1981, E-Y:1779, sifted litter, bush, leg Endrödy-Younga (TMSA); 4♂♂ 3♀♀: S. Afr., E. Transvaal, Mariepskop, 24°35′S 30°50′E, 5.v.1981, E-Y:1776, sifted cloud forest, leg. Endrödy-Younga. (TMSA); 2♂♂ 1♀: Mariepskop For., Transvaal, viii.1960, Humus (no collector given) (TMSA); 5♂♂ 6♀♀: Blyderivierspoort Nature Reserve, nr. Bourke's Luck, 24°39′S 30°52′E, 28.i.1989, D.H. Jacobs (DHJS, TMSA); 2♂♂ 1♀: ditto, 24°39′S 30°54′E (DHJS); 6♂♂ 8♀♀: Yellow-wood forest, Blyderivierspoort Nature Reserve, 24°40′S 30°54′E, 29.i.1989, D.H. Jacobs (DHJS, TMSA); 10♂♂ 2♀♀: Bridal Veil Falls, nr. Sabie, 25°05′S 30°43′E, 5.xi.1988, D.H. Jacobs (DHJS, TMSA); 2♂♂ 3♀♀: Maritzbos, nr. Sabie, 25°06′S 30°41′E, 6.xi.1988, D.H. Jacobs (DHJS); 1♂: S. Afr. Tvl., Uitsoek, Grootkloof ind. for., 25°15′S 30°33′E, 28.ix.1986; E-Y:2294, intercept. trap 28d, leg. Endrödy-Younga (TMSA); 2♀♀: ditto, 16.xii.1986; E-Y:2395, forest litter before rain (TMSA); 4♂♂ 2♀♀: ditto; 17.xii.1986, E-Y:2396, forest litter after rain (TMSA); 2♂♂ 2♀♀: ditto, 6.ii.1987, E-Y:2425, beating in forest (TMSA); 18♂♂ 14♀♀: S. Afr., E. Transvaal, Berlin F.S., gorge, 25°32′S 30°44′E, 22.ix.1986, E-Y:2284, litter in rock crevices, leg. Endrödy-Younga (TMSA); 1♀: ditto 9.xii.1986, E-Y:2366, intercept trap 56d (TMSA); 1♂: S. Afr., Tvl., Nelshoogte, gallery forest below St., 25°51′S 30°53′E, 2.xii.1986, E-Y:2344, beating, leg. Endrödy-Younga (TMSA). **SWAZILAND**. 1♂ 1♀: Pigs Peak, Humus, x-1961 (TMSA).

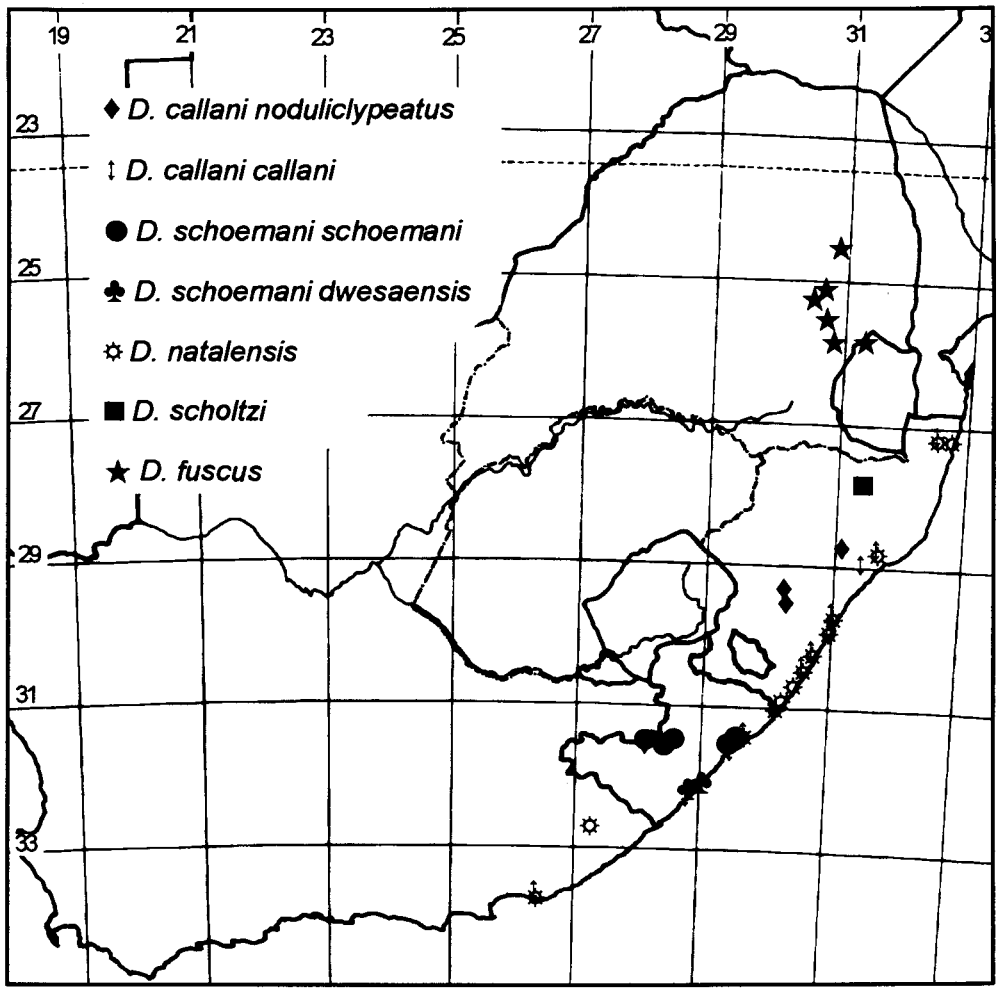


Figure 256. Distribution of *Dundocoris* species and subspecies.

9.1.11 *Dundocoris callani* Hoberlandt., Figs 396-405, 407-425.

D. callani was described in 1959 from a single female collected near Bathurst in the Eastern Cape. It has subsequently proved to be a widespread and common species but also very variable. It is possible that some of populations actually represent separate species but on present information it would be premature to split them up. I was very tempted to describe the population from the Pietermaritzburg area as a separate species as their chromosome number differ and they show some morphological features which set them apart. However, one or two populations in the Eastern Cape seem to be intermediate in some of these morphological characters and I have subsequently decided to allocate only subspecific status to them.

It is the haphazardousness of the variation between the populations that complicates the systematic treatment of this species. It seems that each population has some constant characters that set them apart from adjacent populations but some of these may be shared by geographically distant populations. For example: the specimens from Ngoye forest which is near the northern limit of its distribution area are morphologically much more similar to those from Dwesa which is near the southern limit of its distribution area than both are to the specimens from Umhlanga Rocks in the centre of these locations.

Each population seem to be unique in terms of the combination of characteristics they have, but overall the variation seems to be more or less continuous. An intensive investigation into this species, not based on morphology alone, is needed to elucidate its systematics.

Redescription:

Length: ♂: 3,0 - 3,7 mm; ♀ 3,7 - 4,5 mm.

Width: ♂: 1,4 - 1,9 mm; ♀ 1,8 - 2,4 mm.

Diagnostic measurements are given in Tables 9.16 and 9.17.

Apterous. Male oval, female more ovate. Body coated with a whitish to yellowish incrustation. Heavily incrustate specimens uniformly dark brown, slightly incrustate specimens with thorax lighter than abdomen and checkered pattern on margin of female abdomen prominent, especially in the subspecies *D. callani noduliclypeatus*.

The following description is based on specimens with the incrustation removed.

Head: 1,05 - 1,12x as wide (across eyes) as long (neck not included). Genae straight usually extending beyond clypeus for only a short distance. Antenniferous lobes prominent, usually diverging anteriorly. Postocular lobes variable, prominent and extending beyond level of outer margin of eyes in some populations, nearly absent and obtuse in others. Subapical tubercle on clypeus nearly always absent in the nominate subspecies, present and prominent in *D. callani noduliclypeatus*. Antennae 1,32 - 1,57x as long as width across eyes; length of first segment variable, usually extending beyond apex of genae by distinctly less than half its length, relative lengths of segments about 14:10:16:13, but differing between populations and subspecies.

Thorax: Dorsum. Pronotum about 3,2x as wide as long. Lateral lobes densely granulate, lateral margins slightly concave, anterolateral angles produced anteriorly to level of anterior margin of collar or little beyond, posterolateral angles only slightly produced laterally. Disk irregularly excavated. Transverse ridge behind collar entire or with slight median depression.

Mesonotal median ridge with 2(1+1) longitudinal parallel elevations separated by a prominent median furrow; these elevations may converge and merge at posterior extreme and wedge in between elevations of mesonotal median ridge; elevations longer than length of pronotum excluding collar. Disk with irregular smooth areas and excavations. Lateral lobes densely granulate, lateral margins straight, converging anteriorly. Mesonotum well separated from metanotum by a deep suture except on median ridge where a transverse row of irregular tubercles, which often link up with the posterolateral extremities of the longitudinal elevations, demarcate its posterior margin.

Metanotal median ridge comprising 2(1+1) suboval or subquadrangular elevations separated by a wide furrow with a slight elevation medially which usually reaches posteriorly to the posterior margin of MTg 1 (sometimes even the posterior margin of MTg 2) and anteriorly to the longitudinal elevations of the mesonotal median ridge with which it usually merges. Disk with 2(1+1) irregular smooth areas, often comma-shaped; further with irregular nodules and excavations and a transverse row of nodules along its posterior margin. Lateral lobes densely granulate, lateral margins straight.

MTg 1 usually only moderately elevated relative to metanotum for median half remainder on same level, comprising 2(1+1) transverse ridges, separated medially by a wide furrow; the ridges continues laterally, mainly along the posterior margin, to where it ends at the sublateral elevations to which it is often partially fused, lateral of this a slightly elevated rim at the posterior and lateral margin of MTg 1 may be viewed as a continuation of the ridge. MTg 1 usually totally fused to metanotum but in some populations a weak suture may be present laterally.

MTg 2 subequal or slightly longer than MTg 1, separated laterally by a suture, submedially by the abrupt decline of MTg 1 but medially, at the median furrow, they are usually fused. MTg 2 with 2(1+1) submedian and 2(1+1) sublateral longitudinal ridges, rest fairly smooth.

Venter and legs: Metasternum usually with a well developed tubercle anterolaterally; just behind the mesocoxa (Fig. 407). Legs as for genus.

Abdomen: Dorsum. Tergal disk about 1,3x as wide as long in males and 1,12x in females, moderately elevated along median line. Carinae separating glabrous impressions usually entire and prominent (except in the Umhlanga Rocks and Stainbank Reserve populations where especially the carina between segment 5/6 is usually broken into nodules), Y-shaped. Dorsal hem present but usually not well developed in females. Posteroexterior angles of DELTg 5-7 slightly but increasingly protruding.

Venter. Ventral hem in females not prominent and hardly discernable in some populations. Spiracle 2 ventral; 3 sublateral, about a spiracle width from lateral margin in males and about 2 spiracle widths in females (on inner margin of ventral hem); 4 sublateral, about half a spiracle width from lateral margin in males and 1½ spiracles widths in females; 5 always lateral and visible from above in males, usually lateral but sometimes slightly removed from margin, but visible from above in females; 6-7 lateral and visible from above; 8 subterminal on paratergites. VELTg 7 of males with elevation like in *D. scholtzi* but much less prominent.

Genitalia: Pygophore as in Figs 400-405, 424-425. Removed parameres as in Figs 408-417, 420-423.

Chromosome number: 2n(♂) = 28XY in nominate subspecies or 26XY in *D. callani noduliclypeatus*.

Habitat and distribution: Widely distributed in coastal and montane evergreen forests in Kwazulu-Natal and the Eastern Cape.

Discussion: *D. callani* is characterised by a combination of its small size, position of spiracle 4 which is never visible from above, the absence of the subapical tubercle on the clypeus in the nominate subspecies and elevations of the mesonotal median ridge which are parallel or convergent posteriorly and may merge and wedge in between elevations of metanotal median ridge.

It is closely related to *D. scholtzi* from which it can be distinguished by its relatively shorter antennal segment 1 (extending beyond apex of genae by at most half its length but usually by distinctly less); spiracle 4 which is never visible from above in both sexes; the median depression on MTg 1 which is usually much wider; the elevation on VELTg 7 of males which is less prominent and the absence of the subapical tubercle on the clypeus in the nominate subspecies.

D. callani is also related to *D. natalensis* from which it can be distinguished as discussed under the latter.

MATERIAL EXAMINED: See under subspecies.

9.1.11.1 *Dundocoris callani callani* Hoberlandt, Figs 396-405, 407-417.

Length: ♂ 3,0 - 3,7 mm; ♀ 3,7 - 4,5 mm.
Width: ♂ 1,4 - 1,8 mm; ♀ 1,8 - 2,3 mm.
Diagnostic measurements are given in Table 9.16.

Table 9.16. Measurements (in mm) of *Dundocoris callani callani* Hoberlandt.

	STRUCTURE		DHLINSA FOREST				UMHLANGA ROCKS			
			N	Mean	SD	Range	N	Mean	SD	Range
MALES	Total	length	10	3.41	0.163	3.14-3.62	10	3.20	0.050	3.07-3.26
		width	10	1.64	0.065	1.52-1.74	10	1.59	0.057	1.48-1.66
	Head	length	10	0.70	0.018	0.67-0.73	10	0.63	0.012	0.61-0.66
		width	10	0.75	0.015	0.72-0.77	10	0.71	0.019	0.68-0.74
	Pronotum	length	10	0.40	0.017	0.37-0.43	10	0.38	0.020	0.35-0.42
		width	10	1.26	0.060	1.15-1.36	10	1.17	0.040	1.10-1.22
	Tergal disk	length	10	0.85	0.032	0.80-0.91	10	0.80	0.021	0.77-0.85
		width	10	1.07	0.052	1.00-1.15	10	1.06	0.036	1.00-1.11
	Antennal segments	I	10	0.30	0.010	0.27-0.31	10	0.26	0.006	0.24-0.27
		II	10	0.21	0.009	0.18-0.23	10	0.18	0.006	0.17-0.20
		III	10	0.33	0.015	0.30-0.36	10	0.29	0.006	0.27-0.30
		IV	10	0.26	0.006	0.25-0.28	10	0.25	0.006	0.24-0.26
			N	Mean	SD	Range	N	Mean	SD	Range
FEMALES	Total	length	10	4.22	0.161	4.03-4.43	10	3.89	0.104	3.70-4.01
		width	10	2.06	0.134	1.81-2.27	10	1.96	0.075	1.81-2.09
	Head	length	10	0.78	0.021	0.75-0.81	10	0.70	0.012	0.68-0.73
		width	10	0.81	0.014	0.79-0.83	10	0.77	0.019	0.74-0.81
	Pronotum	length	10	0.44	0.020	0.40-0.48	10	0.41	0.020	0.37-0.44
		width	10	1.40	0.080	1.31-1.56	10	1.30	0.042	1.21-1.37
	Tergal disk	length	10	1.23	0.061	1.14-1.33	10	1.16	0.032	1.10-1.21
		width	10	1.36	0.064	1.25-1.45	10	1.31	0.058	1.23-1.41
	Antennal segments	I	10	0.31	0.009	0.30-0.33	10	0.27	0.007	0.25-0.29
		II	10	0.22	0.009	0.21-0.25	10	0.19	0.004	0.18-0.20
		III	10	0.35	0.025	0.32-0.39	10	0.30	0.019	0.26-0.35
		IV	10	0.28	0.008	0.26-0.29	10	0.26	0.009	0.24-0.27

Chromosome number: 2n(♂) = 28XY.

Antennae less than 1,5x as long as width across eyes; relative lengths of segments: 14:10:15,8:12,5.

The nominate subspecies can be distinguished from *D. callani noduliclypeatus* by the absence of the subapical tubercle on the clypeus (although it is present in the populations from Nquaba forest and Ku-manina forest), the antenna which is shorter relative to the width of the head (less than 1,5x compared to more than 1,5x), the first antennal segment that surpasses the apex of the genae (on average) with distinctly less than half its length (nearly with half its length in *D. callani noduliclypeatus*), the different relative lengths of the antennal segments (especially segment 4 that is distinctly longer than 2) and the different chromosome number.

Habitat and distribution: Particularly widespread in the coastal forests of Kwazulu-Natal and the Eastern Cape but also present in some montane forests in Kwazulu-Natal and Eastern Cape (Fig. 256).

MATERIAL EXAMINED: **SOUTH AFRICA**. **Kwazulu-Natal**. 1♂ 1♀: nr. Manzengwenya, Kwazulu, 27°12′S 32°37′E, 5.xii.1980, D.H. Jacobs (DHJS); 29♂♂ 18♀♀: Ngoye Forest Reserve, nr. Empangeni, 28°50′S 31°43′E, 11-12.xii.1980 D.H. Jacobs (DHJS, TMSA); 3♂♂ 7♀♀: ditto, 22.viii.1985 (DHJS); 47♂♂ 19♀♀: Dhlinsa forest, Eshowe, 28°54′S 31°27′E, 12.iv.1980, D.H. Jacobs (DHJS, TMSA); 7♂♂ 4♀♀: ditto, 21.viii.1985 (DHJS); 19♂♂ 20♀♀: Umhlanga Rocks Nature Reserve, nr. Durban, 29°42′S 31°06′E, 10-11.ix.1991, D.H. Jacobs (DHJS, TMSA); 1♀: nr. Durban, 29°45′S 31°04′E, 8-11.iv.1980, D.H. Jacobs (DHJS); 3♂♂ 5♀♀: Stainbank Nature Reserve, Durban, 29°55′S 30°56′E, 2.xi.1989, D.H. Jacobs, (DHJS, TMSA); 5♂♂ 9♀♀: nr. Scottburgh, 30°15′S 30°46′E, 25.i.1983, D.H. Jacobs (DHJS, TMSA); 2♂♂ 3♀♀: Umdoni Park, nr. Scottburgh, 30°24′S 30°41′E, 27.i.1983, D.H. Jacobs (DHJS). **Eastern Cape**. 1♀: Ntsubane forest, 31°27′S 29°44′E, 25.xi.1987, E-Y: 2537, fungi & for. litter, leg Endrödy-Younga (TMSA); 2♂♂ 3♀♀: Silaka forest Reserve, 31°33′S 29°30′E, 24.xi.1987, E-Y: 2533, indig. forest litter, leg. Endrödy-Younga (TMSA) 3♀♀: Ku-manina forest, nr. Umtata, 31°34′S 28°09′E, 9.xii.1981, D. H. Jacobs (DHJS); 6♂♂ 19♀♀: Nqaba forest, nr. Umtata, 31°36′S 28°07′E, 9.xii.1981, D.H. Jacobs (DHJS, TMSA); 7♂♂ 2♀♀: Mount Thesiger Nature Reserve, Port St. Johns, 31°37′S 29°31′E, 2-6.xii.1981, D.H. Jacobs (DHJS); 13♂♂ 22♀♀: Dwesa forest, 32°18′S 28°50′E, 10-13.xii.1981, D.H. Jacobs (DHJS, TMSA); 2♂♂ 3♀♀: Alexandria forest, nr. Grahamstown, 33°43′S 26°24′E,30.i.1984, D.H. Jacobs (DHJS, TMSA) 1♂ 2♀♀: Alexandria forest station, 33°43′S 26°23′E, 5.xii.1987, E-Y:2553, groundtraps 2 days, leg Endrödy-Younga (TMSA).

9.1.11.2 *Dundocoris callani noduliclypeatus* subspec. nov., Figs 418-425.

Length: ♂ 3,1 - 3,7 mm; ♀ 3,7 - 4,5 mm.
Width: ♂ 1,5 - 1,9 mm; ♀ 1,8 - 2,4 mm.
Diagnostic measurements are given in Table 9.17.

Table 9.17. Measurements (in mm) of *Dundocoris callani noduliclypeatus* subspec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	N	Mean	SD	Range$	AT#	N	Mean	SD	Range$
Total	length	3.46	10	3.48	0.116	3.15-3.66	4.10	10	4.11	0.179	3.76-4.47
	width	1.67	10	1.70	0.054	1.55-1.82	2.11	10	2.12	0.094	1.87-2.33
Head	length	0.68	10	0.69	0.030	0.62-0.73	0.76	10	0.74	0.031	0.68-0.79
	width	0.73	10	0.76	0.022	0.71-0.80	0.82	10	0.82	0.029	0.75-0.87
Pronotum	length	0.39	10	0.39	0.019	0.34-0.41	0.44	10	0.42	0.020	0.38-0.49
	width	1.19	10	1.23	0.044	1.09-1.35	1.38	10	1.37	0.046	1.24-1.46
Tergal disk	length	0.88	10	0.87	0.041	0.80-0.96	1.22	10	1.22	0.058	1.11-1.35
	width	1.14	10	1.14	0.042	1.04-1.24	1.36	10	1.41	0.060	1.29-1.52
Antennal segments	I	0.33	10	0.34	0.006	0.31-0.35	0.35	10	0.36	0.009	0.34-0.38
	II	0.23	10	0.24	0.013	0.21-0.27	0.25	10	0.25	0.010	0.23-0.27
	III	0.36	10	0.36	0.018	0.32-0.39	0.39	10	0.38	0.020	0.34-0.42
	IV	0.26	10	0.26	0.011	0.24-0.28	0.28	10	0.27	0.011	0.24-0.29

* HT = holotype. # AT = allotype.
$ May include measurements of specimens other than those used for statistical analysis.
♦ 5♂♂ 5♀♀ from Town Bush and 5♂♂ 5♀♀ from Shaws Wood farm.

Chromosome number: 2n(♂) = 26XY.

Antennae more than 1,5x as long as width across eyes; relative lengths of segments 14:10:15:10,5.

The differences between it and the nominate subspecies have been discussed under the latter.

Habitat and distribution: Montane evergreen forests in Kwazulu-Natal (Fig. 256). A single specimen from Gwaliweni forest in the Ingwavuma district (TMSA) probably also belong to this subspecies but is not included in the type series because of slight morphological differences and the large distance from its known distribution area.

Etymology: Noduliclypeatus referring to the subapical nodule (tubercle) on its clypeus.

MATERIAL EXAMINED: **SOUTH AFRICA**. **Kwazulu-Natal**. ♂ holotype: Town Bush, Pietermaritzburg, 29°33′S 30°20′E, 31.i.1983, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 663 paratypes as follows: 6♂♂ 6♀♀: Nkandla forest, 28°44′S 31°08′E, 12.iv.1980, D.H. Jacobs (DHJS, TMSA); 8♂♂ 2♀♀: Ehlatini farm, Karkloof, 29°19′S 30°17′E, 1.ii.1983 D.H. Jacobs. (DHJS, TMSA); 77♂♂ 72♀♀: Shaws Wood farm, Karkloof, 29°19′S 30°18′E, 1.ii.1983, D.H. Jacobs (DHJS, TMSA); 311♂♂ 180♀♀: Same data as holotype (DHJS, TMSA); 1♂: Town Bush, Maritzburg District, humus, x.1960 (TMSA).

9.1.12 *Dundocoris natalensis* Kormilev, Figs 406, 426-433.

D. natalensis was described from a single male, collected in the Oribi Gorge nr Port Shepstone, mainly in a comparative way to *D. stuckenbergi*.

The holotype, which should be in the Natal Museum, could not be traced. According to Dr. J.G.H. Londt, assistant director of the Natal museum (in litt, 1977) they didn't receive the holotype of *D. natalensis* back from Kormilev. Kormilev (in litt, April 1978), however, claimed that he returned both types of *D. natalensis* and *D. stuckenbergi* in the same parcel. I visited the Natal Museum in 1978 but could find no trace of the holotype.

The mystery intensified when I received a female specimens labelled "Neo-allotype, *Dundocoris natalensis* N. Kormilev 1962" from the Swedish Museum of Natural History. When I informed Kormilev about this find his reply (in litt, June 1978) was: "How *Dundocoris natalensis* came to Sweden? Who made it neo-allotype? It is very strange. Where is original type, do you find it?"

Because *D. natalensis* also shows some haphazard variation over its wide distribution area and it is possible that it is actually a semi-sibling species complex, it is, to my mind, advisable to designate a neotype to avoid future confusion.

The specimen marked neo-allotype of course has no validity as it is not mentioned in the literature and Kormilev himself seems to be unaware of its existence or origin. For the following reasons I shall not designate this specimen as the neotype:

1) It is of another sex as the original holotype.

2) Its collection locality "Natal" is vague and it could have been collected very far away from the original type locality.

3) It is not in very good condition.

I have decided to designate a ♂ specimen from Southport, which is very close to the Oribi Gorge, as the neotype.

It is most peculiar that the distribution area (Fig. 256) of *D. natalensis* is nearly identical to that of *D. callani callani* and that they occur sympatrically in many forests. *D. natalensis*, however, seems to be much rarer than *D. callani*. From the limited number of specimens at hand it appears that a similar type of haphazard variation as in *D. callani* is present in *D. natalensis* and it is also possible that it comprises a species-complex with more than one semi-sibling species.

Redescription:

Length: ♂ 3,4 - 4,2 mm; ♀ 4,0 - 5,0 mm.
Width: ♂ 1,6 - 2,0 mm; ♀ 2,0 - 2,4 mm.
Diagnostic measurements are given in Table 9.18.

Table 9.18. Measurements (in mm) of *Dundocoris natalensis* Kormilev.

STRUCTURE		MALES					FEMALES				
		NT*	N♂	Mean	SD	Range	NAT#	N♂	Mean	SD	Range
Total	length	4.05	10	3.758	0.243	3.46-4.12	4.50	10	4.39	0.287	4.02-4.91
	width	1.84	10	1.78	0.103	1.67-1.97	2.16	10	2.21	0.122	2.07-2.40
Head	length	0.75	10	0.71	0.039	0.64-0.78	0.76	10	0.76	0.033	0.70-0.80
	width	0.78	10	0.74	0.036	0.70-0.81	0.80	10	0.78	0.035	0.74-0.84
Pronotum	length	0.50	10	0.44	0.040	0.38-0.51	0.46	10	0.46	0.032	0.42-0.52
	width	1.36	10	1.30	0.078	1.20-1.44	1.45	10	1.42	0.072	1.30-1.53
Tergal disk	length	1.01	10	0.94	0.059	0.87-1.04	1.34	10	1.31	0.099	1.18-1.51
	width	1.24	10	1.20	0.075	1.13-1.35	1.51	10	1.48	0.093	1.37-1.65
Antennal segments	I	0.33	10	0.33	0.011	0.31-0.35	0.35	10	0.35	0.017	0.31-0.38
	II	0.23	10	0.23	0.012	0.20-0.25	0.24	10	0.24	0.013	0.22-0.27
	III	0.44	10	0.41	0.026	0.37-0.45	0.45	10	0.43	0.022	0.40-0.47
	IV	0.27	10	0.26	0.013	0.25-0.30	0.29	10	0.27	0.013	0.25-0.30

* NT = neotype. # NAT = neo-allotype.
♦ 3♂♂ 3♀♀ from Umtamvuma forest, 2♂♂ from Umdoni Park, 1♂ 2♀♀ from Stainbank Nature Reserve, 2♂♂ 1♀ from Ngoye forest, 1♂ from Mtwalume, 1♂ from Lake Bhangazi, 1♀ from Ramsgate,1♀ from Durban, 1♀ from South Port, 1♀ from Scottburgh and 1♀ from "Natal" (labelled neo-allotype - Riksmuseum Stockholm).

Apterous. Body oval, coated with a greyish-brown incrustation. Heavily incrustate specimens uniformly dark brown, slightly incrustate specimens greyish brown with thorax slightly lighter coloured than abdomen. Checkered pattern on margin of female abdomen discernable but not prominent. The following description is based on specimens with the incrustation removed.

Head: About 1,05x as wide (across eyes) as long (neck not included). Genae straight, usually extending beyond clypeus for only a short distance. Antenniferous lobes prominent, usually slightly diverging anteriorly. Postocular lobes variable, usually not extending beyond level of outer margins of eyes. Subapical tubercle on clypeus present and usually prominent. Antennae about 1,65x as long as width across eyes; extending beyond apex of genae by little less than half its length; relative lengths of segments 14,5:10:18:11,5.

Thorax: Dorsum. Pronotum about 3,0x as wide as long. Lateral lobes granulate, lateral margins slightly concave, anterolateral angles produced anteriorly beyond level of anterior margin of collar, posterolateral angles only slightly produced laterally. Disk smooth submedially, further with irregular excavations. Transverse ridges behind collar with prominent median depression.

Mesonotal median ridge with 2(1+1) longitudinal elevations separated by a prominent median furrow; these elevations usually diverge posteriad, sometimes forming a slight curve and often widening posteriorly; never converging or merging at posterior extreme; elevations shorter than length of pronotum excluding collar. Disk usually smooth anteriorly, medially and laterally; with some irregular

nodules on posterior margin (which may link up with posterolateral extremity of the elevations of median ridge) and in central area. Lateral lobes granulate with lateral margins straight, converging anteriorly. Mesonotum well separated from metanotum by a deep suture except on median ridge where the irregular nodules usually demarcate it.

Metanotal median ridge comprising 2(1+1) suboval elevations separated by a wide furrow. Disk with 2(1+1) large, more or less comma-shaped, smooth areas anteriorly; laterally nodulated and also with row of nodules on its posterior margin which often link up with elevations on median ridge. Lateral lobes granulate, lateral margins straight.

MTg 1 very moderately elevated relative to metanotum for median two thirds, remainder on lower level; comprising 2(1+1) transverse ridges on posterior margin between submedian and sublateral longitudinal elevations; submedian elevations separated by wide furrow; area lateral of sublateral elevations smooth. MTg 1 usually totally fused to metanotum but a weak suture may be present laterally.

MTg 2 subequal in length to MTg 1, laterally separated from it by a suture, submedially by the abrupt decline of MTg 1 but fused at median furrow; with 2(1+1) submedian and 2(1+1) sublateral longitudinal ridges, rest very smooth.

Venter and legs: Metasternum without a tubercle behind the mesocoxa (Fig. 406). Legs as for genus.

Abdomen: Dorsum. Tergal disk about 1,27x as wide as long in males and 1,13x in females, moderately elevated along median line. Carinae separating glabrous impressions entire and prominent, Y-shaped, not reaching lateral margin of tergal disk. Area between carinae and glabrous impressions very smooth (more so than in *D. callani*). Dorsal hem in females well developed. Posteroexterior angles of DELTg 5-7 only slightly protruding.

Venter. Ventral hem in females usually clearly discernable. Spiracle 2 ventral; 3-4 sublateral, 3 about 1½ spiracle widths from lateral margin and 4 about 1 spiracle width in males, both about 1½ spiracle widths from lateral margin, just mesally from ventral hem, in females; 5-7 lateral and visible from above; 8 subterminal on paratergites. Elevation on VELTg 7 of males not prominent.

Genitalia: Pygophore as in Figs 432-433. Removed parameres as in Figs 428-431.

Chromosome number: 2n(♂) = 28XY.

Habitat and distribution: They occur mainly in coastal evergreen forests in Kwazulu-Natal and the Eastern Cape (Fig. 256).

Discussion: *D. natalensis* is characterised by a combination of its short, usually posteriorly diverging elevations of the mesonotal median ridge, sublateral position of spiracle 4 (which is never visible from above) and the presence of the subapical tubercle on the clypeus.

It is slightly larger (on average) than *D. callani* and can be distinguished from it by the elevations of mesonotal median ridge which are shorter than the length of the pronotum behind the collar and usually diverge, the absence of the tubercle anterolaterally on the metasternum, the antennae which are more than 1,6x as long as the width across the eyes. From the nominate subspecies of *D. callani* (with which it occurs sympatrically) it can also be distinguished by the presence of the subapical tubercle on the clypeus.

In general facies *D. natalensis* is also very similar to *D. nodulicarinus* with which it occurs sympatrically but it can easily be distinguished by the unbroken carinae on the tergal disk.

MATERIAL EXAMINED: **SOUTH AFRICA**. **Kwazulu-Natal**. ♂ neotype: nr. Southport, 30°40′S 30°30′E, 29.i.1983 D.H. Jacobs (TMSA); 1♂ 1♀: nr. Manzengwenya, Kwazulu, 27°12′S 32°37′E, 5.xii.1980, D.H. Jacobs (DHJS); 1♀: Manzengwenya, 27°13′S 32°47′E, 7.xii.1980, D.H. Jacobs (DHJS); 1♂: Ngoye forest Reserve, nr. Empangeni, 28°50′S 31°43′E, 11-12.xii.1980, D.H. Jacobs (DHJS); 1♂ 1♀: ditto, 22.vii.1985 (DHJS, TMSA); 1♂: Hawaan forest, nr. Umhlanga Rocks, 29°42′S 30°05′E, 26.i.1983, D.H. Jacobs (DHJS); 1♀: nr. Durban, 29°45′S 31°04′E, 8-11.iv.1980, D.H. Jacobs (TMSA); 1♂ 2♀♀: Stainbank Nature Reserve, Durban, 29°55′S 30°56′E, 2.xi.1989, D.H. Jacobs (DHJS, TMSA); 1♀: nr. Scottburgh, 30°15′S 30°46′E, 25.i.1983, D.H. Jacobs (TMSA); 2♀♀: Umdoni Park, nr. Scottburgh, 30°24′S 30°41′E, 23.i.1983, D.H. Jacobs (DHJS, TMSA); 1♂ 1♀: nr. Mtwalume, 30°29′S 30°37′E, 29.i.1983, D.H. Jacobs (DHJS); 1♂ 1♀: Same data as neotype (TMSA); 1♀: nr. Ramsgate, 30°55′S 30°19′E, 28.i.1983, D.H. Jacobs (DHJS); 3♂♂ 3♀♀: Umtamvuma forest, nr. Port Edward, 31°03′S 30°11′E, 28.i.1983, D.H. Jacobs (DHJS, TMSA). **Eastern Cape**. 1♂ 1♀: Ntsubane forest, 31°27′S 29°44′E, 25.xi.1987, E-Y:2537 fungi + forest litter, leg. Endrödy-Younga (TMSA); 1♂: Amatole, Pirie Forest, 32°43′S 27°17′E, 8.xii.1987, E-Y:2560, indig. forest litter, leg. Endrödy-Younga (TMSA); 1♂ 1♀: Alexandria forest, nr. Grahamstown, 33°43′S 26°24′E, 30.i.1984, D.H. Jacobs, (DHJS); 5♂♂: ditto, 33°43′S 26°23′E, 4.xii.1987, E-Y:2550; forest litter, leg. Endrödy-Younga (TMSA).

9.2 Cytogenetics of the genus *Dundocoris*

The localities and number of individuals of *Dundocoris* taxa that were cytogenetically studied are presented in Table 9.19. The course of meiosis in all *Dundocoris* species is of the normal Carventine type (similar to that of *Adamanotus uncotibialis*).

Table 9.19. Locality and numbers of individuals of *Dundocoris* species cytogenetically studied

Locality	Co-ordinates	Date collected	No. of individuals cytogenetically studied
Dundocoris nodulicarinus nodulicarinus			
Mpesheni forest, nr. Kokstad	30°38′S 29°40′E	30/xi/1981	3
Lesser Stinkwood forest	30°33′S 29°43′E	29/xi/1981	1
Dundocoris nodulicarinus novenus			
Isidenge forest, nr. Stutterheim	32°40′S 27°17′E	14-17/xii/1981	15
ditto	"	26-31/i/1984	4 + 7 embryos
Qacu Forest Reserve, nr.Stutterheim	32°25′S 27°18′E	17/xii/1981	4
Schwarzwald forest, nr. Hogsback	32°39′S 27°00′E	16/xii/1981	1
Dundocoris nodulicarinus septeni			
Alexandria forest, nr. Grahamstown	33°43′S 26°24′E	18/xii/1981	1
ditto	"	30/i/1984	8 + 1 female

Locality	Co-ordinates	Date collected	No. of individuals cytogenetically studied
Dundocoris marieps			
Mariepskop forest, nr. Hoedspruit	24°33′S 30°54′E	4/x/1981	13
Dundocoris begemanni			
nr. Injasuti, Giants Castle Reserve	29°06′S 29°29′E	3/ii/1983	5
Dundocoris stuckenbergi stuckenbergi			
Town Bush, Pietermaritzburg	29°33′S 30°20′E	31/i/1983	6
Shaws Wood farm, Karkloof	29°19′S 30°18′E	31/i/1983	1
Dundocoris stuckenbergi ngomensis			
Ngome forest station, nr. Louwsburg	27°49′S 31°25′E	20-24/i/1983	17
Dundocoris nigromaculatus			
Ngoye forest reserve, nr Empangeni	28°50'S 31°43'E	11-12/xii/1980	16
Dhlinza forest, Eshowe	24°54'S 31°27'E	21/viii/1985	2
Dundocoris flavilineatus flavilineatus			
Dhlinza forest, Eshowe,	24°54′S 31°27′E	12/iv/1980	1
nr. Durban	29°45′S 31°04′E	4/iv/1980	2
Shaws Wood farm, Karkloof	29°19′S 30°18′E	1/ii/1983	3
Lesser Stinkwood forest, nr. Kokstad	30°33′S 29°43′E	29/xi/1981	2
nr. Manzengwenya, Kwazulu	27°18′S 32°45′E	6/xii/1980	6
Manzengwenya, Kwazulu	27°16′S 32°46′E	3-7/xii/1980	3
nr. Maphelana, Kwazulu-Natal	28°26′S 32°25′E	10/xii/1980	3
Mpsheni forest nr. Kokstad	30°38′S 29°40′E	30/xi/1981	3
Ngoye forest reserve, nr Empangeni	28°50′S 31°43′E	11-12/xii/1980	8
nr. Scottburgh	30°15′S 30°46′E	25/i/1983	6
Sordwana Bay, Kwazulu-Natal	27°32′S 32°40′E	23/vii/1977	1
Dundocoris flavilineatus ndabeniensis			
Ndabeni forest, nr. Josini	27°22′S 32°00′E	24/i/1983	3
Dundocoris schoemani schoemani			
Baziya forest, nr. Umtata	31°34′S 28°25′E	8-9/xii/1981	6
Kambi Forest Reserve, nr. Umtata	31°28′S 28°36′E	8/xii/1981	7
Ku-manina forest, nr. Umtata	31°34′S 28°09′E	9/xii/1981	6
Nquaba forest, nr. Umtata	31°36′S 28°07′E	9/xii/1981	3
Dundocoris schoemani dwesaensis			
Dwesa forest Eastern Cape	32°18′S 28°50′E	10-13/xii/1981	5
Dundocoris scholtzi			
Ngome forest station, nr. Louwsburg	27°49′S 31°25′E	20-24/i/1983	16
Dundocoris fuscus			
Mariepskop forest, nr. Hoedspruit	24°33′S 30°54′E	6/x/1981	5
Dundocoris callani callani			
Dwesa forest	32°18′S 28°50′E	10-13/xii/1981	7
nr. Durban	29°45′S 31°04′E	8-11/iv/1980	1
Alexandria forest, nr. Grahamstown	33°43′S 26°24′E	30/i/1984	5
Ngoye Forest Reserve, nr. Empangeni	28°50′S 31°43′E	11-12/xii/1980	7
Nqaba forest, nr. Umtata	31°36′S 28°07′E	9/xii/1981	5
Mount Thesiger Nature Reserve, Port St. Johns	31°37′S 29°31′E	2-6/xii/1981	8
nr. Scottburgh	30°15′S 30°46′E	25/i/1983	4
Umdoni Park, nr. Scottburgh	30°24′S 30°41′E	27/i/1983	1
Dundocoris callani noduliclypeatus			
Town Bush, Pietermaritzburg	29°33′S 30°20′E	31/i/1983	10
Shaws Wood farm, Karkloof	29°19′S 30°18′E	1/ii/1983	7

Locality	Co-ordinates	Date collected	No. of individuals cytogenetically studied
Dundocoris natalensis			
Alexandria forest, nr. Grahamstown	33°43'S 26°24'E	30/i/1984	4
Manzengwenya	27°13'S 32°47'E	7/xii/1980	1
Ngoye forest Reserve, nr. Empangeni	28°50'S 31°43'E	11-12/xii/1980	2
Umtamvuma forest, nr. Port Edward	31°03'S 30°11'E	28/i/1983	3
Umdoni Park, nr. Scottburgh	30°24'S 30°41'E	23/i/1983	3
Hawaan forest, nr. Umhlanga Rocks	29°42'S 30°05'E	26/i/1983	3

9.2.1 *Dundocoris nodulicarinus* (Figs 257-259, 434-459)

This is a very interesting taxon from a cytogenetic viewpoint. It contains three subspecies which are morphologically indistinguishable but have different chromosome numbers. Furthermore two of the subspecies exhibit a multiple XY_1Y_2 sex chromosome system while the other one has a normal XY sex chromosome system. *D. nodulicarinus septeni* also features the unique situation where both the original X and Y chromosomes were involved in fusions with autosomes.

9.2.1.1 *Dundocoris nodulicarinus nodulicarinus* (Figs 257, 452-453)

The chromosome number of *Dundocoris nodulicarinus nodulicarinus* is 2n(♂) = 14XY. The true and relative chromosome areas for *D. nodulicarinus nodulicarinus* are represented in Table 9.20 and an idiogram in Fig. 257. Although 14XY is probably the ancestral chromosome number of the Aradidae, the karyotype of *D. nodulicarinus nodulicarinus* does not reflect the ancestral karyotype but a highly derived one. Three of the six autosomes are distinctly larger than the other three (in the ancestral karyotype it is presumed that the autosomes form a more or less gradual size series as it is present in *Silvacoris heissi*, *S. pondolandensis*, *Calisius africanus* and a *Brachyrhynchus* species). As most other *Dundocoris* taxa have chromosome numbers of 26XY or 28XY and there are strong indications that 28XY is the ancestral number for *Dundocoris* it seems that *D. nodulicarinus nodulicarinus* originated from a 28XY ancestor by means of at least 7 autosomal fusions. The three large chromosomes each probably consist of at least three of the original chromosomes while the fourth largest chromosome probably originated by the fusion of two of the smallest original chromosomes.

Table 9.20. True and relative chromosome areas of *D. nodulicarinus nodulicarinus*.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Mpesheni forest	Mpesheni forest
Individuals	1	1
Cells	6	6
A1	5.50(±1.00)	25.16(±0.73)
A2	5.17(±0.91)	23.68(±0.62)
A3	4.92(±0.81)	22.59(±0.48)
A4	2.39(±0.37)	10.99(±0.55)
A5	1.96(±0.33)	8.99(±0.40)
A6	1.88(±0.34)	8.60(±0.45)
X	5.35(±1.22)	24.37(±2.78)
Y	4.96(±1.08)	22.67(±2.66)
Autosomes	21.83(±3.68)	
All chromosomes	32.14(±5.76)	

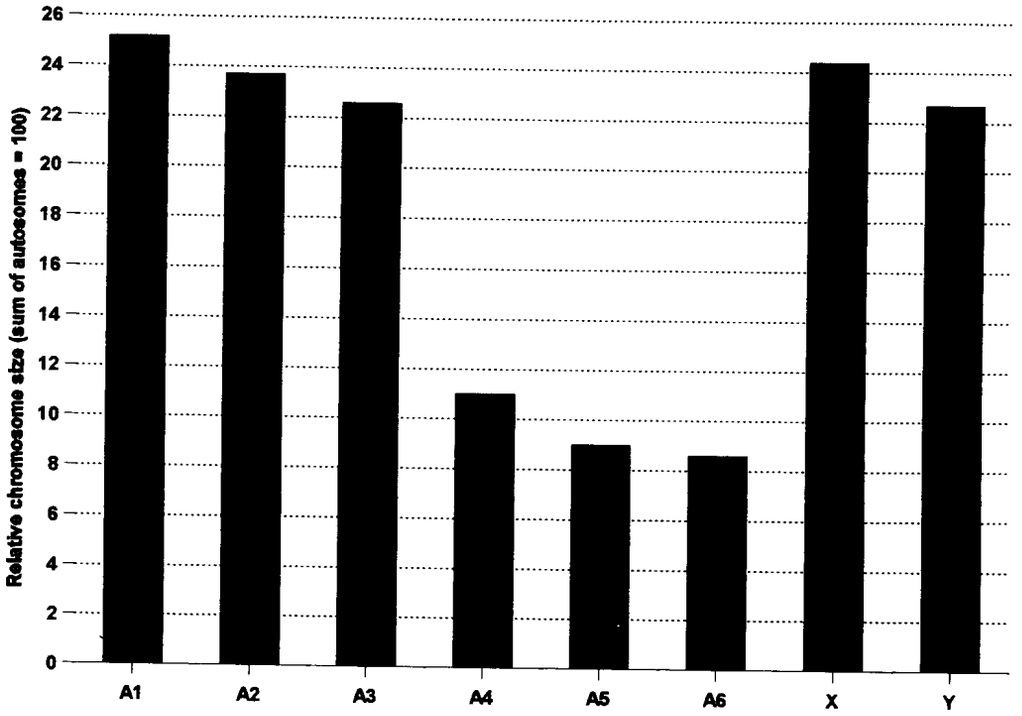


Figure 257. Idiogram of *Dundocoris nodulicarinus nodulicarinus*.

9.2.1.2 *Dundocoris nodulicarinus novenus* (Figs 258, 434-451)

The chromosome number of *Dundocoris nodulicarinus novenus* is $9XY_1Y_2$ (where Y_1 represents a neo-Y and X a neo-X which originated by the fusion of an autosome with the X-chromosome). The true and relative chromosome areas for *D. nodulicarinus novenus* are presented in Table 9.21 and an idiogram

in Fig. 258. The karyotype consists of one very large autosome, two small autosomes, a large neo-X chromosome (the result of a fusion between an autosome and the original X-chromosome), the neo-Y chromosome (indicated by Y_1) which represents the homologue of the autosome involved in the autosome-X fusion and the original Y-chromosome (indicated by Y_2).

Table 9.21. True and relative chromosome areas of *D. nodulicarinus novenus*.

True chromosome areas (μm^2) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.	Relative chromosome areas (% of total area of all chromosomes) and standard deviation.
Chromosome	Isidenge forest	Isidenge forest	Isidenge forest
Individuals	3	3	3
Cells	9	9	9
A1	12.24(±2.31)	72.92(±1.85)	32.02(±0.93)
A2	2.51(±0.47)	14.98(±1.29)	6.58(±0.58)
A3	2.02(±0.33)	12.10(±0.87)	5.31(±0.37)
X	10.31(±1.93)	61.46(±1.80)	26.97(±0.81)
Y_1	6.24(±1.13)	37.25(±1.47)	16.34(±0.46)
Y_2	4.87(±0.87)	29.11(±1.94)	12.77(±0.77)
Autosomes	16.77(±3.03)		
All chromosomes	38.19(±6.86)		

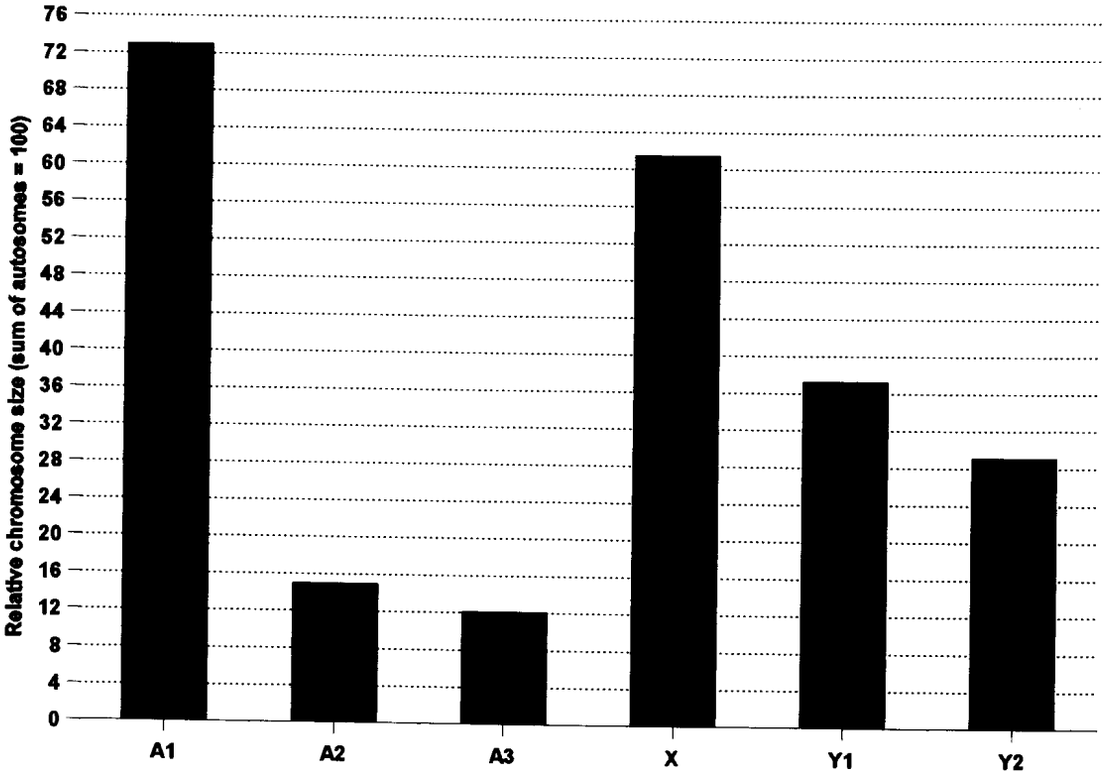


Figure 258. Idiogram of *Dundocoris nodulicarinus novenus*.

D. nodulicarinus novenus presumably originated from *D. nodulicarinus nodulicarinus* by means of three fusions namely (not necessarily in the indicated order):

1. Fusion between one of the small and one of the large autosomes.
2. Fusion between two of the large autosomes.
3. Fusion between one of the large autosomes and the X-chromosome.

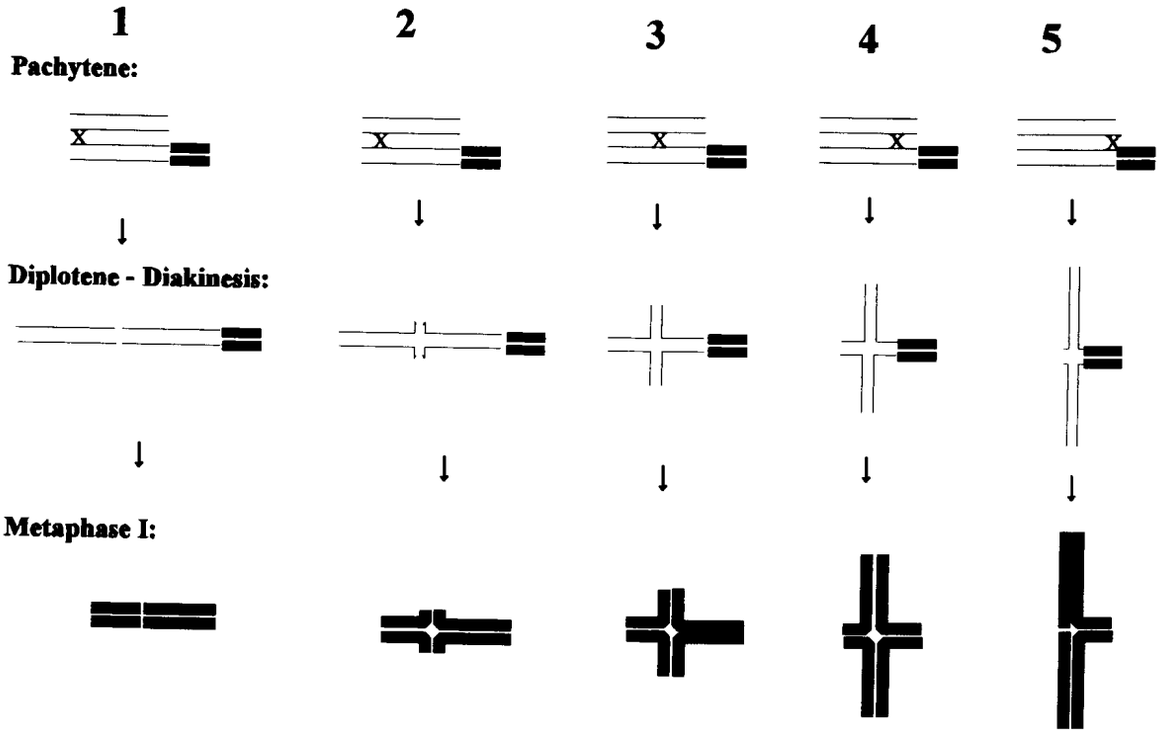
The behaviour of the neo-XY chromosome structure during meiosis is of particular interest because, in the Heteroptera, the sex chromosomes are positively heterochromatic during prophase I and undergo chromatid segregation at AI while the autosomes are euchromatic and exhibit normal crossovers and segregation

During Leptotene-Pachytene the original sex chromosomes are heterochromatic and associated to form a single circular body with the individual chromosomes not discernable while all the autosomes and the autosomal part of the neo-X are euchromatic and form the usual pachytene strands (Fig. 434). A very lightly stained nucleolus, which is at least the size of the heterochromatic body, is usually associated with it.

During the diffuse stage all the autosomes and the autosomal part of the neo-X become fuzzy and the chromatids are not discernable. The original sex chromosomes stay positively heterochromatic and associated and form a smooth, circular body (Fig. 453). The lightly stained round nucleolus is still visible and associated with this body.

During diplotene-diakinesis the individual bivalents become visible and the individual chromatids become discernable so that the chiasmata are clearly visible in the large autosomal bivalent and the neo-XY structure. The two small autosomal bivalents usually form two quadripartite structures where the four chromatids are loosely connected by thin strands (Figs 436-438). The original sex chromosomes are still positively heterochromatic but become detached from each other. The original X-chromosome is often some distance apart from its fused autosomal part and only connected to it by a very thin strand (Figs 436-437). At late diakinesis this strand becomes more visible and the heterochromatic X part of the neo-X moves closer to its autosomal part.

During diplotene-diakinesis the neo-XY shows one chiasma without exception and the structure of the 'bivalent' depends on where the crossing over took place as follows:



Forty diakinese cells were scored for types 1-5 structures (as defined in the figure above) for the neo-XY 'bivalent' and their percentages are as follows:

TYPE	1	2	3	4	5
PERCENTAGE	32.5	27.5	27.5	5	7.5

It is clear that the most crossovers are located in the distal part of the 'bivalent' (as defined relative to the position of the original X). The same cells were scored for the chiasmata of the large autosomal bivalent with the following results:

BIVALENT TYPE	2/0	2/1	2/2	1/0	1/1
PERCENTAGE	45	37.5	7.5	7.5	2.5

At metaphase I the autosomes and the original sex chromosomes become isochromatic. Five structures are visible namely the three autosomal bivalents, the neo-XY 'bivalent' and the original Y-chromosome (= Y_2). The original X and the autosomal part of the neo-X form an unbroken unit and the fusion site is not discernable. In the type 1 neo-XY structures a small gap indicates the terminalized chiasma (Figs 439-440). The large autosome is usually visible as a more or less solid roundish structure where it is difficult to determine the exact position of the chiasmata, especially if both chiasmata are not terminalized. Where both chiasmata are terminalized (2/2) it forms the usual donut-shaped structure. In the cases where only one chiasma is present it usually occurs interstitially (Fig. 440). In the 1/0 large

autosomal bivalent in Fig. 443 crossing over has occurred near one end and the bivalent has orientated with its long axis parallel to the equatorial plate. This is not always the case and it often orientates with its long axis perpendicular to the equatorial plate - it seems that this depends on at which telomere the spindle fibres have attached. In *Triatoma infestans* Pérez et al. (1997) have shown that the chromosome ends may show kinetic activity independent of the chiasma position and it is also probably the case here. The small autosomal bivalents usually form a square or rectangular structure and their quadripartite structure is usually still visible.

Forty-five metaphase cells were scored for the five types of the neo-XY 'bivalent' with the following results:

TYPE	1	2	3	4	5
PERCENTAGE	42	18	33	2	4

The results are similar to that of diakinesis and again indicate the distal localisation of the crossovers. It also demonstrates that there is not terminalization of chiasmata.

The large autosomal bivalent shows the following percentages of chiasmatic types:

BIVALENT TYPE	2/0	2/1	2/2	1/0	1/1
PERCENTAGE	53	31	9	7	0

Again it is very similar to the results for diakinesis, arguing against terminalization of chiasmata.

During anaphase I five structures move to each pole, namely the three autosomes, one chromatid of the original Y-chromosome (Y_2) and one chromatid of the neo-X together with a chromatid of the neo-Y (Y_1) (Figs 444-446). The chromosomes of the large autosomal bivalent often move to the poles with their long axes perpendicular to the spindle axis, indicating that the spindle has probably attached to more than one point along the chromosome (Figs 444, 446), but this is not always the case and sometimes it is clearly attached to one of the chromosome ends as is usual for the Heteroptera (refer to the discussion at 9.2.1.4).

Metaphase II (Figs 447-448) follows directly after AI and four structures are present at this stage, namely the three autosomes and the tripartite sex chromosome structure which consist of the neo-X on the one side and the neo-Y (Y_1) and original Y (Y_2) on the other side. The latter undergo the usual touch-and-go pairing with the original X part of the neo-X. It is interesting to note that the large autosome usually lies with its long axis parallel to the equatorial plate and it often seems if there is bi-telomeric attachment of the spindle fibres resulting in each chromatid forming a C-shaped structure (Fig. 448).

At anaphase II four chromatids (= daughter chromosomes) (two large and two small, representing the large autosome, large neo-X and two small autosomes) segregate to one pole and five (one large, two medium and two small, representing the large autosome, medium sized neo-Y and original Y and the two small autosomes) to the opposite pole. No early AII cells were found (indicating the short duration of this stage), but from late AII cells it looks possible that the larger chromosomes move broadside to the poles.

Spermatogonial mitosis (Fig. 450) clearly shows 9 chromosomes (two large autosomes, four small autosomes, large neo-X and medium sized neo-Y and Y-chromosomes) while oogonial mitosis (Fig. 451) shows 8 chromosomes (two large autosomes, four small autosomes and two large neo-X chromosomes).

9.2.1.3. *Dundocoris nodulicarinus septeni*. (Figs 259, 454-459).

The chromosome number of *Dundocoris nodulicarinus septeni* is $2n(\sigma^{\prime}) = 7XY_1Y_2$ (where Y_1 represents the neo-Y that originated by the fusion of an autosome with the X-chromosome - like in *D. nodulicarinus novenus*; Y_2 represent a neo-Y that originated by the fusion of an autosome to the Y-chromosome; X represent a neo-X comprising the original X which has fused to a large autosome (like in *D. nodulicarinus novenus*) on the one side and to a small autosome - the homologue of the autosome that fused with the Y-chromosome - on the other side).

The true and relative chromosome areas of *D. nodulicarinus septeni* are presented in Table 9.22 and an idiogram in Fig. 259.

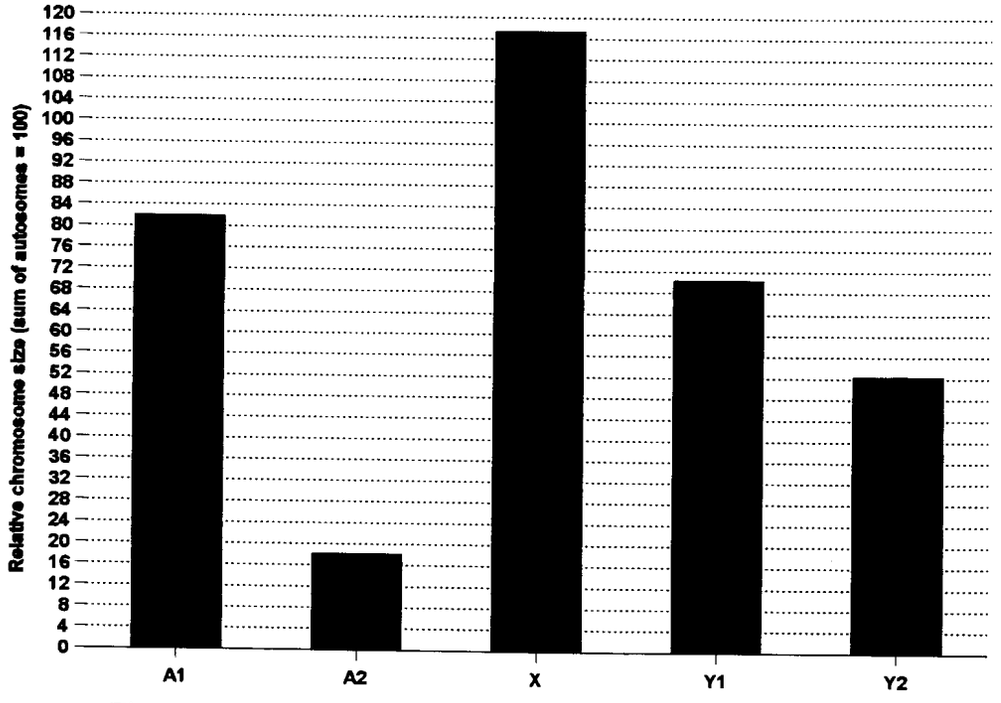


Figure 259. Idiogram of *Dundocoris nodulicarinus septeni*.

Table 9.22. True and relative chromosome areas of *D. nodulicarinus septeni*.

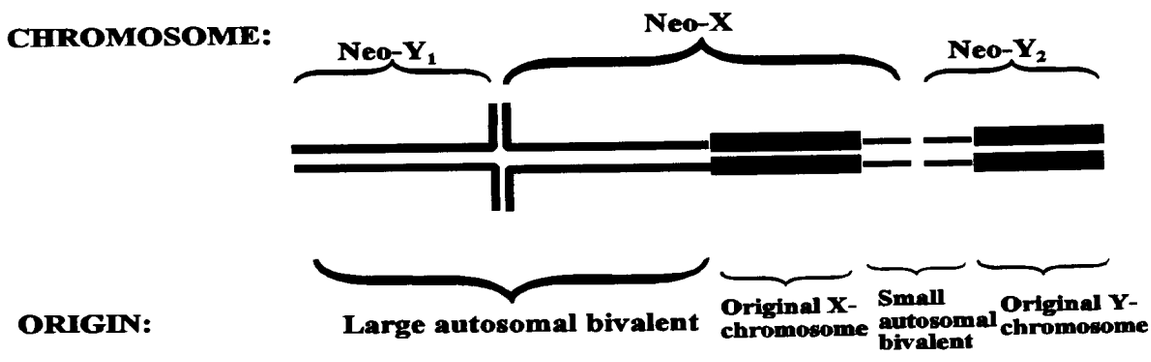
True chromosome areas (µm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.	Relative chromosome areas (% of total area of all chromosomes) and standard deviation.
Chromosome	Alexandria forest	Alexandria forest	Alexandria forest
Individuals	3	3	3
Cells	8	8	8
A1	9.12(±1.61)	81.94(±2.28)	24.13(±1.18)
A2	1.99(±0.24)	18.06(±2.28)	5.31(±0.58)
X	13.00(±1.93)	117.28(±3.14)	34.49(±0.18)
Y_1	7.82(±1.31)	70.39(±1.94)	20.70(±0.45)
Y_2	5.77(±0.64)	52.36(±4.41)	15.38(±0.96)
Autosomes	11.11(±1.75)		
All chromosomes	37.70(±5.55)		

The karyotype consists of one large autosome, one small autosome and the three neo sex chromosomes as described above. *D. nodulicarinus septeni* possibly originated from *D. nodulicarinus novenus* by means of two fusions namely:

1. Fusion between one of the small autosomes and the original Y-chromosome.
2. Fusion between the homologue of the same small autosome and the neo-X of *D. nodulicarinus novenus*.

The two homologues of one small autosome have thus been involved in fusions with the original X and Y chromosomes respectively.

The course of meiosis is basically similar to that of *D. nodulicarinus novenus* and mainly differences are pointed out in the following description. During diakinesis and MI only three structures are present namely the two autosomes and the composite sex chromosome structure consisting of the neo-X and both the neo-Y chromosomes. The composition and origin of this structure are schematically presented as follows:



During diplotene-diakinesis the two original sex chromosomes that form the positively heterochromatic structure, become separated. The original X part of the neo-X usually lies, from the time the chromosomes become discernable, close to its autosomal part and neo-Y_1 while the neo-Y_2 (which embodies the original Y) usually lies well removed from this structure and is only connected to it with two very thin, nearly invisible strands. At late diakinesis it is apparent that this gap is situated between the two parts of the small autosomal 'bivalent' and represents a terminal chiasma. (This is equivalent to the situation in *D. nodulicarinus novenus* where there is usually a gap between the two chromosomes of the small autosomal bivalents.) During metaphase I the neo-Y_2 moves closer to the neo-X but a small gap always remains visible. The two strands that attach them, however, become clearly detectable. The two chromatids of the original Y-chromosome usually lie somewhat directed towards the poles with its free end, suggesting spindle attachment to them.

The crossover pattern of both the large autosomal bivalent and the neo-Y_1 - neo-X 'bivalent' differs markedly from that of *D. nodulicarinus novenus*. The large autosomal bivalent exhibits the following percentages of chiasmatic types (37 MI cells were analysed):

BIVALENT TYPE	2/0	2/1	2/2	1/0	1/1
PERCENTAGE	3	24	73	0	0

Although no 1/0 or 1/1 chiasmic types were observed they probably occur in a very low frequency.

The neo-X - neo-Y part of the sex chromosome structure was also scored for the five types of single crossovers as defined for *D. nodulicarinus novenus*. In addition to the five types a substantial number of them have two crossovers. The observed percentages for the 37 analysed MI cells are as follows:

TYPE	1	2	3	4	5	2 chiasmata
PERCENTAGE	11	5	30	5	3	46

The neo-Y_1 - neo-X 'bivalent' with two chiasmata have interesting complications for segregation as discussed in 9.2.1.4.

During AI three bodies move to each pole namely the two autosomes and the tripartite neo-X-neo-Y_1-neo-Y_2 (one chromatid of each of the latter). Although no early AI cells were observed, late AI cells often suggest the broadside movement of the larger chromosomes.

At MII (Fig. 457) three structures are present namely the two autosomes and the tripartite sex chromosome structure which incorporates the neo-X on the one side and the neo-Y_1 and neo-Y_2 on the other. Both the large autosome and the neo-X lie with their long axis parallel to the equatorial plate. At AII four daughter chromosomes (the large autosome, the small autosome and the medium sized neo-Y_1 and Y_2) segregate to one pole and three (the large autosome, the small autosome and the large neo-X) to the opposite pole.

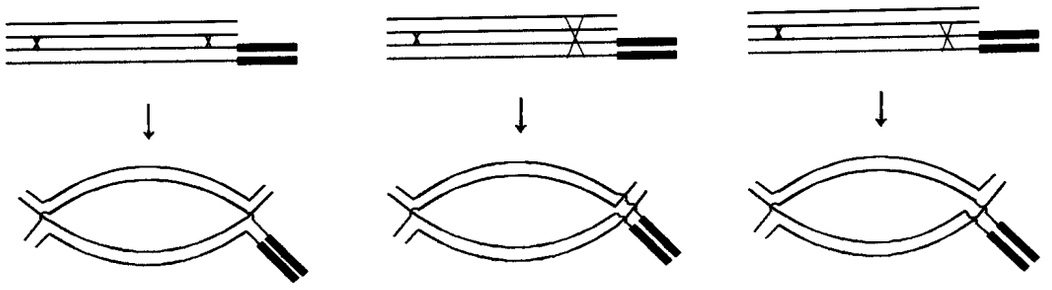
Spermatogonial mitosis (Fig. 458) shows seven chromosomes as expected, namely (from large to small) the neo-X, two large autosomes, neo-Y_1, neo-Y_2 and two small autosomes. Oogonial mitosis (Fig. 459) shows the expected six chromosomes, namely (from large to small) the two neo-X chromosomes, two large autosomes and two small autosomes.

As mentioned above *D. nodulicarinus septeni* possibly originated from *D. nodulicarinus novenus* by means of the fusions of the homologous chromosomes of a small autosome to the original X- and Y-chromosomes respectively. The relative sizes of the chromosomes (compare Tables 9.21 and 9.22), however, suggest that they may have originated independently from *D. nodulicarinus nodulicarinus* or another ancestor. It is evident that the large autosome is larger in *D. nodulicarinus novenus* than in *D. nodulicarinus septeni* (32% versus 24% of the total chromosome area) while the neo-X is larger in *D. nodulicarinus septeni* (34.5% versus 27%). Although the latter is to be expected because of the extra autosome fused to it, the difference is larger than can be explained by the fusion. Further confirmation of this is that the neo-Y_1 (which is the homologue of the large autosomal part of the neo-X) is also larger in *D. nodulicarinus septeni* (20.7% versus 16.3%). The different frequency and location of the crossovers in the large autosome and neo-X-neo-Y_1 'bivalent' between these taxa are also indicative of the size and structural differences between them and support their independent origin. Further study and analysis would be necessary to confirm this.

9.2.1.4. Discussion.

In *D. nodulicarinus septeni* two crossovers often occur between the neo-Y_1 and neo-X chromosomes (in 46% of the cells) and this has complications for the segregation of the chromosomes and may throw some light on the location of spindle attachment. It is known that in the Heteroptera the spindle usually attaches over a large part of the length of the chromosomes during mitosis (Buck 1967, Comings & Okada 1972, Ruthmann.& Permantier 1973) while it usually attaches to the chromosome ends during meiosis (Schrader 1935, Hughes-Schrader & Schrader 1961, Nokkala 1985, González-García *et al.* 1996, Pérez *et al.* 1997) although Nokkala & Nokkala (1996) suggested that microtubules may also attach to those regions of chromatids lying parallel to the equatorial plane during meiosis. In *Psylla försteri* (Homoptera) the large bivalent/chromosome always orientates with its long axis parallel to the equatorial plate at MI and MII and the spindle fibres apparently attach themselves to its whole poleward surface (Suomalainen & Halkka 1963).

From the following figure, which depicts the case in *D. nodulicarinus septeni*, it is obvious that if the spindle attaches to the free distal ends of the 'bivalent', it would follow that all two and four strand double crossovers (50% of the cases) would result in the original X part of the neo-X (as well as the original Y) undergoing chromosome and not chromatid segregation. Only three strand double crossovers (50% of the cases) would result in chromatid segregation of the original X (and Y). However, all AI and MII cells show that chromatid segregation of the original X and Y is the rule without exception.



To ensure the regularly observed segregation pattern there are the following possibilities:
The spindle may attach to the two chromatids of the original X-chromosome and not to its large autosomal part. This is, however, unlikely because:

a. Both ends of the original X are fused with autosomes which are involved in chiasmata. This would imply that the spindle fibres attach to the main body of the X-chromosome and not to the chromosome ends as is usually the case in Heteropteran meiosis. Although this may be possible and even likely (see point 4.), one would then expect that it would also happen to the autosomal and neo-Y_2 parts of structure and not to the original X alone.

b. It would imply that there are no spindle fibres attached to the neo-Y_1 and that they are dragged along to the poles by their chiasmatic association with the neo-X. It is, however, the rule that the chiasmata break down during early AI and one would expect that they would be unable to segregate to the poles but form laggards on the equatorial plate. This as well as the presumed deletion MII cells, was never observed.

1. The distal chiasmata may terminalize completely before the spindle attaches. This would, however, require the attachment of the spindle to each pair of adjacent chromatids although they have originated from different chromosomes. This is unlikely and it has been demonstrated that the chiasmata do not terminalize in the Heteroptera (Nokkala & Nokkala 1996, Pérez et al. 1997).
2. The spindle may attach to the free ends of the neo-Y_2 (= original Y-chromosome). The neo-Y_2 is, however, attached to the rest of the structure by means of a terminal chiasma and would thus be unable to drag along the other chromosomes (see point 1b).
3. The spindle fibres do not attach to the chromosome ends as is normally the case but to the main body of the chromosome between the two chiasmata (probably at various points) as is the case during mitosis. The crossover between the spindle attachment area and the original X would then assure the chromatid segregation of the latter. It is also probable that the spindle simultaneously attaches to the chromatids of the original X (and possibly to the original Y as well - although it is more probable that the spindle attaches to its free ends as its orientation at MI suggests) to assist their segregation.

This type of spindle attachment could also explain the broadside movement of the large chromosomes during AI (as was also observed in *D. nodulicarinus novenus*) and it can be argued that the large chromosomes have various potential attachment areas. The large chromosomes are the result of the fusion of various small chromosomes and it is possible that interstitial telomeric sequences may serve as attachment points for the spindle.

The following arguments against this mode of spindle attachment can be raised:

a. It would probably imply different modes of spindle attachment depending on the location and number of chiasmata (two chiasmata or a single terminal chiasma ➜ interstitial spindle attachment; single interstitial chiasma ➜ telomeric spindle attachment).

b. Although interstitial or holocentric spindle attachment has been suggested for large chromosomes and the broadsided movement of chromosomes has been described previously (Schrader 1935, Suomalainen & Halkka 1963), most of the recent investigations support the telomeric attachment of the spindle during meiosis.

Further investigation is necessary to elucidate the spindle attachment to this structure.

Very few XY_n sex chromosome systems have thus far been reported in the Heteroptera. Pfaler-Collander (1941) reported that some individuals of *Lygaeus equestris* have two Y chromosomes that are smaller than the usual small Y-chromosome. The same situation was subsequently described for *L. hospes* and *L. pandurus* (Barik et al. 1981, Manna & Deb-Mallick 1986). They found that in both these species there are two types of X-chromosomes and three types of Y-chromosomes namely the usual original X, a smaller X_1 that probably originated after a small segment broke off the original X, the original Y, a smaller Y_1 that probably originated after a small segment broke off the original Y, and Y_2 which is presumably the fusion product of the small parts that broke off the X and Y.

In the above three lygaeid bugs only a few individuals in the population exhibit the XY_1Y_2 sex chromosome system (11 of 230 specimens in *L. hospes* and 6 of 80 specimens in *L. pandurus*). These individuals could not morphologically or otherwise be told apart from the rest of the population.

A few cases of polymorphism for sex chromosome systems where "supernumery" Y-chromosomes occur have been reported in the Heteroptera. Wilson (1907, 1909, 1910) described the situation in three species of *Acanthocephala* (as *Metapodius*)(Coreidae) namely *A. femoratus*, *A. granulosa* and *A. terminalis*. All three species have the basic coreid type chromosome constitution of 2n(♂) = 21 (18A + 2m + X0) but many of the individuals have in addition one to five supernumery Y-chromosomes. The Y elements form a chain with the single X at MII and segregate regularly to the opposite pole than the X. The extra Y-chromosomes were suspected to be supernumeraries because they seemed to have no genetical or morphological effect.

The only two species that have been reported as having an XY_n sex chromosome system as the norm is *Rhyparochromus angustatus* (Lygaeidae) [reported by Takenouchi & Muramoto (1968) as cited by Ueshima (1979)] and *Cryptostemma pusillimum* (Dipsocoridae) (Grozeva & Nokkala 1996).

I have not read the original paper of Takenouchi & Muramoto (which is in Japanese) and therefore do not know how many specimens they studied and how many details of their findings are presented. If one, however, compares the chromosome number of *Rhyparochromus angustatus* (2n(♂) = 15 (10A + 2m + XY_1Y_2) with that of two other *Rhyparochromus* species (listed by Ueshima 1979) which both have 2n(♂) = 14 (10A + 2m + XY) it is evident that the XY_1Y_2 system in *R. angustatus* probably originated by means of fragmentation of the Y-chromosome. It must, however, be noted that the findings of Takenouchi & Muramoto have often been in disagreement with the findings of other authors. For example: they (1967) listed *Saldula saltatoria* as having 2n(♂) = 36XY while Cobben (1968) found it to be 2n(♂) = 35X0; they (1968) found *Gerris paludum* to have 2n(♂) = 24XY while Wilke (1913) reported it to be 2n(♂) = 23X0; they (1968) found *Hydrometra procera* to be 2n(♂) = 20XY while two other *Hydrometra* species are 2n(♂) = 19X0 (Jande 1959, Cobben 1968).

In the well documented case of *Cryptostemma pusillimum* the two Y-chromosomes are rather small, only slightly larger than the m-chromosomes and much smaller than the autosomes and X-chromosome. Grozeva & Nokkala came to the conclusion that "there is certainly no doubt that these multiple Y chromosomes of *C. pusillimum* have evolved from the Y chromosome by fragmentation". Unfortunately they did not state how many individuals they studied.

In all of the above cases the multiple Y-chromosomes originated by means of fragmentation. The XY_1Y_2 sex chromosome system of *Dundocoris nodulicarinus novenus* and *D. nodulicarinus septeni* are thus the first reported cases in the Heteroptera where such a system originated by a X-chromosome-autosome fusion. The case of *D. nodulicarinus septeni* where three autosome-sex chromosome (two X-autosome and one Y-autosome) fusions were involved in the creation of its sex chromosome system and where the two homologous autosomes were both involved in fusions with the X- and Y-chromosome respectively, have, to my knowledge, not previously been encountered in any organism.

9.2.2 ***Dundocoris marieps*** (Figs 260, 460-461)

The chromosome number of *D. marieps* is 2n(♂) = 28XY. The true and relative chromosome areas of *D. marieps* are presented in Table 9.23 and an idiogram in Fig. 260.

Table 9.23. True and relative chromosome areas of *D. marieps*.

True chromosome areas (µm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Mariepskop forest	Mariepskop forest
Individuals	2	2
Cells	9	9
A1	4.02(±0.36)	9.63(±0.26)
A2	3.88(±0.37)	9.29(±0.18)
A3	3.69(±0.37)	8.84(±0.22)
A4	3.60(±0.42)	8.60(±0.28)
A5	3.38(±0.35)	8.08(±0.19)
A6	3.32(±0.32)	7.95(±0.13)
A7	3.24(±0.31)	7.77(±0.13)
A8	3.19(±0.28)	7.65(±0.15)
A9	3.08(±0.31)	7.39(±0.22)
A10	2.94(±0.27)	7.05(±0.14)
A11	2.77(±0.24)	6.65(±0.30)
A12	2.38(±0.25)	5.70(±0.23)
A13	2.26(±0.27)	5.41(±0.23)
X	8.35(±0.88)	20.02(±1.21)
Y	6.37(±0.72)	15.23(±0.67)
Autosomes	41.75(±3.98)	
All chromosomes	56.47(±5.43)	

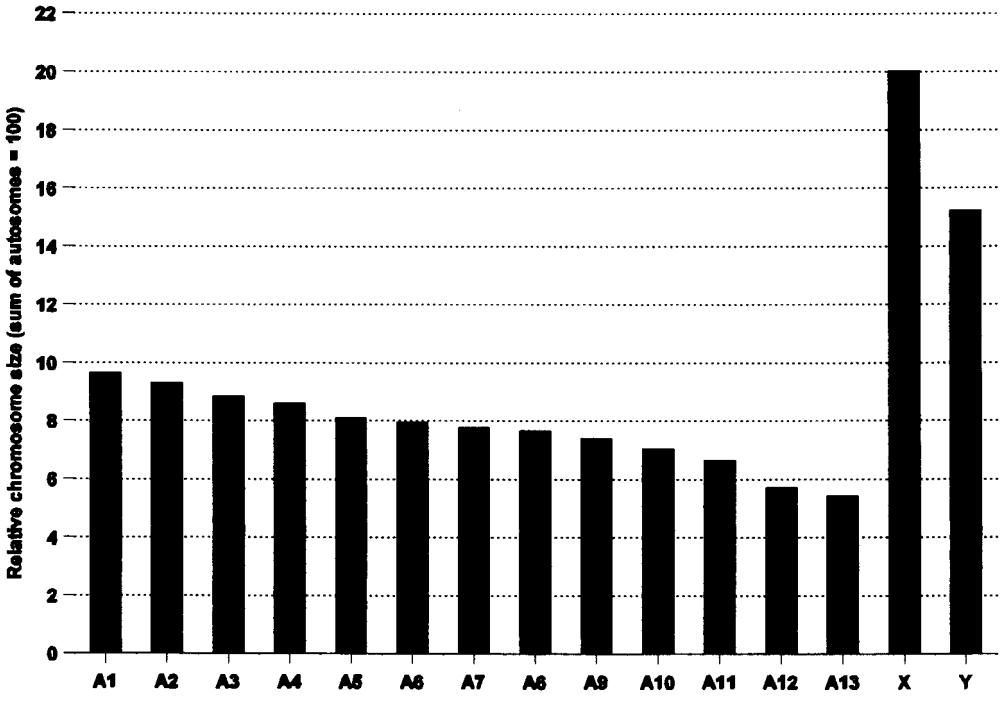


Figure 260. Idiogram of *Dundocoris marieps*.

The autosomes form a gradual size series except for A12 and A13 which is set apart by a slight step in the series. The sex chromosomes are by far the largest chromosomes in the complement - the X-chromosome is more than twice the size of the largest autosome while the Y-chromosome is nearly 1.6x as large as the largest autosome.

D. marieps occurs sympatrically with *D. fuscus* at Mariepskop and individuals of both species are often found in close proximity to each other. The chromosome number of *D. fuscus* is also 2n(♂) = 28XY and its karyotype is very similar to that of *D. marieps* except for the sex chromosomes that are distinctly smaller.

9.2.3 *Dundocoris begemanni* (Figs 261, 462).

The chromosome number of *D. begemanni* is 2n(♂) = 26XY. The true and relative chromosome areas are presented in Table 9.24 and an idiogram in Fig. 261. Although cytogenetic preparations of 5 individuals were made the MII cells found were not well spread and therefore MI cells were used for measurements. The largest autosome (A1) is much larger (1.4x) than the second largest autosome (A2). A2-A12 form a more or less gradual size series but small steps set apart A2 and A12. The sex chromosomes are large as in the previous species. The X-chromosome is the largest chromosome in the complement, about twice the size of A2. The latter probably represents the largest autosome of an ancestor before a fusion gave rise to the large A1 and is thus comparable with A1 of the previous species. The Y-chromosome is about 1.35x the size of A2 and slightly smaller than A1.

Table 9.xx. True and relative chromosome areas of *D. begemanni* at metaphase 1.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Injasuti forest	Injasuti forest
Individuals	1	1
Cells	2	2
A1	9.94(±0.68)	14.65(±0.30)
A2	7.00(±0.13)	10.32(±0.68)
A3	6.19(±0.16)	9.13(±0.17)
A4	5.94(±0.08)	8.76(±0.28)
A5	5.85(±0.19)	8.60(±0.14)
A6	5.53(±0.14)	8.14(±0.19)
A7	5.31(±0.35)	7.82(±0.17)
A8	5.06(±0.21)	7.46(±0.03)
A9	4.79(±0.08)	7.06(±0.22)
A10	4.51(±0.39)	6.65(±0.29)
A11	4.21(±0.77)	6.21(±0.87)
A12	3.53(±0.22)	5.20(±0.07)
X	13.33(±0.34)	19.71(±0.32)
Y	9.51(±0.26)	14.07(±0.96)
Autosomes	67.86(±3.14)	
All chromosomes	90.70(±3.22)	

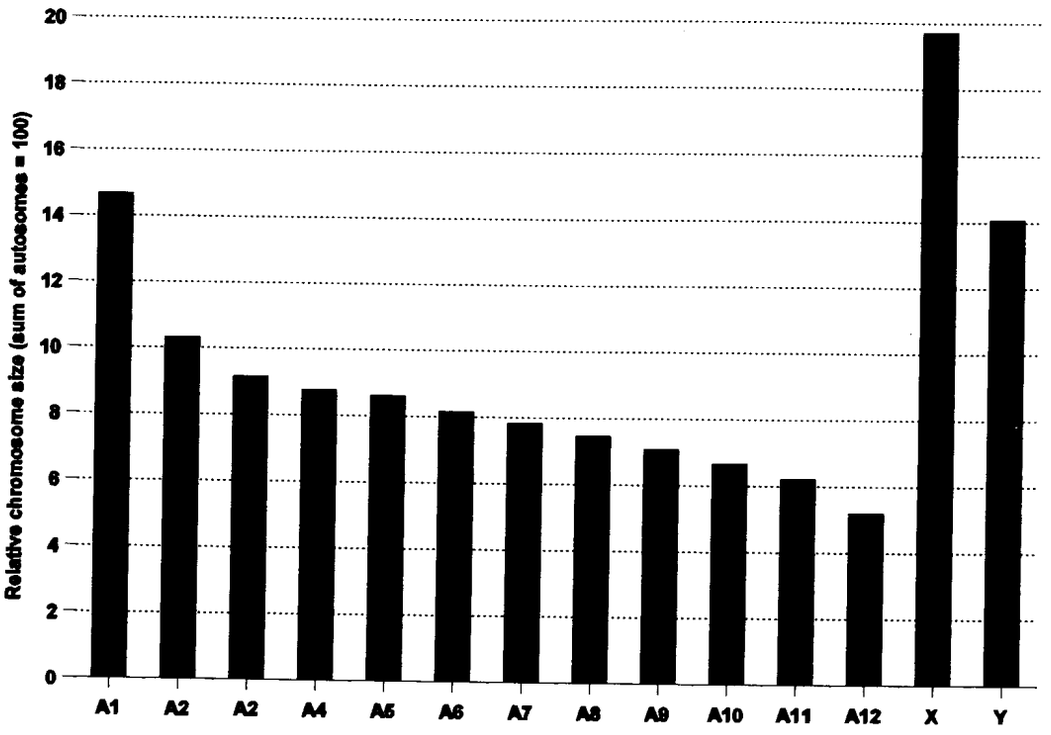


Figure 261. Idiogram of *Dundocoris begemanni*.

D. begemanni probably originated from a 28XY ancestor (refer also to the discussion in 9.2.12) by means of a fusion of two autosomes. It is possible that one of the smallest autosomes (A12 or A13) of the ancestor fused with the second largest autosome (A2) to form the large autosome of *D. begemanni*. The small steps between A2/A3 and A11/A12 support this hypothesis.

9.2.4 ***Dundocoris stuckenbergi*** (Figs 262-263, 263A, 463-468).

D. stuckenbergi encompasses two subspecies that are morphologically indistinguishable but have different chromosome numbers and karyotypes. Two specimens of a possible third subspecies were also collected - they are smaller than specimens of the other subspecies and although their autosomal karyotype is very similar to that of one of the described subspecies (*D. stuckenbergi ngomensis*) the sex chromosomes are markedly smaller.

9.2.4.1. ***Dundocoris stuckenbergi stuckenbergi*** (Figs 262, 463-464).

The chromosome number of *D. stuckenbergi stuckenbergi* is 2n(♂) = 26XY. The true and relative chromosome areas are presented in Table 9.25 and an idiogram in Fig. 262. The largest autosome (A1) is about 1.5x as large as A2. A2-A12 form a more or less gradual size series with a slight step between A2 and A3 and autosomes A11 and A12 also seem to be set apart by a small step. The sex chromosomes

are subequal in size and by far the largest chromosomes in the complement. The X-chromosome is about 2.37x and the Y-chromosome about 2.23x as large as A2.

D. stuckenbergi stuckenbergi probably originated from *D. stuckenbergi ngomensis* or an ancestor with similar karyotype by means of the fusion of two autosomes. A fusion between the second largest chromosome (A2) and one of the smaller chromosomes, maybe A10 or A11 (but not A12 or A13 as they are set apart by a small step in the ancestor as well - see discussion in 9.2.12) of the ancestor will be consistent with the observed steps in the karyotype of *D. stuckenbergi stuckenbergi* as well as with the size of A1.

Table 9.25. True and relative chromosome areas of *D. stuckenbergi stuckenbergi*.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Town Bush	Town Bush
Individuals	1	1
Cells	6	6
A1	2.76(±0.47)	15.31(±0.80)
A2	1.86(±0.28)	10.35(±0.64)
A3	1.60(±0.18)	8.92(±0.38)
A4	1.57(±0.18)	8.76(±0.32)
A5	1.50(±0.20)	8.36(±0.20)
A6	1.45(±0.19)	8.05(±0.18)
A7	1.37(±0.14)	7.66(±0.26)
A8	1.33(±0.14)	7.41(±0.27)
A9	1.29(±0.15)	7.18(±0.36)
A10	1.22(±0.16)	6.79(±0.26)
A11	1.07(±0.18)	5.91(±0.40)
A12	0.96(±0.17)	5.31(±0.57)
X	4.41(±0.79)	24.43(±2.15)
Y	4.15(±0.85)	22.90(±2.32)
Autosomes	18.00(±2.31)	
All chromosomes	26.56(±3.88)	

9.2.4.2. *Dundocoris stuckenbergi ngomensis* (Figs 263, 465-467).

The chromosome number of *D. stuckenbergi ngomensis* is 2n(♂) = 28XY. The true and relative chromosome areas are presented in Table 9.26 and an idiogram in Fig. 263. It has the typical *Dundocoris* ancestral karyotype where the autosomes form a gradual size series except for A12 and A13 which are set apart by a slight step in the series. The sex chromosomes are, however, extremely large, the largest of all *Dundocoris* taxa. The X-chromosome is 3.3x and the Y-chromosome is about 2.8x as large as the largest autosome.

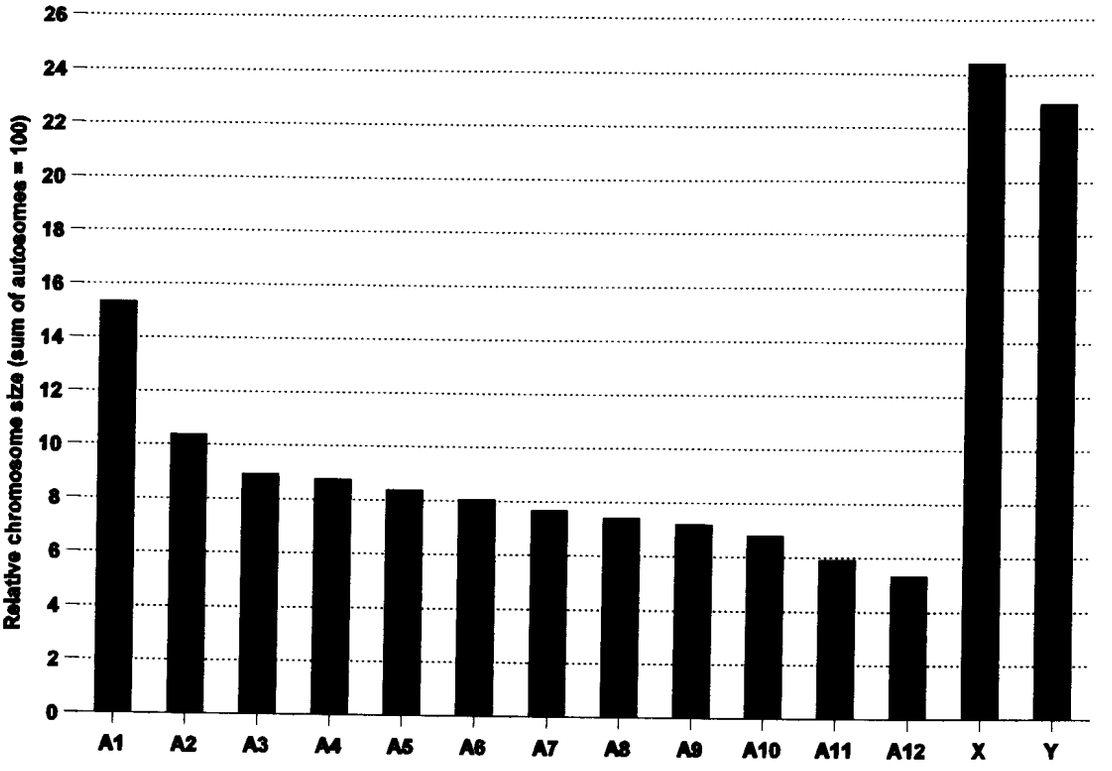


Figure 262. Idiogram of *Dundocoris stuckenbergi stuckenbergi*.

Table 9.xx. True and relative chromosome areas of *D. stuckenbergi ngomensis*.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Ngome forest	Ngome forest
Individuals	2	2
Cells	6	6
A1	2.39(±0.47)	9.75(±0.36)
A2	2.19(±0.42)	8.91(±0.11)
A3	2.14(±0.40)	8.72(±0.14)
A4	2.10(±0.41)	8.55(±0.11)
A5	2.03(±0.36)	8.28(±0.10)
A6	1.99(±0.37)	8.10(±0.19)
A7	1.95(±0.36)	7.96(±0.14)
A8	1.92(±0.35)	7.82(±0.12)
A9	1.81(±0.39)	7.36(±0.28)
A10	1.69(±0.34)	6.85(±0.15)
A11	1.64(±0.33)	6.68(±0.17)
A12	1.42(±0.28)	5.76(±0.31)
A13	1.29(±0.23)	5.26(±0.11)
X	7.93(±1.73)	32.21(±1.78)
Y	6.64(±1.29)	27.10(±0.85)
Autosomes	24.55(±4.67)	
All chromosomes	39.12(±7.64)	

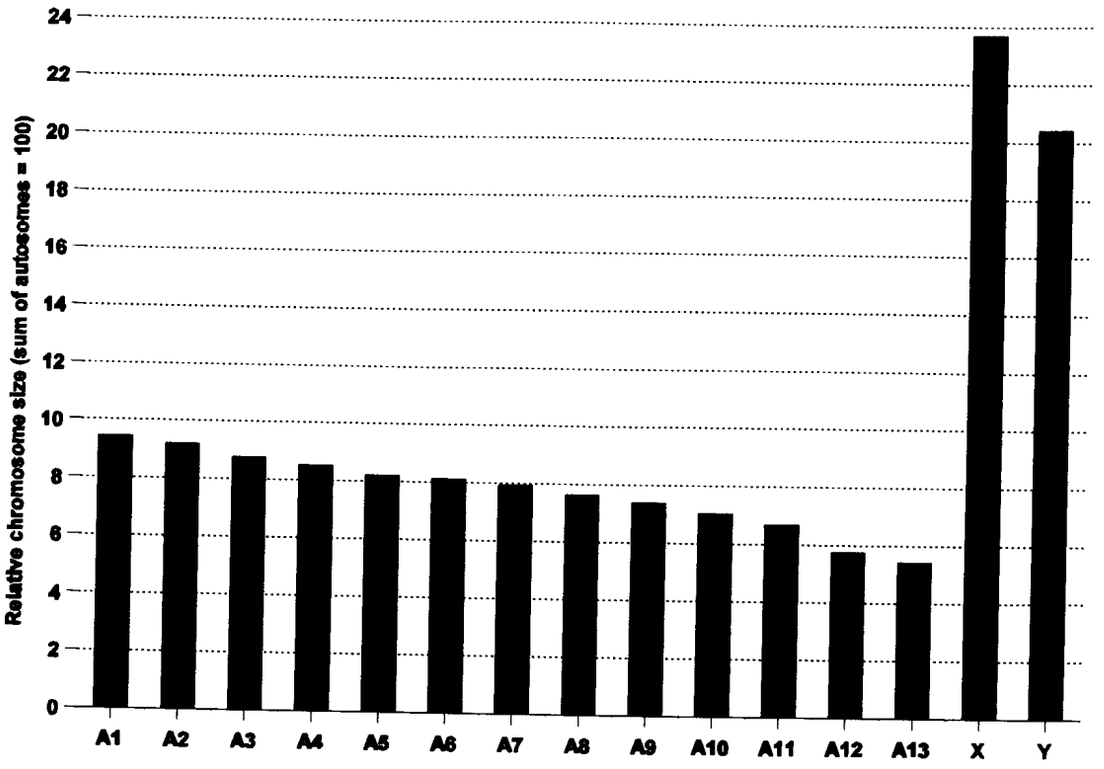


Figure 263A. Idiogram of *Dundocoris stuckenbergi subspec.* nov?

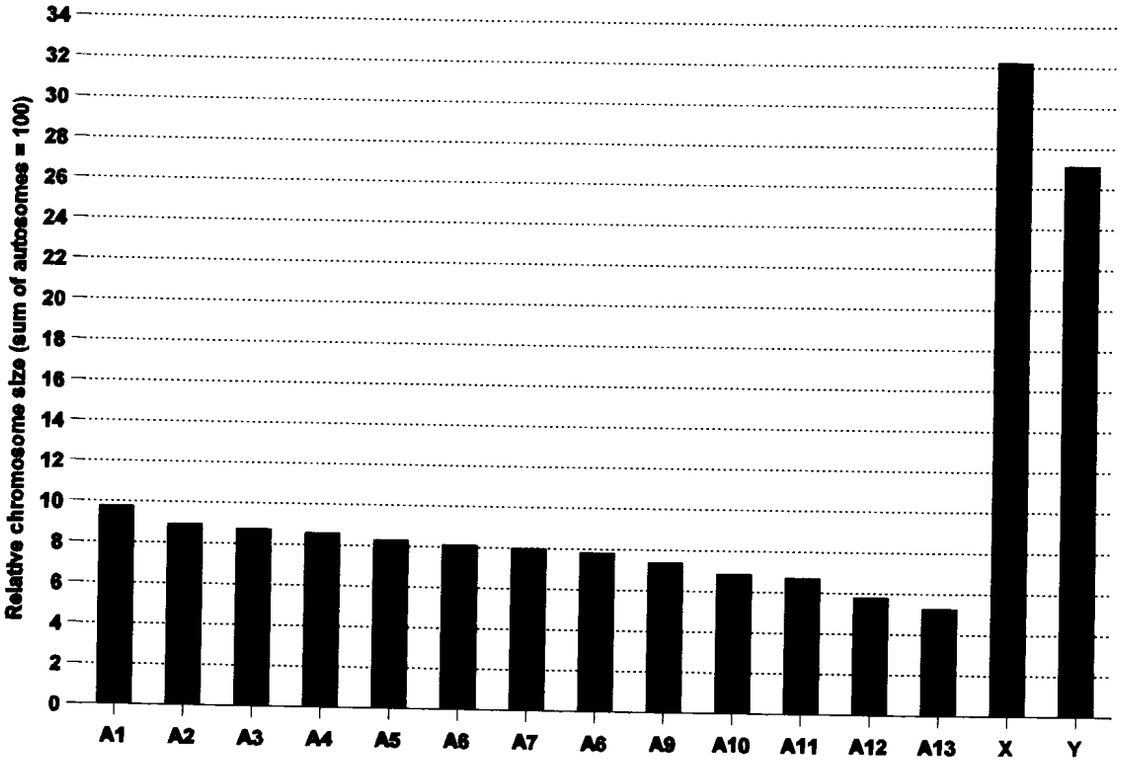


Figure 263. Idiogram of *Dundocoris stuckenbergi ngomensis.*

9.2.4.3. *Dundocoris stuckenbergi subspec.* nov? (Figs 263A, 468).

A male and female of a possibly undescribed subspecies were collected in Ngoye forest in northern Kwazulu-Natal. Its chromosome number is 2n(♂) = 28XY and an idiogram of its karyotype is presented in Fig. 263A. Its karyotype is very similar to that of *D. stuckenbergi ngomensis* except that the sex chromosomes are smaller. The X-chromosome is 2.5x and the Y-chromosome 2.17x as large as the largest autosome.

9.2.5. *Dundocoris nigromaculatus.* (Figs 264, 469-470).

The chromosome number of *D. nigromaculatus* is 2n(♂) = 20XY. The true and relative chromosome areas are presented in Table 9.27 and an idiogram in Fig. 264. There is a substantial difference in size between the five largest autosomes (A1-A5) while A6-A9 form a more gradual size series. The sex chromosomes are relatively small; the X-chromosome is just larger than A3 but smaller than A1 & A2, while the Y-chromosome is only slightly larger than A5.

D. nigromaculatus supposedly originated from an 28XY ancestor by means of four fusions. Two of the largest autosomes of the ancestor probably fused to form A1 while two of the smallest autosomes fused to form A4. A2 and A3 were formed by indeterminable fusions of some of the other autosomes.

Table 9.27. True and relative chromosome areas of *D. nigromaculatus*.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Ngoye forest	Ngoye forest
Individuals	1	1
Cells	6	6
A1	5.87(±0.87)	21.49(±0.86)
A2	4.30(±0.76)	15.67(±0.58)
A3	3.68(±0.68)	13.38(±0.50)
A4	3.15(±0.48)	11.52(±0.25)
A5	2.58(±0.48)	9.39(±0.26)
A6	2.18(±0.36)	7.95(±0.23)
A7	2.06(±0.35)	7.52(±0.08)
A8	1.87(±0.29)	6.83(±0.18)
A9	1.71(±0.26)	6.25(±0.37)
X	3.87(±0.62)	14.13(±0.56)
Y	2.76(±0.49)	10.05(±0.42)
Autosomes	27.40(±4.46)	
All chromosomes	34.03(±5.54)	

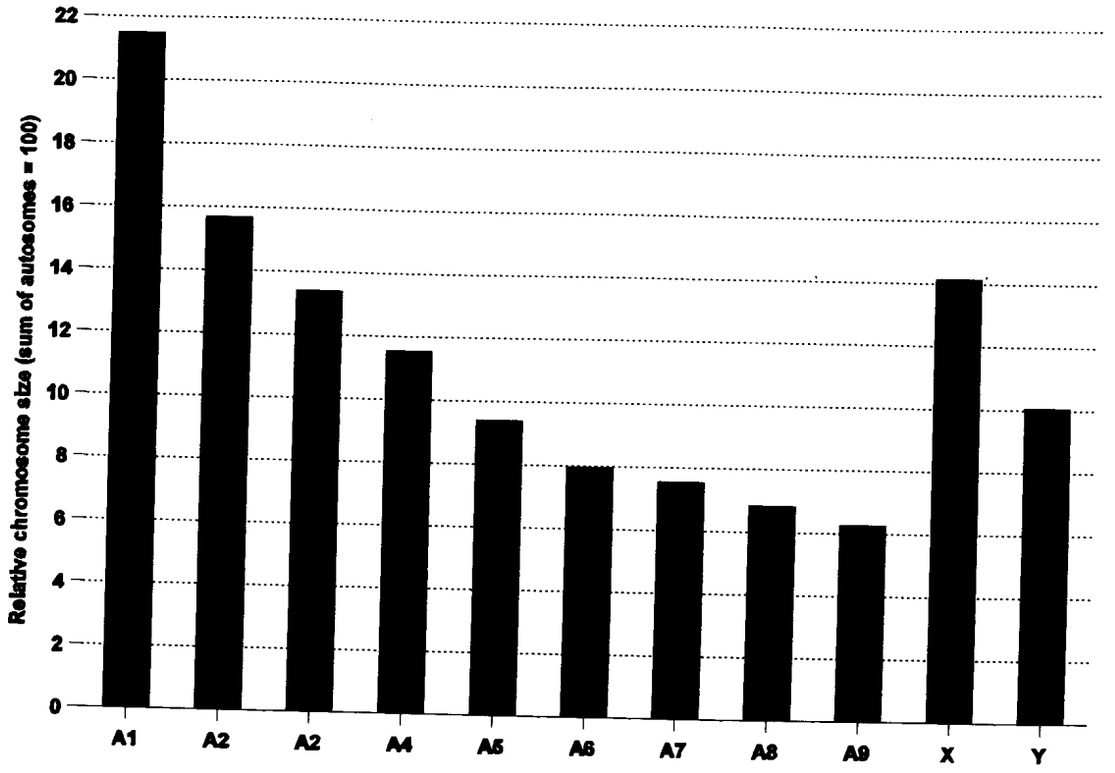


Figure 264. Idiogram of *Dundocoris nigromaculatus*.

9.2.6. ***Dundocoris flavilineatus.*** (Figs 265-266, 471-487).

Two subspecies are recognized, mainly on account of their different chromosome number although there also seems to be a slight size difference between them. *D. flavilineatus flavilineatus* has a chromosome number of 2n = 28XY and is slightly smaller than *D. flavilineatus ndabeniensis* with 2n = $27X_1X_2Y$. The nominate subspecies occurs widespread in Kwazulu-Natal and also in the Eastern Cape while *D. flavilineatus ndabeniensis* is probably restricted to the Ndabeni forest in northern Kwazulu-Natal.

9.2.6.1. ***Dundocoris flavilineatus flavilineatus.*** (Figs 265, 471-474).

The chromosome number of *D. flavilineatus flavilineatus* is 2n(♂) = 28XY. The true and relative chromosome areas for three localities are presented in Table 9.28 and idiograms for the three localities in Fig. 265. *D. flavilineatus flavilineatus* exhibit the typical ancestral *Dundocoris* karyotype where the autosomes form a more or less gradual size series with perhaps a small step that sets apart A11 and A12, and large X- and Y-chromosomes.

The three populations used for the idiograms come from localities that are far apart from each other (at least 120 km) without interconnecting forests between them. Given the low vagility of the apterous Carventinae it can be assumed that they have been isolated for at least several thousands of years. The idiograms of the populations at the three localities are very similar in respect to the autosomes - the differences between them can probably be accounted to variation in the squashing and measurement errors. The sex chromosomes, however, differ markedly between the three localities. The X-chromosome of the Mpsheni Forest population is markedly smaller than those of the other populations

and the Y-chromosome of the Ngoye Forest population is markedly larger than those of the other populations. Size differences in the sex chromosomes between populations and even between individuals of the same population is fairly common in the Heteroptera.

Table 9.28. True and relative chromosome areas of *D. flavilineatus flavilineatus*.

True chromosome areas (μm²) and standard deviation.				
Chromosome	Mpesheni forest	Ngoye forest	Scottburgh	TOTAL
Individuals	1	1	2	4
Cells	3	11	4	18
A1	2.89(±0.06)	2.46(±0.18)	3.70(±1.12)	2.81(±0.71)
A2	2.68(±0.17)	2.27(±0.14)	3.29(±0.85)	2.56(±0.57)
A3	2.48(±0.19)	2.22(±0.15)	3.18(±0.90)	2.48(±0.56)
A4	2.45(±0.19)	2.15(±0.14)	3.08(±0.88)	2.41(±0.55)
A5	2.36(±0.11)	2.07(±0.15)	2.95(±0.83)	2.31(±0.52)
A6	2.23(±0.07)	1.95(±0.15)	2.76(±0.75)	2.17(±0.47)
A7	2.13(±0.08)	1.92(±0.15)	2.63(±0.67)	2.11(±0.43)
A8	2.02(±0.02)	1.87(±0.17)	2.56(±0.66)	2.05(±0.42)
A9	2.01(±0.03)	1.83(±0.17)	2.47(±0.62)	2.00(±0.39)
A10	1.93(±0.08)	1.77(±0.16)	2.38(±0.70)	1.93(±0.41)
A11	1.82(±0.06)	1.61(±0.12)	2.23(±0.63)	1.78(±0.38)
A12	1.60(±0.06)	1.55(±0.11)	2.03(±0.59)	1.66(±0.33)
A13	1.50(±0.01)	1.35(±0.14)	1.75(±0.45)	1.46(±0.27)
X	3.97(±0.30)	4.60(±0.40)	5.99(±1.26)	4.80(±0.93)
Y	3.10(±0.18)	3.51(±0.30)	4.12(±1.12)	3.58(±0.62)
Autosomes	28.09(±0.85)	25.01(±1.83)	35.01(±9.64)	27.75(±5.98)
All chromosomes	35.17(±1.24)	33.12(±2.40)	45.12(±11.98)	36.13(±7.34)
Relative chromosome areas (% of total area of autosomes) and standard deviation.				
A1	10.31(±0.46)	9.84(±0.29)	10.51(±0.35)	10.07(±0.43)
A2	9.54(±0.32)	9.08(±0.24)	9.42(±0.20)	9.24(±0.30)
A3	8.83(±0.40)	8.90(±0.20)	9.07(±0.15)	8.92(±0.23)
A4	8.71(±0.41)	8.62(±0.19)	8.78(±0.09)	8.67(±0.22)
A5	8.41(±0.18)	8.28(±0.17)	8.40(±0.26)	8.33(±0.19)
A6	7.91(±0.06)	7.79(±0.14)	7.88(±0.04)	7.83(±0.12)
A7	7.57(±0.24)	7.66(±0.16)	7.53(±0.19)	7.62(±0.18)
A8	7.20(±0.14)	7.46(±0.19)	7.36(±0.17)	7.39(±0.20)
A9	7.13(±0.12)	7.33(±0.18)	7.11(±0.25)	7.25(±0.21)
A10	6.87(±0.09)	7.06(±0.24)	6.76(±0.21)	6.97(±0.25)
A11	6.48(±0.16)	6.42(±0.14)	6.36(±0.11)	6.42(±0.14)
A12	5.69(±0.38)	6.18(±0.17)	5.79(±0.19)	6.01(±0.30)
A13	5.35(±0.14)	5.38(±0.28)	5.01(±0.12)	5.29(±0.27)
X	14.13(±0.72)	18.41(±1.01)	17.39(±1.38)	17.47(±1.88)
Y	11.04(±0.49)	14.04(±0.81)	11.80(±0.59)	13.04(±1.48)

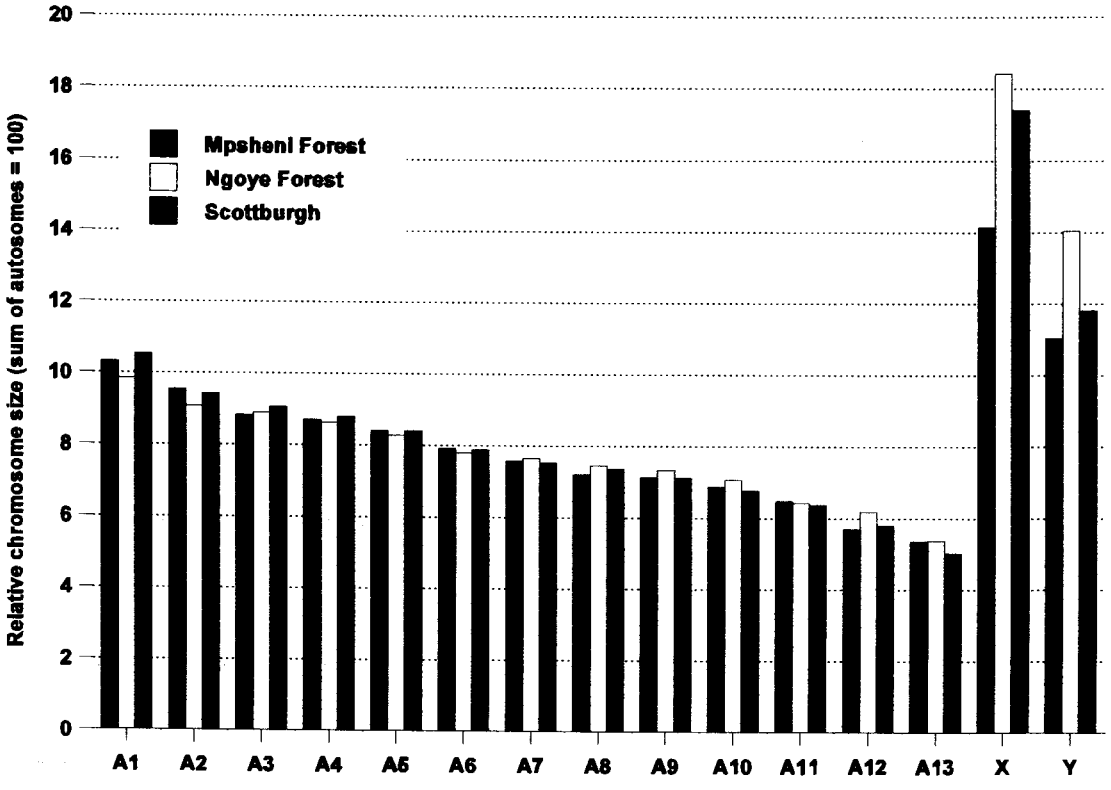


Figure 265. Idiogram of *Dundocoris flavilineatus flavilineatus.*

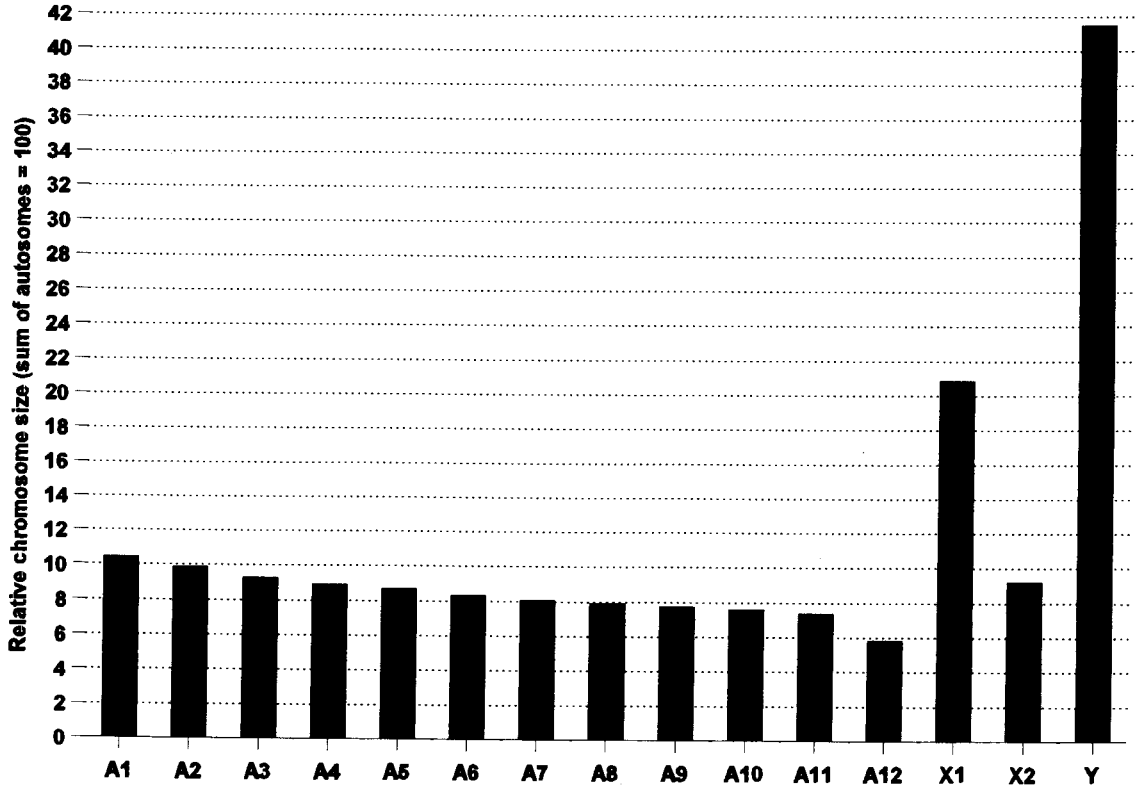


Figure 266. Idiogram of *Dundocoris flavilineatus ndabeniensis.*

9.2.6.2. *Dundocoris flavilineatus ndabeniensis.* (Figs 266, 475-487).

The chromosome number of *D. flavilineatus ndabeniensis* is $2n(\sigma^{\prime}) = 27X_1X_2Y$, although the possibility exists that it is actually $27XY_1Y_2$ as no females were studied (refer to 9.2.6.3). The true and relative chromosome areas are presented in Table 9.29 and an idiogram in Fig. 266. The autosomes form a gradual size series but a small step sets off A12. The Y-chromosome (actually a neo-Y) is by far the largest chromosome in the complement, being about 4x the size of the largest autosome. The original X-chromosome (X_1) is the second largest chromosome, about twice the size of the largest autosome while the neo-X (X_2) chromosome is about the size of A3. The multiple sex chromosome system of *D. flavilineatus ndabeniensis* also originated by a fusion between a sex chromosome and an autosome but the details and behaviour of the chromosomes differ markedly from that described in *D. nodulicarinus*.

At pachytene the original X-chromosome (X_1) forms a positive heterochromatic body which is usually roundish in shape but sometimes its linear shape is apparent as it is twisted and folded in various ways. The Y-chromosome is usually also positively heterochromatic but more or less linear in shape and the junction between the original Y-chromosome part and the autosomal part (which probably incorporate X_2 as well) is often evident as a constriction (Fig. 475). The two sex chromosome structures are often associated but apart from each other in a significant number of cells. When they are apart nucleoli are often associated with both these structures - in the neo-Y it occurs near the free end of the original Y-chromosome. It is unclear whether true synapsis forms between the neo-X (X_2) and the autosomal part of the neo-Y.

Table 9.29. True and relative chromosome areas of *D. flavilineatus ndabeniensis*.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Ndabeni forest	Ndabeni forest
Individuals	2	2
Cells	11	11
A1	1.99(±0.15)	10.43(±0.37)
A2	1.88(±0.13)	9.85(±0.33)
A3	1.77(±0.10)	9.28(±0.21)
A4	1.70(±0.09)	8.92(±0.20)
A5	1.66(±0.09)	8.70(±0.20)
A6	1.59(±0.10)	8.32(±0.17)
A7	1.54(±0.09)	8.08(±0.13)
A8	1.51(±0.09)	7.92(±0.14)
A9	1.48(±0.09)	7.75(±0.13)
A10	1.44(±0.09)	7.57(±0.14)
A11	1.40(±0.09)	7.35(±0.17)
A12	1.11(±0.05)	5.83(±0.18)
X_1	3.97(±0.29)	20.85(±1.12)
X_2	1.75(±0.15)	9.20(±0.75)
Y	7.91(±0.59)	41.47(±1.22)
Autosomes	19.07(±1.05)	
All chromosomes	32.70(±1.91)	

During the diffuse stage X_1 and the neo-Y are positively heterochromatic and nearly always associated. The X_1 usually forms a smooth, circular body with the more or less thick filamentous neo-Y attached to it with it original Y-chromosome end. The distal autosomal subdivision of the neo-Y often exhibits chromomere-like nodules. The nucleoli usually occur in the region where the X_1 and Y are associated. The individual autosomes are not discernable at this stage. As the diffuse stage gradually advances to diplotene the autosomal bivalents become discernable, firstly as filamentous patches with heterochromatic chromomere-like nodules without the individual chromosomes and chromatids discernable but later the they can be distinguished as nodulated filaments. At this stage it also becomes evident that the euchromatic X_2, which may be a considerable distance away, is attached to the heterochromatic neo-Y by means of thin, often nearly invisible filaments, supposedly representing a terminalized chiasma. It now becomes apparent that the X_2-neo-Y 'bivalent' contain three distinct subdivisions namely:

1. A thick, heterochromatic, relatively smooth part that is also the largest and represents the original Y-chromosome.
2. A somewhat thinner, heterochromatic, nodulated part that is slightly smaller than the previous part and represent the autosomal part of the neo-Y.
3. A thin, euchromatic, usually distant part that represent the neo-X (X_2) which is probably attached to the second part by a terminalized chiasma.

The first two subdivisions stay visible until late diakinesis and the third until AI.

At diplotene the chiasmata also become visible. Roughly a third of the bivalents have non terminal chiasmata (1/0) while the rest are associated at their ends by means of terminal chiasmata or perhaps non chiasmate associations. The sex chromosomes are usually still associated at this stage. In cells where they are separate, nucleoli are often associated with both the X_1 and neo-Y, indicating that both probably have NOR's.

At diakinesis the chromosomes spiralize so that during the latter part of this stage the chromosomes become isopicnotic or the sex chromosomes are only slightly heteropicnotic. The X_1 and neo-Y invariably detach and the tripartite structure of the X_2-neo-Y 'bivalent' is very clear. The first two subdivisions are now the same thickness but separated by a less intensely stained constriction while the third subdivision (X_2) is thinner and separated by an unstained area except for the thin filaments that attach it to the neo-Y. Nucleoli are usually not present but rarely small fragments persist that are associated with the X_1 or neo-Y or both. As result of spiralization all bivalents look more or less the same and it is not possible to tell the bivalents with a non-terminal chiasma (1/0) apart from those with a terminal chiasma (1/1), thus making chiasma analysis at this stage and at MI unreliable.

At MI all the chromosomes are isochromatic. The autosomes together with the sex chromosomes form a peripheral ring, although one or two autosomes sometimes lie inside the ring. The neo-Y-X_2 structure always orientates with its long axis parallel to the equatorial plane. Each chromatid of the neo-Y is now a solid thick rod and its two subdivisions are not discernable any more, while the X_2 subdivision is much

thinner and each chromatid is more or less spherical. The X_2 is set apart from the neo-Y by a less intensely stained constriction.

During AI the autosomes segregate regularly (12 chromosomes to each pole) while the X_1, X_2 and neo-Y undergo chromatid segregation and one chromatid of each segregates to each pole.

At MII the autosomes form a peripheral ring with the tripartite sex chromosome structure (consisting of a chromatid each of the X_1, X_2 and neo-Y) in the centre of the ring. The sex chromosome structure always orientates with the neo-Y towards one pole and the X_1 and X_2 towards the opposite pole and during AII they also segregate in this fashion. In two of the individuals a few polyploid MII cells (Fig. 485) were observed. They probably originated as a result of failed cytokinesis.

Spermatogonial mitosis (Figs 486-487) shows 27 chromosomes. The large neo-Y and X_1 chromosomes are clearly distinguishable while all the autosomes and the X_2 are in the same size order.

9.2.6.3. Discussion.

D. flavilineatus ndabeniensis probably originated from *D. flavilineatus flavilineatus* by means of a fusion between its Y-chromosome and an autosome. If we, however, compare the size of X_2 with that of the 'autosomal' part that is attached to the original Y-chromosome it is clear that other structural modifications also took place. The 'autosomal' part of the neo-Y is at least twice the size of X_2 (Fig. 481). It also seems to be permanently heterochromatic while the X_2 is euchromatic. Whether the size difference is the result of the heterochromatization process or of duplications or other reasons is unclear. If we compare the size of X_2 with that of the autosomes it indicates that probably one of the larger autosomes was involved in the fusion. The karyotype of *D. flavilineatus ndabeniensis* where only one small chromosome is set apart by a step in the size series, however, suggests that rather one of the small autosomes (A12 or A13) was involved. It is thus possible that some structural changes also took place in X_2.

One of the main differences between *D. flavilineatus ndabeniensis* and *D. nodulicarinus* is that the autosomal part of the neo-sex chromosome stays euchromatic in the latter while it is heterochromatic in the former from the onset of meiosis. This gives rise to the question of the nature of the association between X_2 and its homologous part on the neo-Y in *D. flavilineatus ndabeniensis* during pachytene - does true synapsis and crossing-over take place? Invariably an end to end association between the X_2 and the neo-Y exist from diplotene to MI but whether it is chiasmate or non-chiasmate [as John & King (1985) found in some of the small bivalents of the grasshoppers *Cryptobothrus chrysophorus* and *Heteropternis obscurella*] is unclear.

It seems as if the two subdivisions of the neo-Y exert an influence on one another. The Y-chromosome which normally forms a spherical, smooth structure at the diffuse and diplotene stages, usually forms

an extended or folded rod-like structure in *D. flavilineatus ndabeniensis*. The autosomal part has become heterochromatic but not to the same extent as the Y-chromosome as is evident from its nodulated structure during diplotene. It is unclear why the same has not happened in *D. nodulicarinus* but one possible explanation is that the Y-chromosome is usually constitutive heterochromatic and inert while the X-chromosome is only facultative heterochromatic (in the females the two X-chromosomes are normally euchromatic).

No cytogenetic studies were done on females of *D. flavilineatus ndabeniensis*. By convention its sex chromosome system was described as X_1X_2Y but it could as well be a XY_1Y_2 system. There are no strong indicators to favour the one above the other. Nucleolus organizer regions are usually situated on the X-chromosomes of Heteroptera but here they seem to be present on both of the original sex chromosomes of *D. flavilineatus ndabeniensis*. At diakinesis (Fig. 481) it seems that the original Y-chromosome part of the neo-Y is larger than the original X-chromosome (X_1) indicating that if it is a X_1X_2Y system the Y-chromosome was probably larger than the X-chromosome in its ancestor and thus probably in *D. flavilineatus flavilineatus*. In a XY sex chromosome system the larger of the sex chromosomes is conventionally assigned as the X-chromosome if no females were studied, and although it is usually correct it is not necessarily so. It is possible (and even probable) that in some cases the X and Y chromosomes were assigned incorrectly in *Dundocoris* and the other genera.

9.2.7. ***Dundocoris schoemani.*** (Figs 267-268, 488-492).

D. schoemani contains two subspecies which are nearly identical in morphology, have the same chromosome number and can only reliably be distinguished by their different karyotypes. The nominate subspecies has thus far only been recorded from the montane forests and *D. schoemani dwesaensis* from the coastal forests of the Eastern Cape (former Transkei).

9.2.7.1. ***Dundocoris schoemani schoemani.*** (Figs 267, 488-490).

The chromosome number of *D. schoemani schoemani* is 2n(♂) = 26XY. The true and relative chromosome areas for three localities are presented in Table 9.30 and idiograms for the three localities in Fig. 267. The autosomes form a gradual size series with A1 set apart by a small step. The smallest one or two autosomes are not set apart at all. The sex chromosomes are very large, the X-chromosome is about twice and the Y-chromosome about 1.65x the size of the largest autosome. The idiograms of the populations of the three localities (that are only about 50km apart) are nearly identical for both the autosomes and the sex chromosomes and the differences can probably be attributed to measuring errors.

Table 9.30. True and relative chromosome areas of *D. schoemani schoemani*.

True chromosome areas (μm²) and standard deviation.				
Chromosome	Baziya forest	Ku-manina forest	Nquaba forest	TOTAL
Individuals	4	3	3	10
Cells	12	9	11	32
A1	2.20(±0.48)	2.38(±0.43)	2.49(±0.49)	2.35(±0.47)
A2	1.98(±0.39)	2.22(±0.42)	2.23(±0.46)	2.13(±0.43)
A3	1.93(±0.39)	2.07(±0.37)	2.17(±0.44)	2.05(±0.40)
A4	1.87(±0.38)	2.02(±0.39)	2.14(±0.43)	2.01(±0.40)
A5	1.82(±0.37)	1.97(±0.37)	2.05(±0.44)	1.94(±0.39)
A6	1.70(±0.33)	1.89(±0.35)	1.90(±0.34)	1.82(±0.34)
A7	1.66(±0.34)	1.82(±0.34)	1.87(±0.34)	1.78(±0.35)
A8	1.63(±0.34)	1.75(±0.30)	1.83(±0.33)	1.73(±0.33)
A9	1.58(±0.33)	1.69(±0.32)	1.79(±0.34)	1.68(±0.33)
A10	1.49(±0.27)	1.64(±0.29)	1.73(±0.30)	1.62(±0.30)
A11	1.44(±0.27)	1.60(±0.28)	1.65(±0.31)	1.56(±0.29)
A12	1.38(±0.26)	1.53(±0.29)	1.55(±0.30)	1.48(±0.29)
X	4.39(±0.86)	4.85(±0.88)	5.02(±1.05)	4.73(±0.95)
Y	3.49(±0.51)	3.99(±0.66)	4.26(±0.94)	3.90(±0.78)
Autosomes	20.69(±4.11)	22.58(±4.11)	23.39(±4.49)	22.15(±4.28)
All chromosomes	28.57(±5.41)	31.42(±5.61)	32.67(±6.44)	30.78(±5.93)
Relative chromosome areas (% of total area of autosomes) and standard deviation.				
A1	10.61(±0.44)	10.57(±0.45)	10.63(±0.42)	10.61(±0.42)
A2	9.59(±0.23)	9.81(±0.30)	9.51(±0.23)	9.62(±0.27)
A3	9.30(±0.20)	9.17(±0.22)	9.25(±0.21)	9.25(±0.21)
A4	9.06(±0.21)	8.95(±0.18)	9.12(±0.20)	9.05(±0.20)
A5	8.81(±0.25)	8.73(±0.17)	8.72(±0.30)	8.76(±0.25)
A6	8.24(±0.16)	8.34(±0.27)	8.14(±0.21)	8.24(±0.22)
A7	8.02(±0.16)	8.06(±0.27)	8.02(±0.21)	8.03(±0.21)
A8	7.85(±0.17)	7.77(±0.21)	7.82(±0.17)	7.82(±0.18)
A9	7.61(±0.14)	7.49(±0.19)	7.66(±0.16)	7.59(±0.17)
A10	7.24(±0.25)	7.27(±0.18)	7.41(±0.16)	7.31(±0.21)
A11	6.98(±0.20)	7.09(±0.23)	7.06(±0.22)	7.04(±0.21)
A12	6.69(±0.20)	6.75(±0.18)	6.65(±0.27)	6.69(±0.22)
X	21.23(±1.29)	21.50(±0.94)	21.41(±0.82)	21.37(±1.03)
Y	17.04(±1.29)	17.76(±1.06)	18.15(±0.96)	17.62(±1.19)

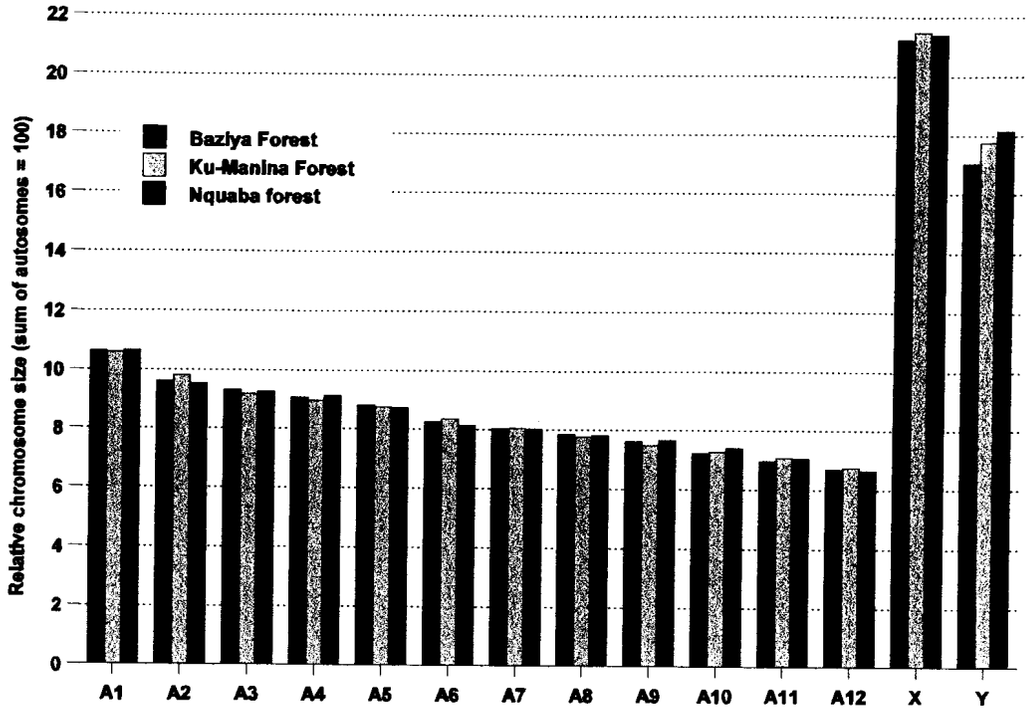


Figure 267. Idiogram of *Dundocoris schoemani schoemani*.

D. schoemani schoemani is the only 26XY *Dundocoris* species where A1 is not markedly larger than the rest of the autosomes. That, together with the fact that the two small chromosomes are not set apart as usual strongly indicates that it originated from a 28XY ancestor by the fusion of the two smallest autosomes. Its karyotype thus resemble that of the hypothetical 26XY ancestor of *Dundocoris* (refer to the discussion at 9.2.12).

9.2.7.2. *Dundocoris schoemani dwesaensis*. (Figs 268, 491-492).

The chromosome number of *D. schoemani dwesaensis* is 2n(♂) = 26XY. The true and relative chromosome areas are presented in Table 9.31 and an idiogram in Fig. 268.

A1 is about 1.32x as large as A2. Autosomes A2-A12 form a more or less gradual size series with definite steps between A2/A3 and A11/A12 and a small step between A10/A11. The sex chromosomes are the largest chromosomes in the complement: the X-chromosome is twice and the Y-chromosome about 1.47x as large as A2.

D. schoemani dwesaensis probably originated independently of *D. schoemani schoemani* from the same 28XY ancestor by means of the fusion of two of the smaller autosomes.

Table 9.31. True and relative chromosome areas of *D. schoemani dwesaensis*.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Dwesa forest	Dwesa forest
Individuals	1	1
Cells	6	6
A1	3.92(±0.24)	13.64(±0.33)
A2	2.98(±0.26)	10.35(±0.40)
A3	2.63(±0.20)	9.13(±0.25)
A4	2.58(±0.18)	8.98(±0.21)
A5	2.49(±0.18)	8.65(±0.22)
A6	2.40(±0.13)	8.35(±0.18)
A7	2.32(±0.15)	8.08(±0.26)
A8	2.25(±0.14)	7.84(±0.18)
A9	2.12(±0.06)	7.39(±0.28)
A10	1.95(±0.13)	6.79(±0.16)
A11	1.70(±0.13)	5.92(±0.44)
A12	1.41(±0.12)	8.89(±0.31)
X	5.94(±0.24)	20.75(±1.42)
Y	4.37(±0.32)	15.22(±1.19)
Autosomes	28.73(±1.68)	
All chromosomes	39.04(±1.81)	

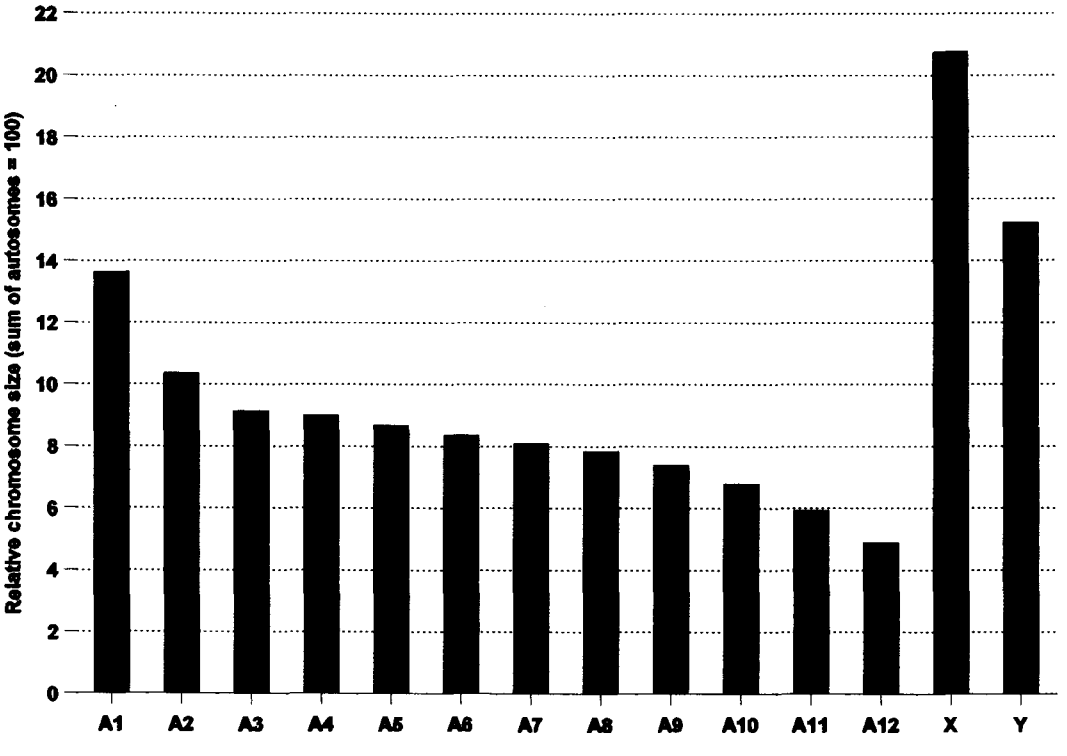


Figure 268. Idiogram of *Dundocoris schoemani dwesaensis*.

9.2.8. *Dundocoris scholtzi.* (Figs 269, 493-494).

The chromosome number of *D. scholtzi* is 2n(♂) = 26XY. The true and relative chromosome areas are presented in Table 9.32 and an idiogram in Fig. 269. A1 is distinctly larger than the rest of the autosomes (1.35x as large as A2). A2-A12 form a more or less gradual size series but a distinct step sets off the smallest two autosomes. The sex chromosomes are large: the X-chromosome is twice the size of A2 while the Y-chromosome is the same size as A1 (1.35x the size of A2).

Table 9.32. True and relative chromosome areas of *D. scholtzi*.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Ngome forest	Ngome forest
Individuals	2	2
Cells	4	4
A1	3.86(±0.46)	13.06(±0.48)
A2	2.87(±0.37)	9.69(±0.39)
A3	2.70(±0.33)	9.13(±0.21)
A4	2.60(±0.28)	8.79(±0.18)
A5	2.56(±0.25)	8.68(±0.17)
A6	2.48(±0.31)	8.37(±0.19)
A7	2.44(±0.31)	8.23(±0.23)
A8	2.35(±0.28)	7.94(±0.29)
A9	2.19(±0.19)	7.41(±0.30)
A10	2.14(±0.22)	7.22(±0.28)
A11	1.75(±0.12)	5.92(±0.36)
A12	1.64(±0.14)	5.57(±0.23)
X	5.84(±1.09)	19.72(±2.19)
Y	3.90(±0.68)	13.14(±1.08)
Autosomes	29.60(±3.13)	
All chromosomes	39.34(±4.71)	

D. scholtzi probably originated from a 28XY ancestor by the fusion of two autosomes. The definite size step between A10 and the smallest two autosomes suggests that A9 and A10 of the ancestor were possibly involved in this fusion.

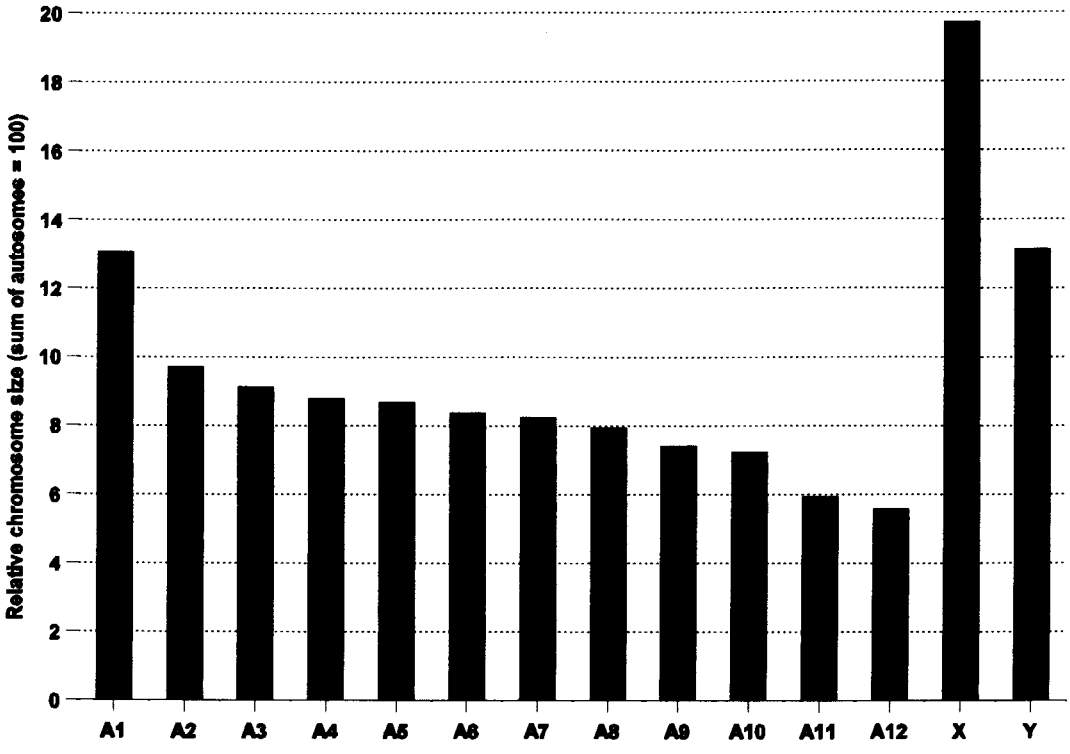


Figure 269. Idiogram of *Dundocoris scholtzi*.

One of the 16 individuals that were cytogenetically studied has an aberrant chromosome number of $2n(♂) = 25X_1X_2Y$. This also proved to be a neo-X_1X_2Y sex chromosome system that originated by the fusion of the largest autosome with the Y-chromosome. The autosomal part of the neo-Y remained euchromatic and underwent normal synapsis and crossovers with the neo-X (X_2).

It is unknown if this individual alone has this fusion or if it perhaps belongs to a sub-population where it has become fixed. I collected the specimens I used for cytogenetic studies from various localities in the large Ngome Forest and was unable to keep track of the exact spot where each individual was collected. This individual, however, shows that sex chromosome polymorphism does occur in natural populations.

9.2.9. ***Dundocoris fuscus.*** (Figs 270, 495-496).

The chromosome number of *D. fuscus* is $2n(♂) = 28XY$. The true and relative chromosome areas are presented in Table 9.33 and an idiogram in Fig. 270. *D. fuscus* possesses the typical ancestral *Dundocoris* karyotype. The autosomes form a gradual size series with small steps between A1/A2, A11/A12 and A12/A13. The sex chromosomes are the largest chromosomes in the complement but in comparison with those of the other *Dundocoris* species they are relatively small: the X-chromosome is about 1.34x and the Y-chromosome 1.25x as large as the largest autosome.

Table 9.33. True and relative chromosome areas of *D. fuscus*.

True chromosome areas (µm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Mariepskop forest	Mariepskop forest
Individuals	2	2
Cells	8	8
A1	2.76(±0.20)	10.05(±0.50)
A2	2.52(±0.18)	9.17(±0.24)
A3	2.42(±0.16)	8.82(±0.34)
A4	2.33(±0.14)	8.49(±0.19)
A5	2.26(±0.14)	8.20(±0.28)
A6	2.20(±0.12)	8.00(±0.27)
A7	2.15(±0.14)	7.80(±0.18)
A8	2.08(±0.15)	7.56(±0.18)
A9	2.01(±0.15)	7.30(±0.22)
A10	1.93(±0.17)	7.01(±0.29)
A11	1.83(±0.16)	6.65(±0.29)
A12	1.60(±0.11)	5.83(±0.41)
A13	1.41(±0.14)	5.12(±0.45)
X	3.70(±0.25)	13.46(±0.29)
Y	3.47(±0.26)	12.62(±0.50)
Autosomes	27.51(±1.62)	
All chromosomes	34.68(±2.10)	

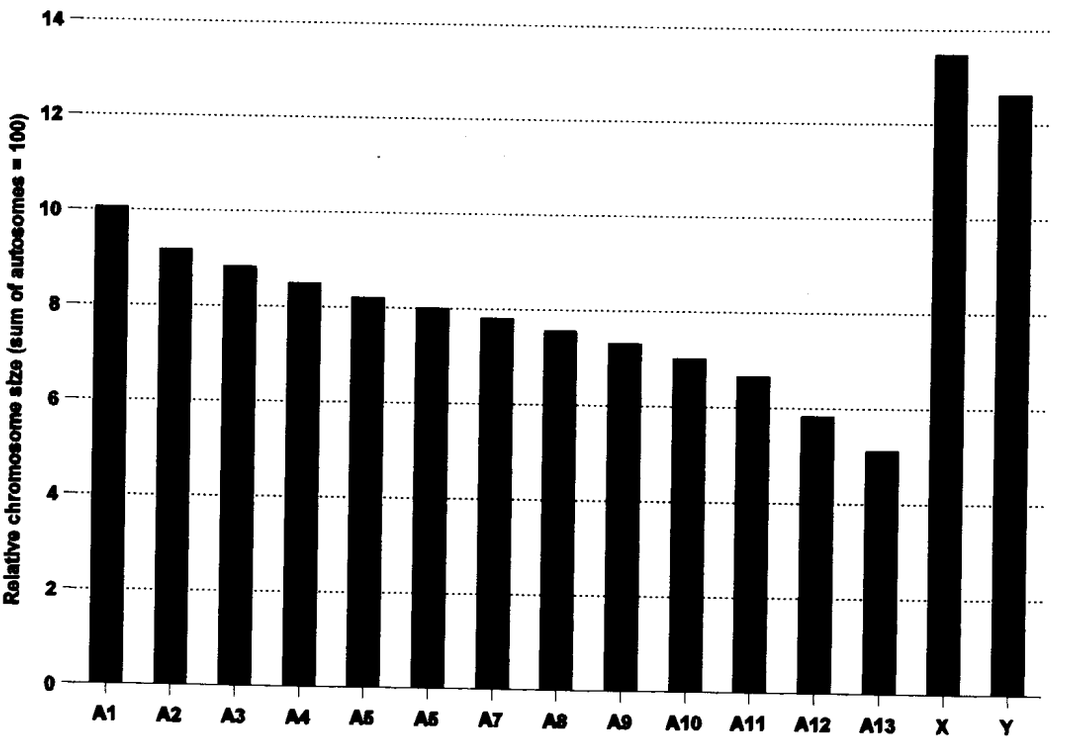


Figure 270. Idiogram of *Dundocoris fuscus*.

9.2.10. *Dundocoris callani.* (Figs 271-272, 497-503).

D. callani is a very variable species that is widespread in the forests of Kwazulu-Natal and the Eastern Cape. Two subspecies are currently recognised but it is possible that the nominate subspecies actually consists of an assemblage of sibling species. The chromosome number of the nominate subspecies is 2n(♂) = 28XY while that of *D. callani noduliclypeatus* is 2n(♂) = 26XY.

Table 9.34. True and relative chromosome areas of *D. callani callani*.

True chromosome areas (μm²) and standard deviation.				
Chromosome	Ngoye forest	Nquaba forest	Scottburgh	TOTAL
Individuals	2	2	1	5
Cells	10	8	7	25
A1	2.37(±0.39)	3.46(±0.74)	2.69(±0.50)	2.81(±0.70)
A2	2.27(±0.38)	3.23(±0.63)	2.53(±0.55)	2.65(±0.64)
A3	2.18(±0.33)	3.14(±0.62)	2.47(±0.53)	2.57(±0.63)
A4	2.04(±0.31)	3.00(±0.57)	2.37(±0.44)	2.44(±0.59)
A5	1.96(±0.32)	2.94(±0.56)	2.22(±0.47)	2.35(±0.60)
A6	1.93(±0.32)	2.87(±0.55)	2.15(±0.43)	2.29(±0.58)
A7	1.88(±0.33)	2.78(±0.51)	2.11(±0.40)	2.23(±0.55)
A8	1.85(±0.29)	2.69(±0.50)	2.02(±0.41)	2.17(±0.53)
A9	1.81(±0.31)	2.59(±0.46)	1.98(±0.39)	2.11(±0.49)
A10	1.76(±0.27)	2.48(±0.45)	1.89(±0.35)	2.02(±0.46)
A11	1.64(±0.24)	2.34(±0.39)	1.84(±0.37)	1.92(±0.43)
A12	1.40(±0.24)	1.98(±0.38)	1.46(±0.28)	1.60(±0.38)
A13	1.32(±0.22)	1.84(±0.29)	1.34(±0.23)	1.49(±0.33)
X	7.59(±1.29)	5.86(±1.03)	5.32(±0.98)	6.40(±1.48)
Y	6.00(±0.96)	3.05(±0.60)	4.30(±0.90)	4.58(±1.51)
Autosomes	24.42(±3.37)	35.35(±6.55)	27.07(±5.30)	28.66(±6.85)
All chromosomes	38.00(±5.48)	44.27(±8.13)	36.69(±7.14)	39.64(±7.35)
Relative chromosome areas (% of total area of autosomes) and standard deviation.				
A1	9.71(±0.35)	9.75(±0.42)	9.97(±0.20)	9.80(±0.35)
A2	9.30(±0.19)	9.13(±0.27)	9.33(±0.28)	9.26(±0.25)
A3	8.92(±0.17)	8.88(±0.31)	9.10(±0.26)	8.96(±0.25)
A4	8.36(±0.22)	8.50(±0.11)	8.76(±0.18)	8.52(±0.24)
A5	8.04(±0.09)	8.31(±0.12)	8.18(±0.25)	8.17(±0.19)
A6	7.89(±0.11)	8.11(±0.14)	7.94(±0.19)	7.98(±0.17)
A7	7.70(±0.12)	7.88(±0.13)	7.80(±0.16)	7.79(±0.15)
A8	7.57(±0.12)	7.61(±0.14)	7.46(±0.10)	7.55(±0.13)
A9	7.41(±0.20)	7.35(±0.18)	7.33(±0.11)	7.37(±0.17)
A10	7.21(±0.22)	7.02(±0.12)	6.98(±0.18)	7.08(±0.20)
A11	6.74(±0.38)	6.61(±0.42)	6.81(±0.20)	6.72(±0.35)
A12	5.74(±0.22)	5.61(±0.19)	5.38(±0.23)	5.60(±0.25)
A13	5.40(±0.18)	5.24(±0.36)	4.97(±0.19)	5.23(±0.30)
X	31.08(±1.66)	16.64(±0.58)	19.70(±0.53)	23.27(±6.71)
Y	24.62(±1.66)	8.63(±0.55)	15.90(±0.99)	17.06(±7.02)

9.2.10.1. *Dundocoris callani callani.* (Figs 271, 497-501).

The chromosome number of *D. callani callani* is 2n(♂) = 28XY. The true and relative chromosome areas for three localities are presented in Table 9.34 and idiograms for the three localities in Fig. 271. *D. callani callani* exhibits the typical ancestral *Dundocoris* karyotype. The autosomal karyotypes of all three populations are very similar - the autosomes form a gradual size series but the smallest two (A12 & A13) are set apart by a slight step in the series. The sex chromosomes, however, differ markedly between the populations: In the Ngoye Forest population the sex chromosomes are very large, the X-chromosome is about 3.2x and the Y-chromosome about 2.5x the size of the largest autosome; in the Scottburgh population they are much smaller, the X being about 2x and the Y 1.6x as large as the largest autosome; in the Nquaba Forest population they are still smaller and there is a big difference between the sizes of the X and Y - the X is about 1.7x the size of the largest autosome while the Y is smaller than the largest autosome, about the same size as A4.

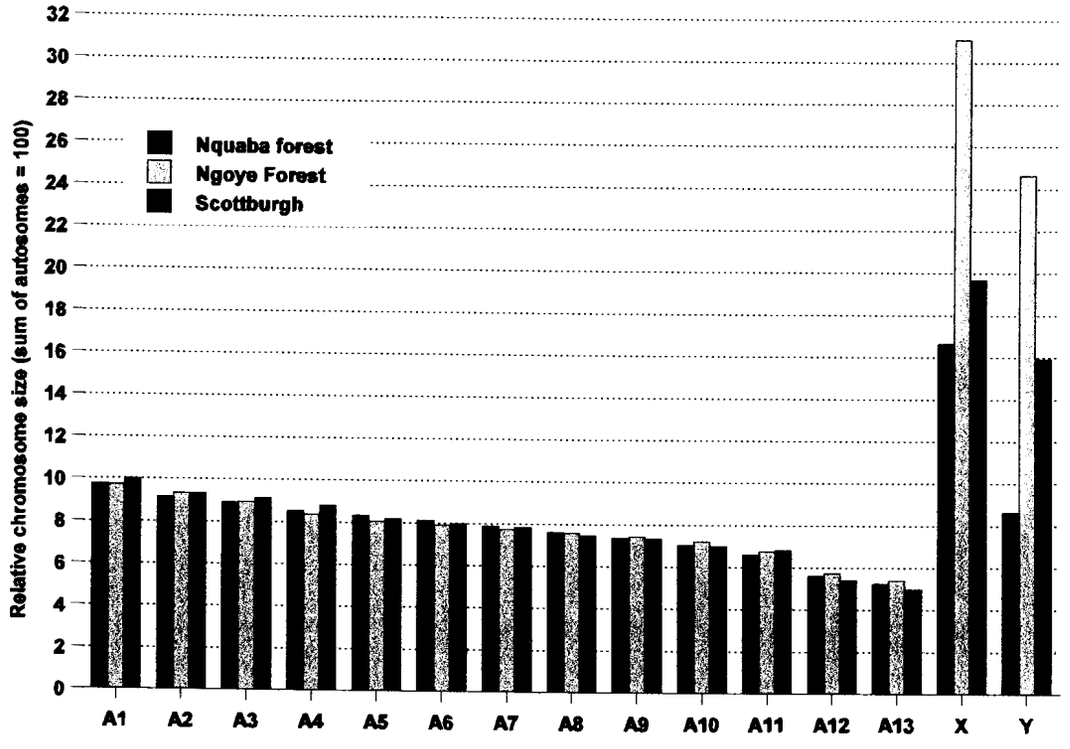


Figure 271. Idiogram of Dundocoris callani callani Hoberlandt.

9.2.10.2. *Dundocoris callani noduliclypeatus.* (Figs 272, 502-503).

The chromosome number of *D. callani noduliclypeatus* is 2n(♂) = 26XY. The true and relative chromosome areas are presented in Table 9.35 and an idiogram in Fig. 272. A1 is much (1.73x) larger than A2. Autosomes A2-A12 form a gradual size series but the smallest two autosomes are set apart by a slight step in the series. The sex chromosomes are very large: the X-chromosome is 2.7x and the Y-chromosome about 2.3x the size of A2.

Table 9.35. True and relative chromosome areas of *D. callani noduliclypeatus*.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	Town Bush	Town Bush
Individuals	1	1
Cells	5	5
A1	4.77(±0.41)	16.26(±0.68)
A2	2.76(±0.34)	9.38(±0.23)
A3	2.66(±0.36)	9.01(±0.34)
A4	2.53(±0.28)	8.59(±0.09)
A5	2.45(±0.28)	8.32(±0.23)
A6	2.38(±0.28)	8.06(±0.23)
A7	2.30(±0.27)	7.79(±0.22)
A8	2.20(±0.23)	7.49(±0.16)
A9	2.15(±0.24)	7.31(±0.18)
A10	1.99(±0.23)	6.75(±0.18)
A11	1.71(±0.22)	5.78(±0.30)
A12	1.55(±0.21)	5.26(±0.29)
X	7.46(±1.05)	25.35(±1.49)
Y	6.26(±0.74)	21.34(±1.77)
Autosomes	29.45(±3.23)	
All chromosomes	43.17(±4.82)	

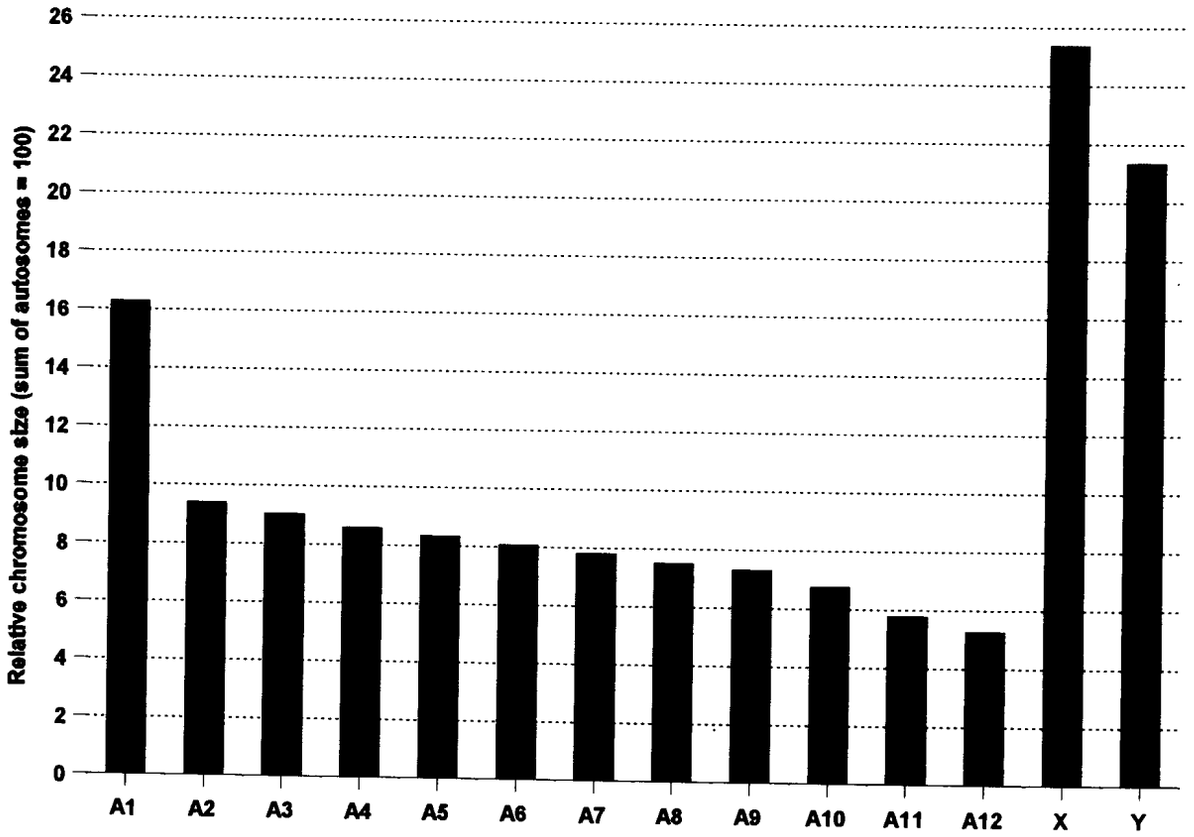


Figure 272. Idiogram of *Dundocoris callani noduliclypeatus*.

D. callani noduliclypeatus probably originated from *D. callani callani* by the fusion of two autosomes. The relatively small size of A2 in *D. callani noduliclypeatus* suggests that probably A1 and one of the smaller autosomes (but not A12 orA13) were involved.

9.2.11. *Dundocoris natalensis.* (Figs 273, 504-505).

The chromosome number of *D. natalensis* is 2n(♂) = 28XY. The true and relative chromosome areas for two localities are presented in Table 9.36 and idiograms for the two localities in Fig. 273. *D. natalensis* also has the typical *Dundocoris* karyotype. The karyotypes of the populations from the two localities are very similar in respect of both the autosomes and sex chromosomes. The autosomes form the usual gradual series with the two smallest chromosomes set apart by a small step in the series. The sex chromosomes are large, the X-chromosome is about twice and the Y-chromosome about 1.47x the size of the largest autosome.

Table 9.36. True and relative chromosome areas of *D. natalensis*.

True chromosome areas (μm²) and standard deviation.				Relative chromosome areas (% of total area of autosomes) and standard deviation.		
Chromosome	Hawaan forest	Ngoye forest	TOTAL	Hawaan forest	Ngoye forest	TOTAL
Individuals	2	2	4	2	2	4
Cells	15	11	26	15	11	26
A1	3.28(±0.65)	2.95(±0.72)	3.14(±0.68)	9.74(±0.31)	9.98(±0.46)	9.85(±0.39)
A2	3.02(±0.52)	2.78(±0.72)	2.92(±0.61)	9.01(±0.24)	9.39(±0.43)	9.17(±0.38)
A3	2.92(±0.54)	2.58(±0.62)	2.77(±0.59)	8.69(±0.17)	8.73(±0.14)	8.70(±0.16)
A4	2.83(±0.54)	2.47(±0.63)	2.68(±0.59)	8.42(±0.19)	8.35(±0.24)	8.39(±0.21)
A5	2.73(±0.49)	2.43(±0.61)	2.60(±0.56)	8.14(±0.15)	8.20(±0.21)	8.16(±0.18)
A6	2.69(±0.50)	2.31(±0.53)	2.53(±0.54)	7.99(±0.14)	7.85(±0.18)	7.93(±0.17)
A7	2.64(±0.50)	2.26(±0.53)	2.48(±0.53)	7.84(±0.13)	7.67(±0.13)	7.77(±0.15)
A8	2.58(±0.49)	2.21(±0.52)	2.42(±0.53)	7.66(±0.14)	7.50(±0.16)	7.59(±0.17)
A9	2.52(±0.48)	2.17(±0.52)	2.38(±0.52)	7.50(±0.14)	7.37(±0.16)	7.44(±0.16)
A10	2.38(±0.45)	2.10(±0.48)	2.27(±0.48)	7.09(±0.24)	7.14(±0.20)	7.12(±0.22)
A11	2.22(±0.42)	2.02(±0.46)	2.13(±0.44)	6.60(±0.29)	6.85(±0.26)	6.71(±0.30)
A12	1.96(±0.34)	1.66(±0.40)	1.83(±0.39)	5.84(±0.23)	5.64(±0.38)	5.76(±0.31)
A13	1.84(±0.33)	1.58(±0.41)	1.73(±0.38)	5.47(±0.19)	5.32(±0.32)	5.41(±0.26)
X	6.78(±1.20)	5.64(±1.57)	6.30(±1.46)	20.22(±1.08)	18.96(±1.17)	19.69(±1.27)
Y	4.85(±0.92)	4.33(±1.18)	4.63(±1.05)	14.43(±0.85)	14.60(±1.03)	14.50(±0.91)
Autosomes	33.61(±6.20)	29.52(±7.07)	31.88(±6.76)			
All chromosomes	45.24(±8.25)	39.50(±9.77)	42.81(±9.20)			

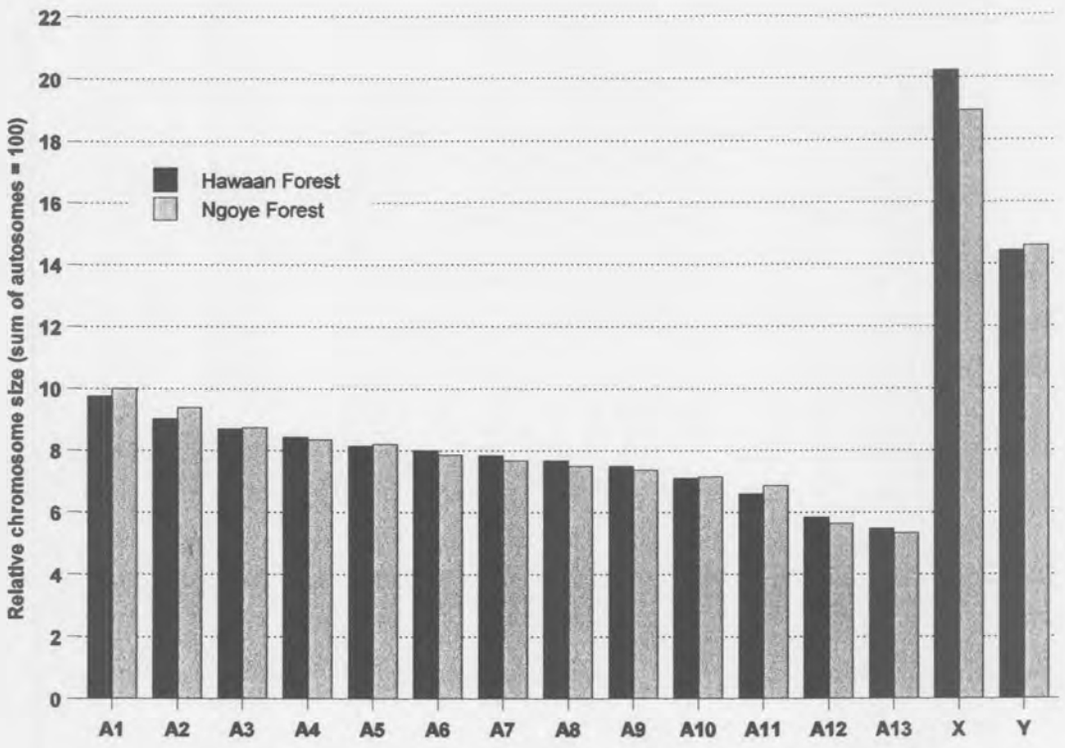


Figure 273. Idiogram of *Dundocoris natalensis Kormilev*.

9.2.12. Discussion.

Most *Dundocoris* taxa have a chromosome number of 2n(♂) = 26XY or 28XY. In an effort to determine which is the ancestral number for the genus the six taxa with 28XY were compared (Fig. 273A) as well as the six taxa with 26XY (Fig. 273B). The autosomal karyotypes of all the 28XY taxa are very similar - the autosomes form a gradual size series with the two smallest chromosomes set apart by a small step. The autosomal karyotypes of the 26XY taxa, however, differ markedly from one another, mainly in respect of the size of the largest chromosome. This strongly indicates that 28XY is the ancestral chromosome number for *Dundocoris* and that all the 26XY taxa originated independently from 28XY ancestors by the fusions of different combinations of autosomes. This notion is further supported by the fact that the taxa that are widespread (*D. callani callani*, *D. flavilineatus flavilineatus* and *D. natalensis*) exhibit a 28XY chromosome number. Most of the 26XY taxa have a limited distribution and often seem to occur only in a single forest like *D. scholtzi* and *D. begemanni* or group of nearby forests as *D. schoemani schoemani*, *D. schoemani dwesaensis*, *D. stuckenbergi stuckenbergi* and *D. callani noduliclypeatus*. The sex chromosomes of both the 28XY and 26XY taxa vary greatly in size but they are usually large: the X-chromosome is always the largest chromosome in the complement and the Y-chromosome usually the second largest. There exists thus, little doubt that 2n(♂) = 28XY is the ancestral chromosome number of *Dundocoris*.

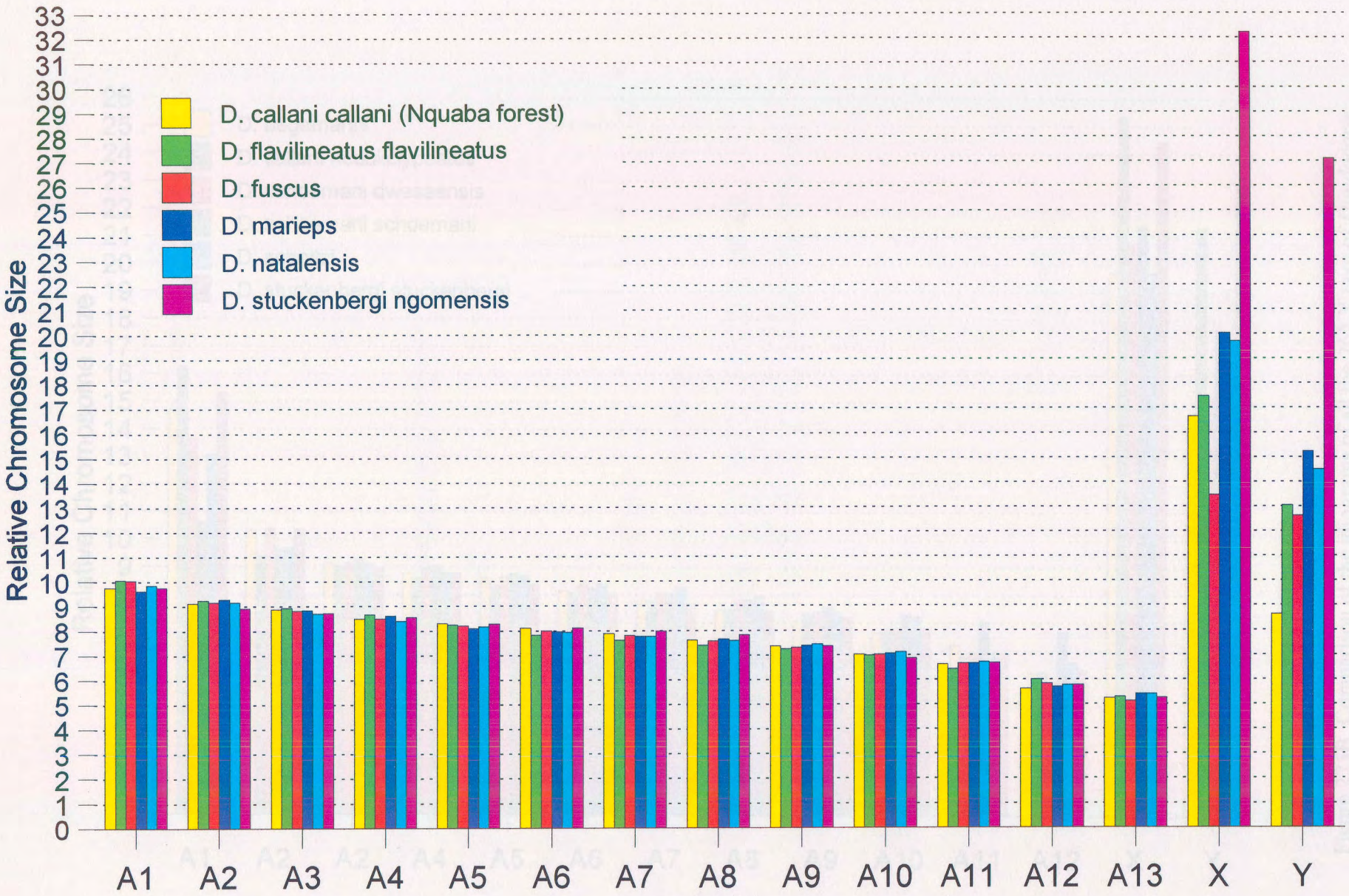


Figure 273A. Comparison of the idiograms of all the 28XY taxa of *Dundocoris*.

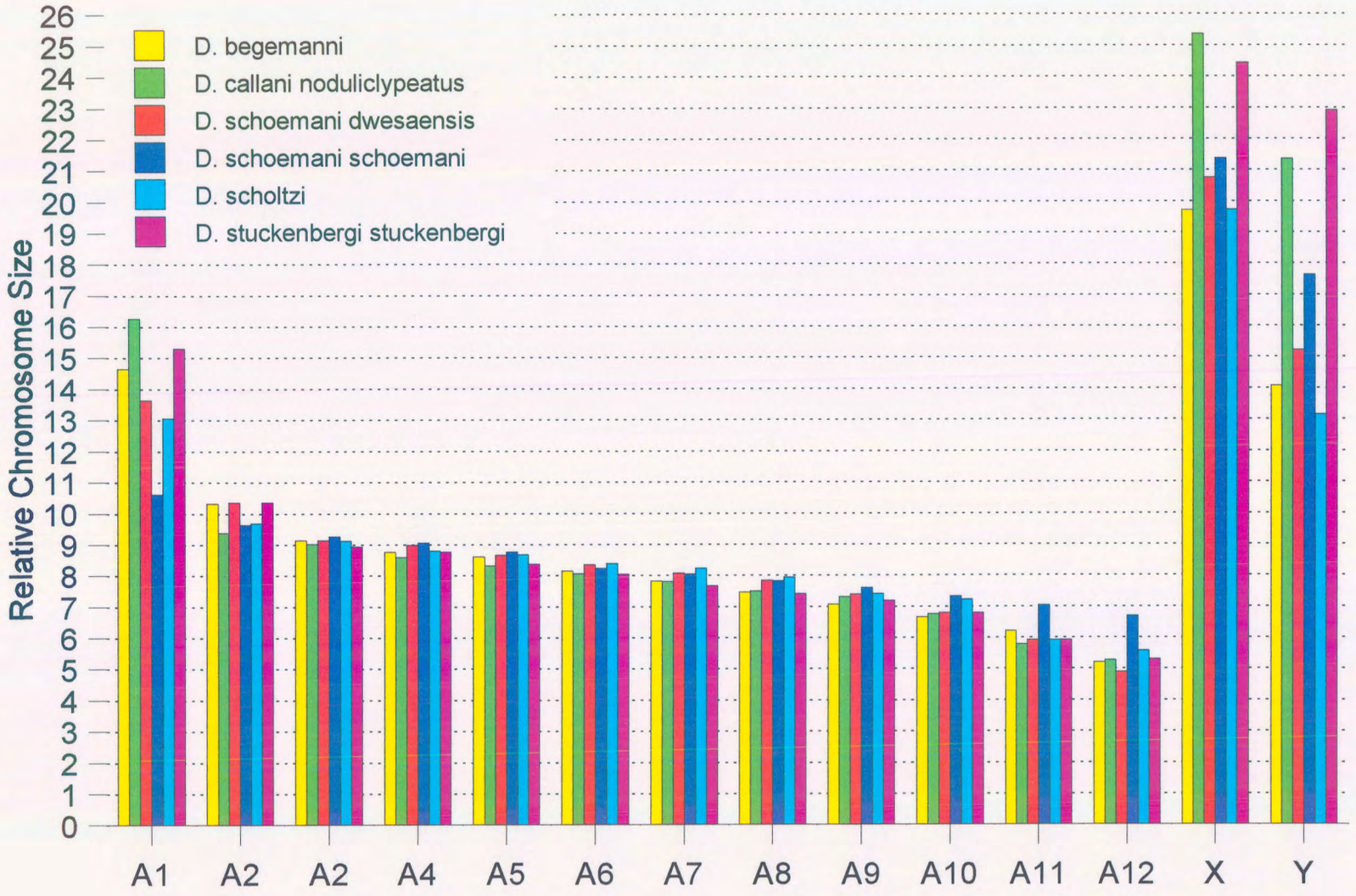


Figure 273B. Comparison of the idiograms of all the 26XY taxa of *Dundocoris*.

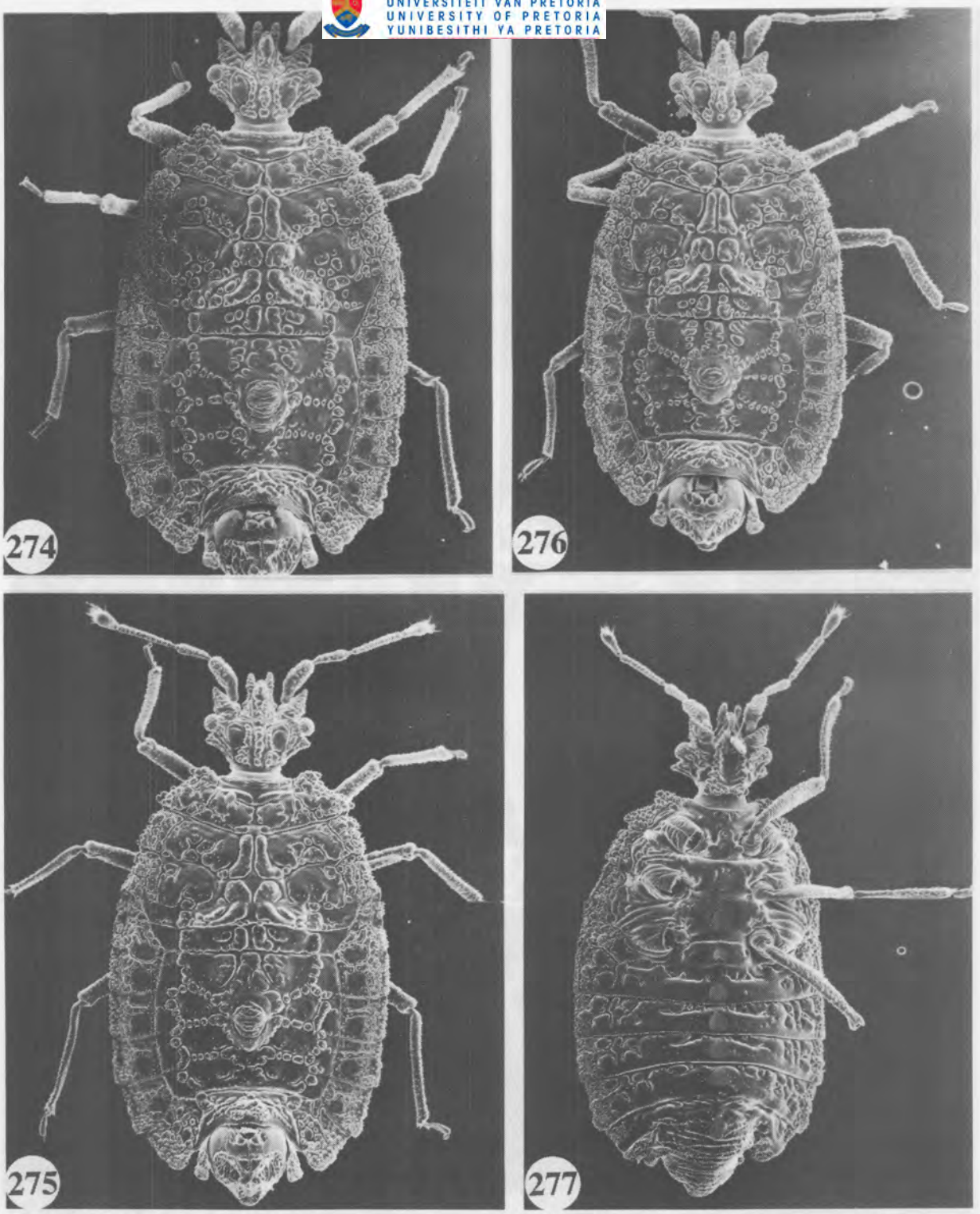
The ancestral 28XY karyotype of *Dundocoris* can be characterized as follows:

1. The autosomes form a more or less gradual size series.
2. The two smallest autosomes (A12 & A13) are set apart by a slightly larger step in the size series.
3. The sex chromosomes are the largest chromosomes in the complement - the X-chromosome is usually about twice and the Y-chromosome about 1.4x the size of the largest autosome.

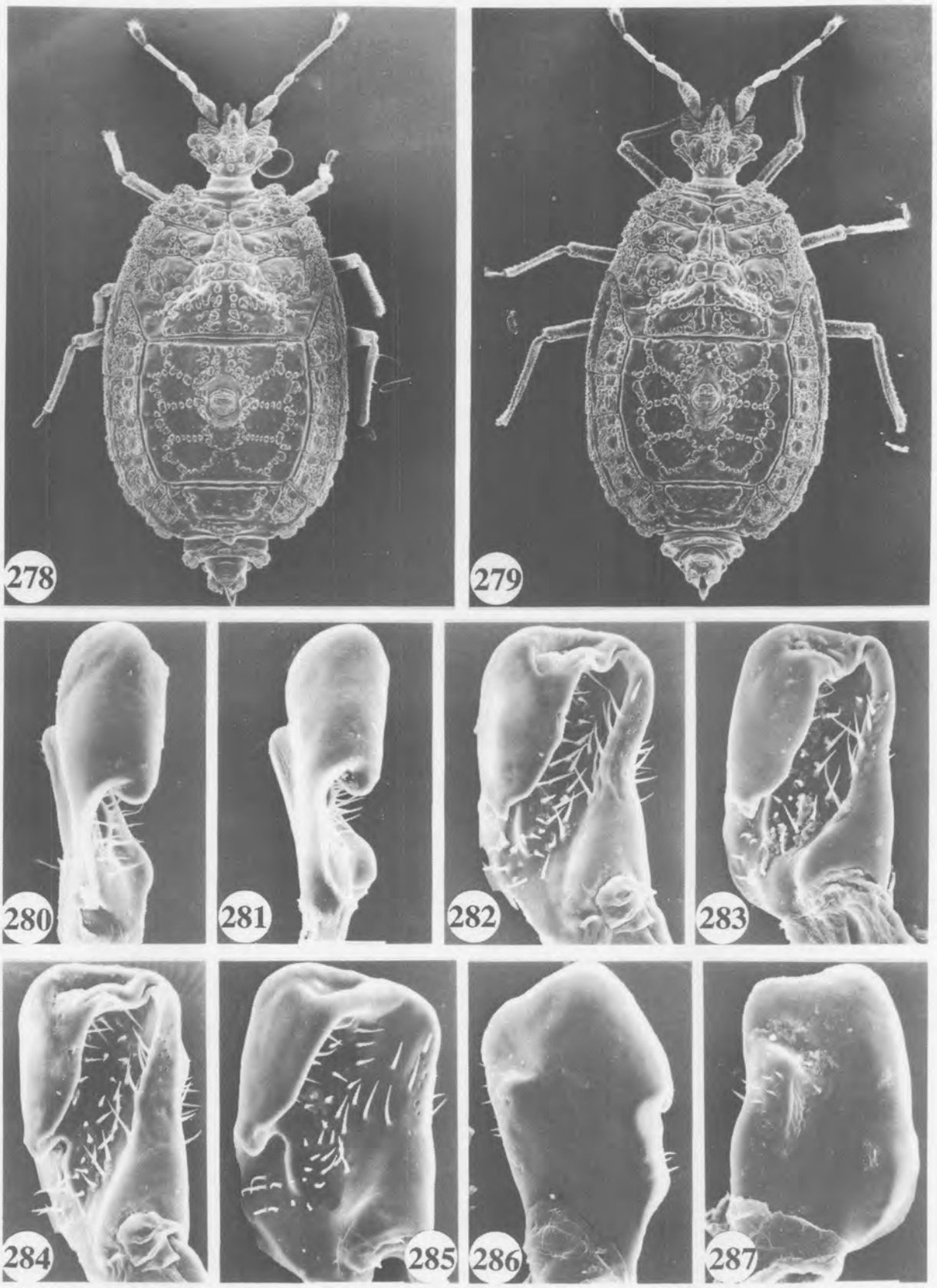
If we accept that 2n(♂) = 14XY is the ancestral chromosome number of the Aradidae and also for the Carventinae (as genera like *Silvacoris*, *Adamanotus* and *Spiculanotus* indicate) then the 28XY karyotype of *Dundocoris* must have evolved from a 14XY karyotype. This probably happened only once in the way proposed for *Trichocarventus* (refer to discussion at 7.2.3) and it demonstrates a relationship between the genera *Trichocarventus*, *Miteronotus* and *Dundocoris*. The karyotype of *D. schoemani schoemani* is of particular interest as it represents the karyotype of the hypothetical 26XY predecessor of the 28XY archetype of the three genera. It is, however, clear that this resemblance is secondary and originated by the fusion of the same autosomes that originally fragmented to form the 28XY archetype.

In the karyotype evolution within the genus *Dundocoris* many chromosome fusions took place (there is evidence for 23 fusions in the above taxa) while there is no indication of any fissions. It is evident that fusions played a very important role in the karyotype evolution of *Dundocoris* while fragmentations did not seem to have played any role at all. This is contrary to what has been generally postulated for the Hetroptera. Ueshima (1979) for example stated: "The possibility that fusion also occurs in organisms with holocentric chromosomes has been discussed by many workers. If indeed it does occur, and the evidence is far from convincing, there can be no doubt that fusion takes place relatively rarely in comparison with fragmentation." Thomas (1987) rightfully criticises the emphasis that Ueshima and others placed on fragmentation and suggested that other processes like fusions, simple aneuploidy and even polyploidy may also have played an important role in the chromosomal evolution in the Heteroptera.

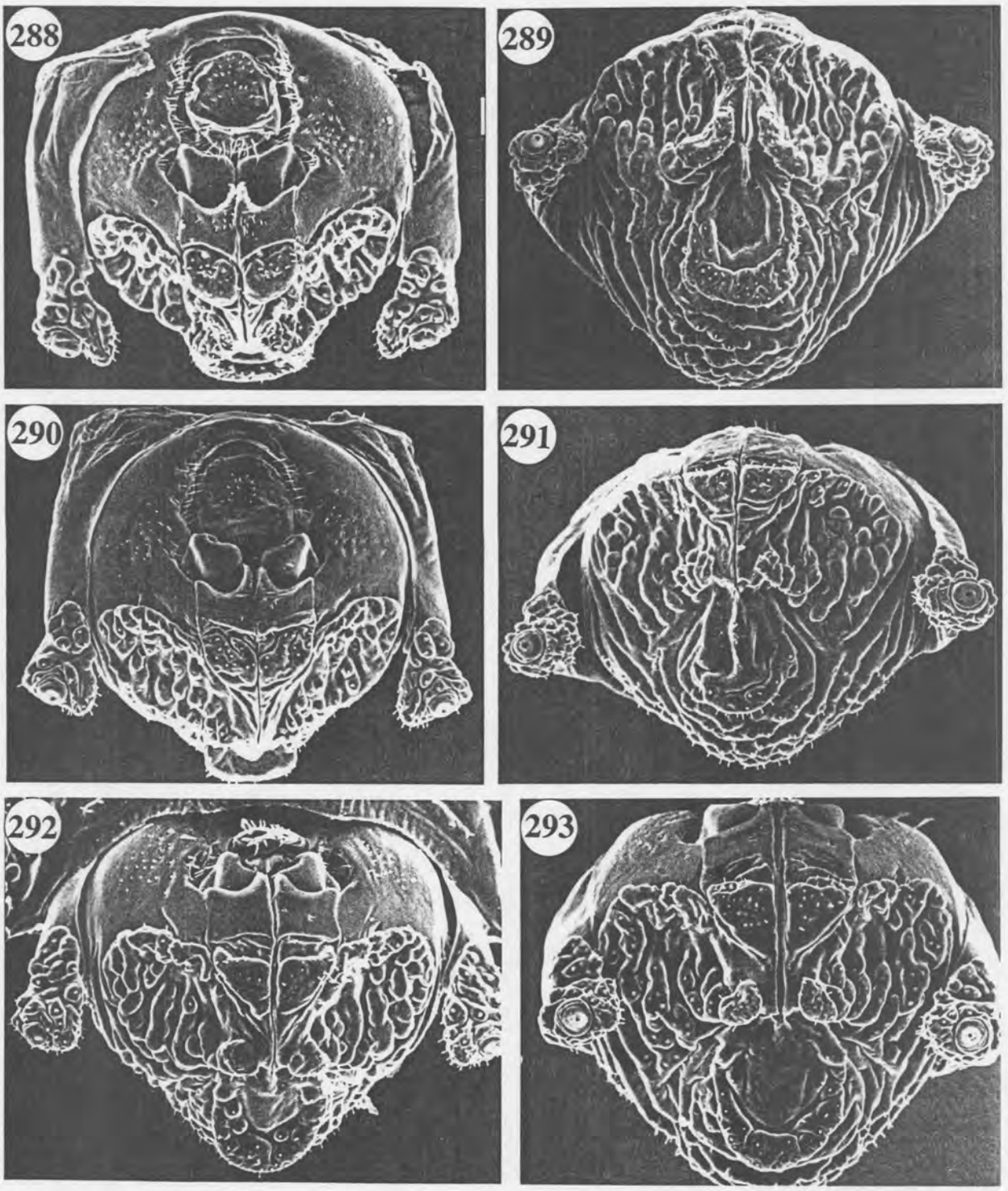
Not only did fusions play such an important role in the evolution of *Dundocoris* but three taxa feature multiple sex chromosome systems that originated by autosome-sex chromosome fusions. At present these are the only known cases in the Heteroptera where that has happened. The case of *D. scholtzi* where one out of sixteen studied individuals has an autosome-Y-chromosome fusion indicates that such fusions may be more common than realized and perhaps happen regularly but very infrequently become fixed in populations.



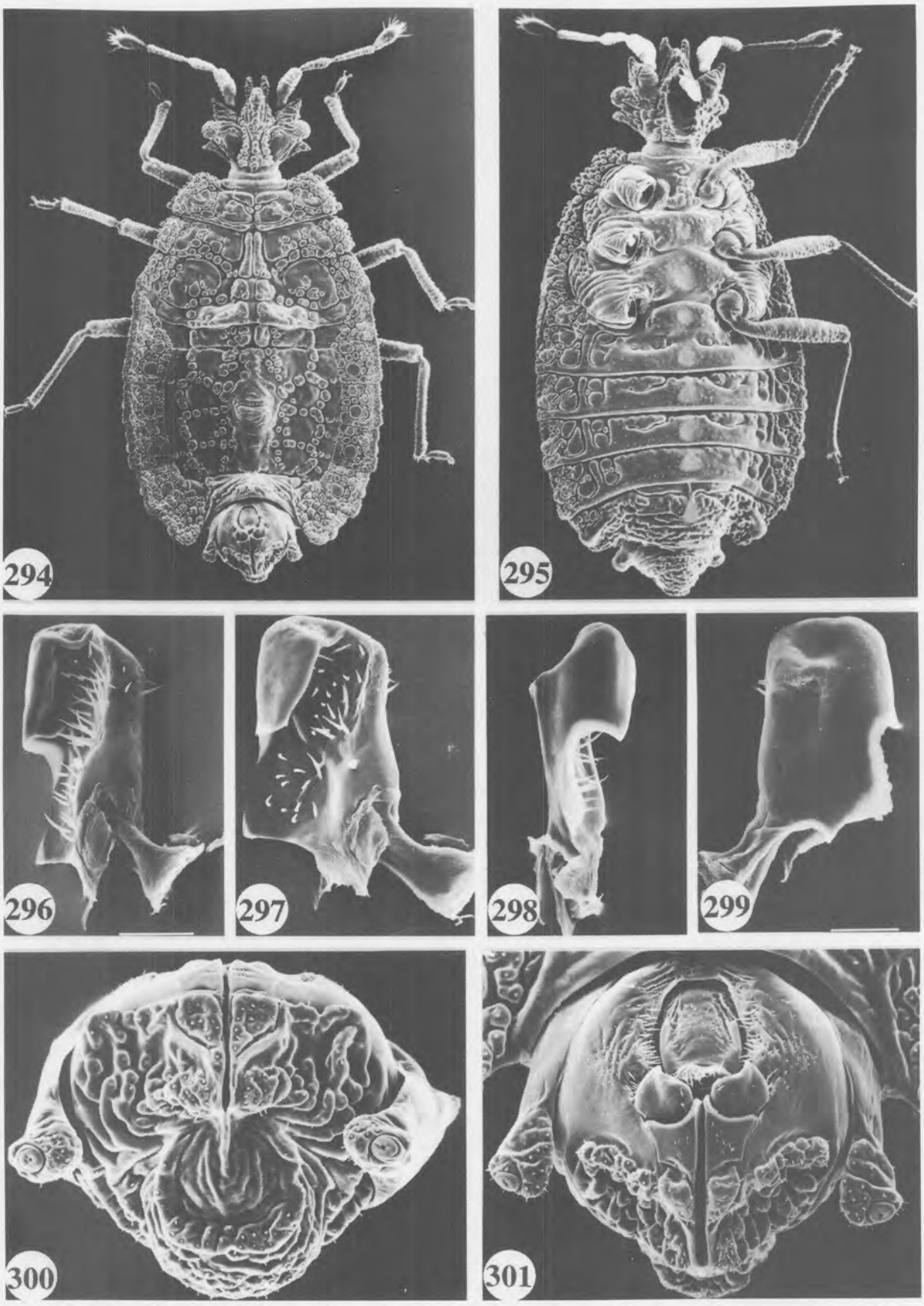
Figs 274-277. Scanning electron photomicrographs of the subspecies of *Dundocoris nodulicarinus* **spec. nov.** 274. *D. nodulicarinus nodulicarinus* **spec. nov.**, dorsal aspect of male paratype. 275. *D. nodulicarinus septeni* **spec. et subspec. nov.**, dorsal aspect of male paratype. 276-277. *D. nodulicarinus novenus* **spec. et subspec. nov.** 276. Dorsal aspect of male paratype. 277. Ventral aspect of male paratype.



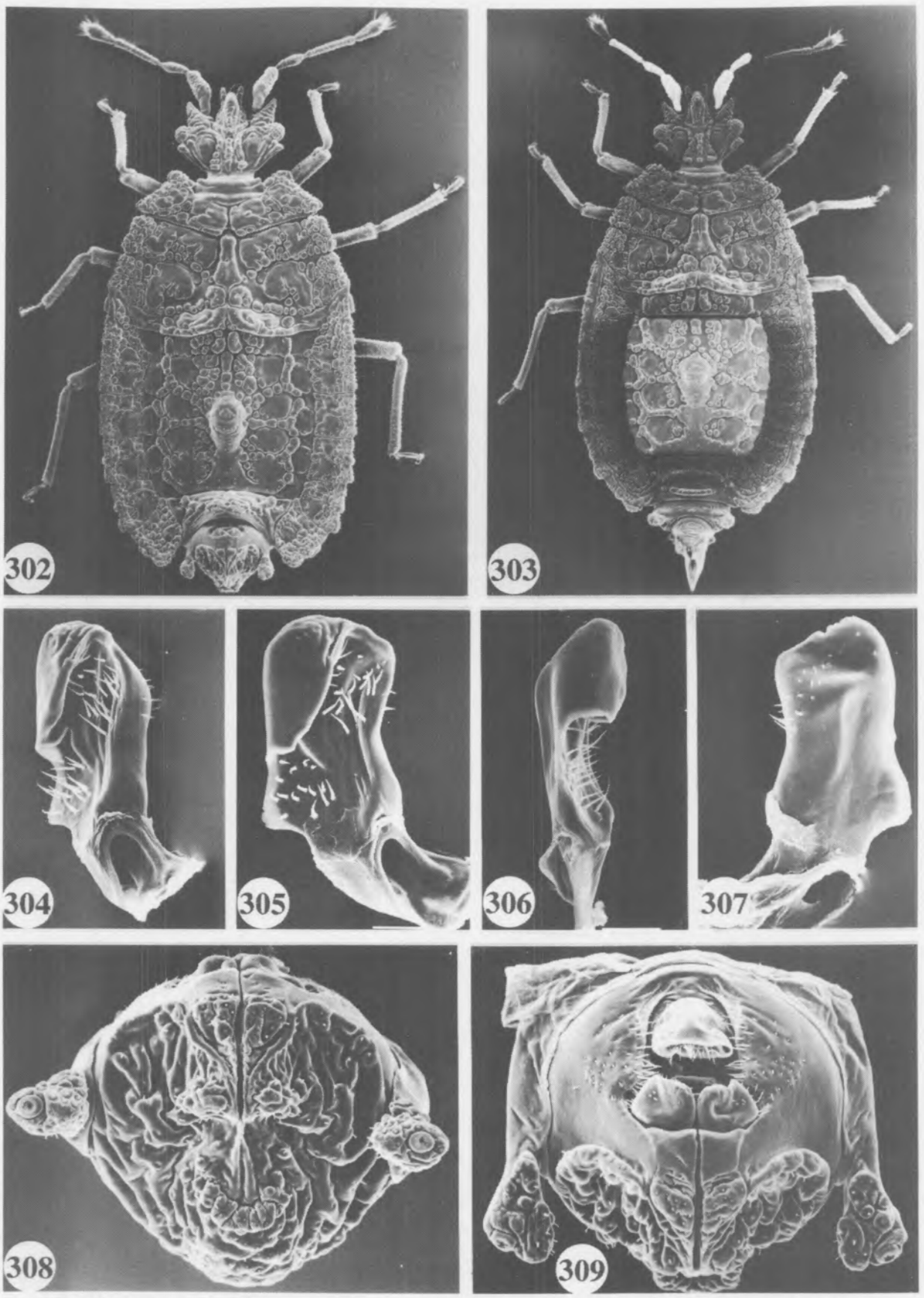
Figs 278-287. Scanning electron photomicrographs of the subspecies of *Dundocoris nodulicarinus* **spec. nov.** 278. *D. nodulicarinus nodulicarinus* **spec. nov.**, dorsal aspect of female paratype. 279. *D. nodulicarinus novenus* **spec. et subspec. nov.**, dorsal aspect of female paratype. 280-287. Different aspects of the left parameres of males (scale bar = 50 μm). 282 & 284. *D. nodulicarinus nodulicarinus* **spec. nov.** 281, 283 & 287. *D. nodulicarinus novenus* **spec. et subspec. nov.** 280, 285-286. *D. nodulicarinus septeni* **spec. et subspec. nov.**



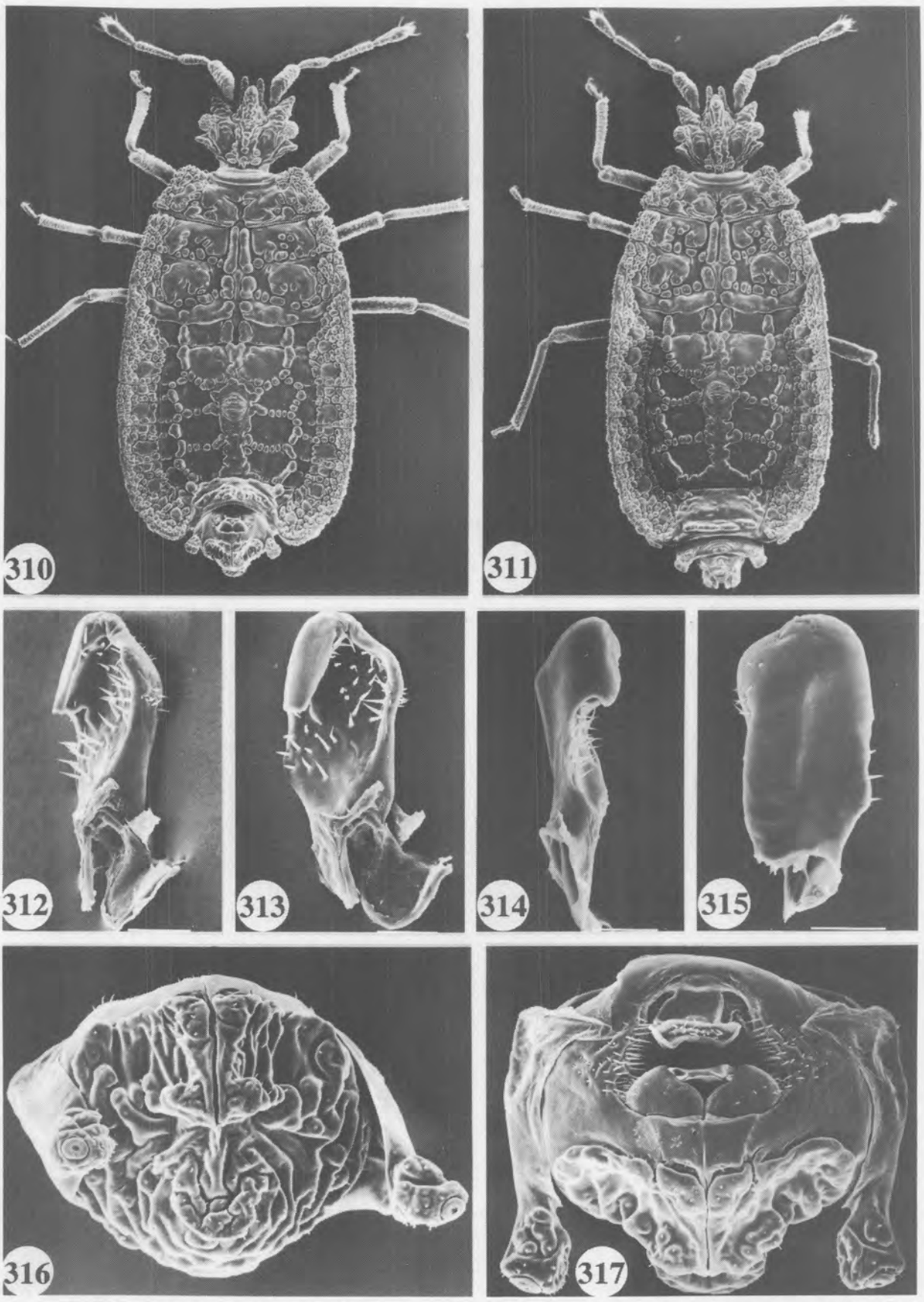
Figs 288-293. Scanning electron photomicrographs of the pygophores of the subspecies of *Dundocoris nodulicarinus* **spec. nov.** 288-289. *D. nodulicarinus nodulicarinus* **spec. nov.** 288. Dorsal aspect (scale bar = 50 μm). 289. Caudal aspect. 290-291. *D. nodulicarinus novenus* **spec. et subspec. nov.** 290. Dorsal aspect. 291. Caudal aspect. 292-293. *D. nodulicarinus septeni* **spec. et subspec. nov.** 292. Dorsal aspect. 293. Caudal aspect.



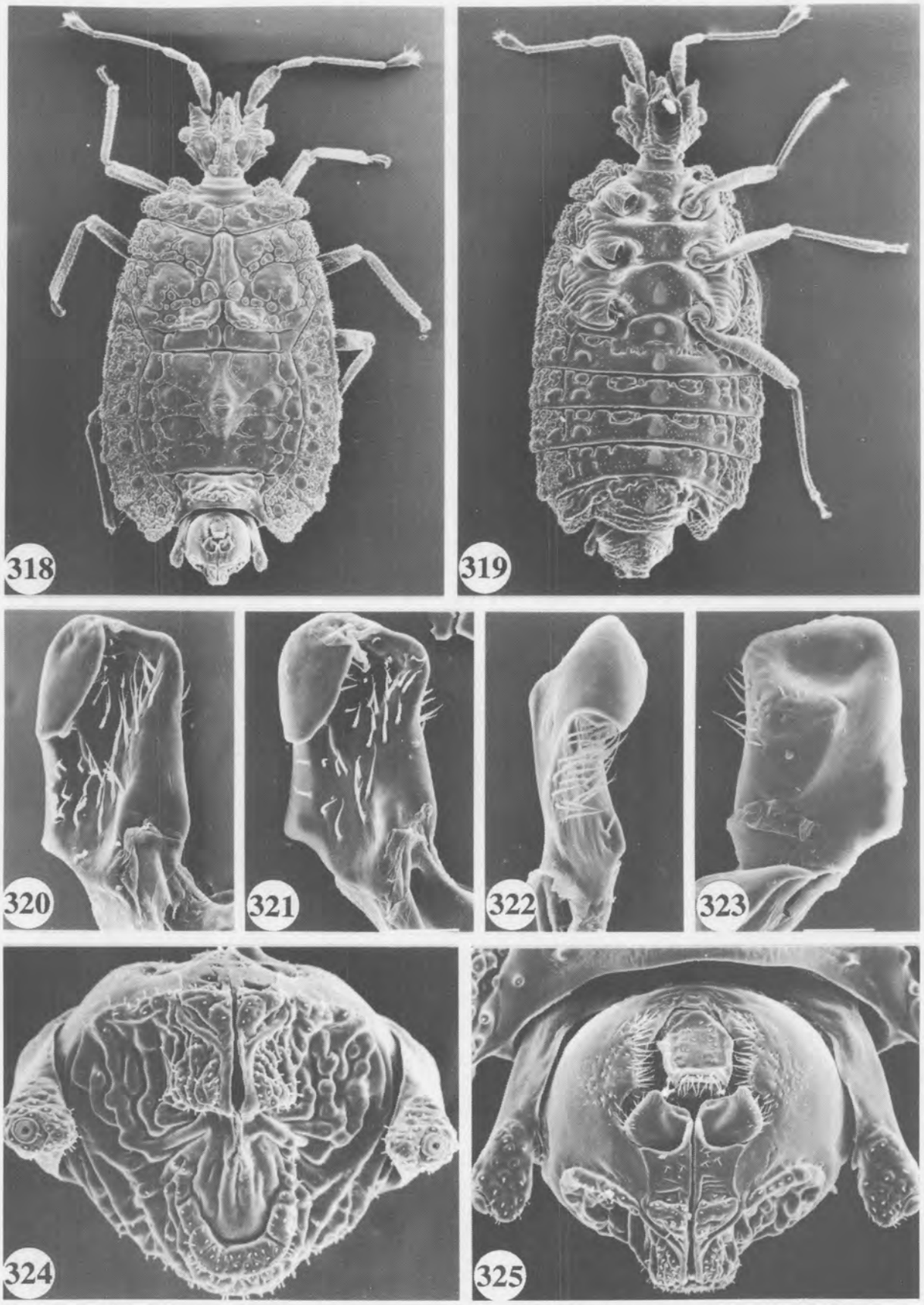
Figs 294-301. Scanning electron photomicrographs of *Dundocoris transvaalensis* **spec. nov.** 294-295. Male paratype. 294. Dorsal aspect. 295. Ventral aspect. 296-299. Different aspects of the left paramere (scale bar = 50 μm). 300-301. Pygophore. 300. Caudal aspect. 301. Dorsal aspect.



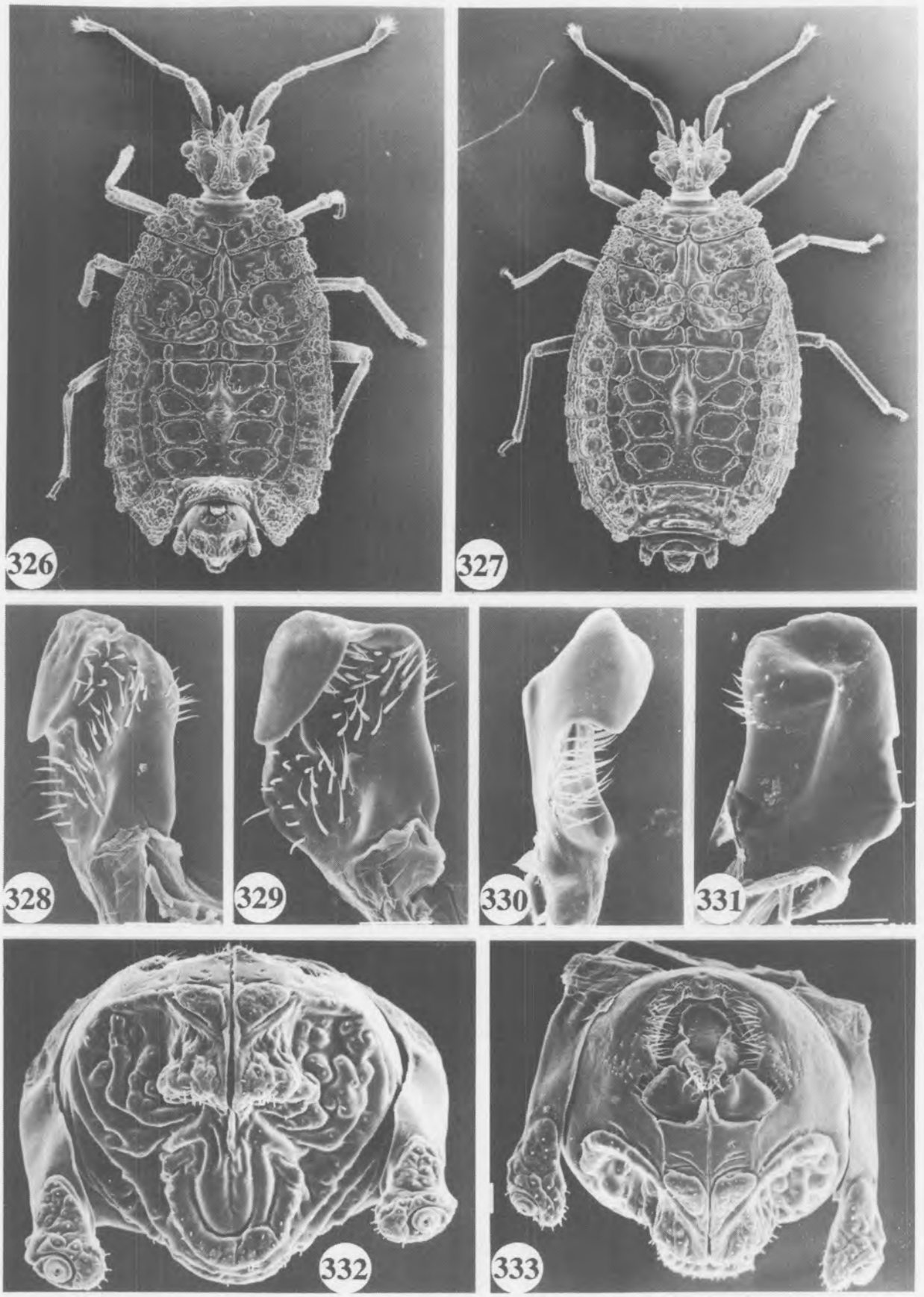
Figs 302-309. Scanning electron photomicrographs of *Dundocoris marieps* **spec. nov.** 302. Male paratype, dorsal aspect. 303. Female paratype, dorsal aspect. 304-307. Different aspects of the left paramere (scale bar = 50 μm). 308-309. Pygophore. 308. Caudal aspect. 309. Dorsal aspect.



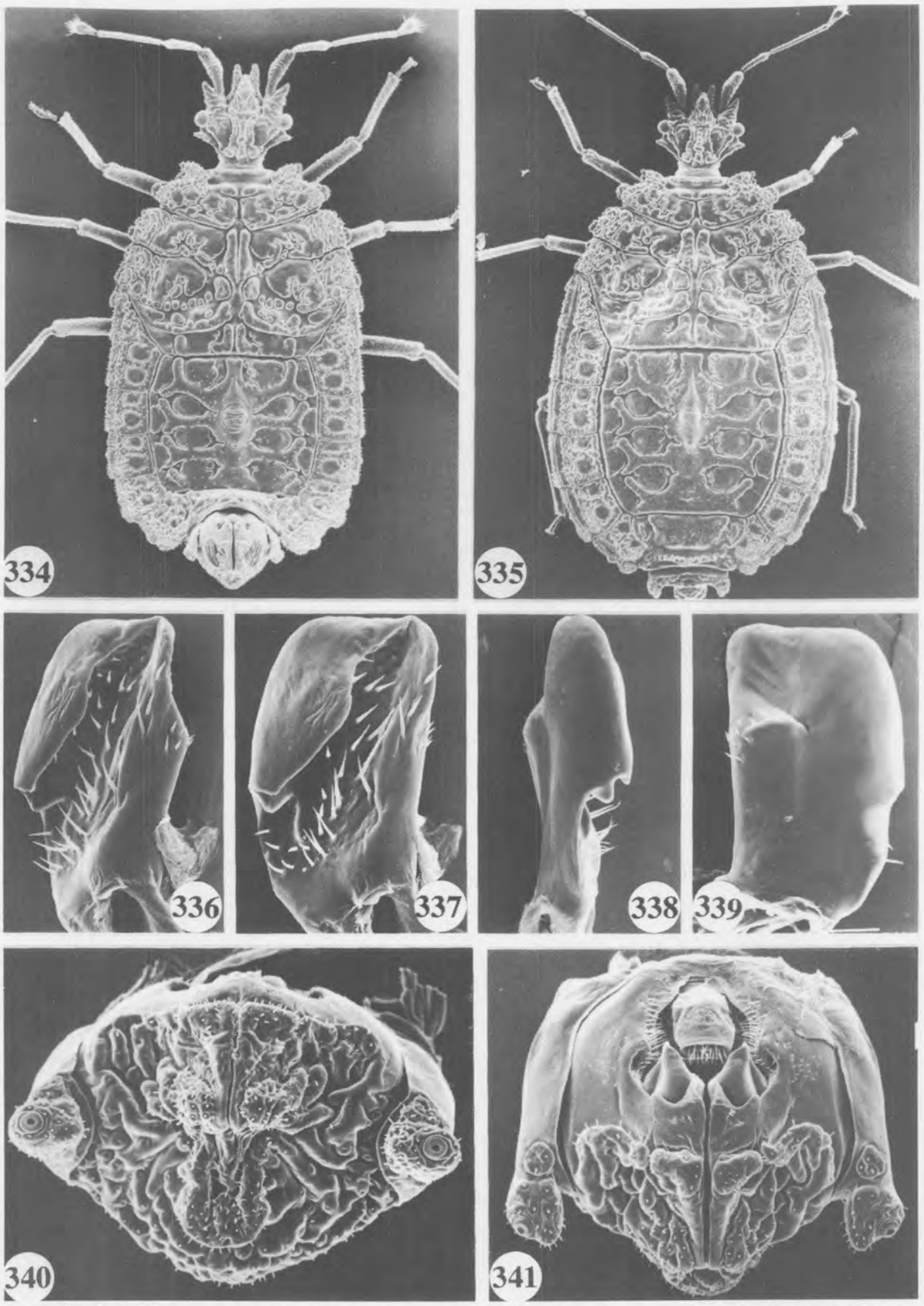
Figs 310-317. Scanning electron photomicrographs of *Dundocoris begemanni* **spec. nov.** 310. Male paratype, dorsal aspect. 311. Female paratype, dorsal aspect. 312-315. Different aspects of the left paramere (scale bar = 50 μm). 316-317. Pygophore. 316. Caudal aspect. 317. Dorsal aspect.



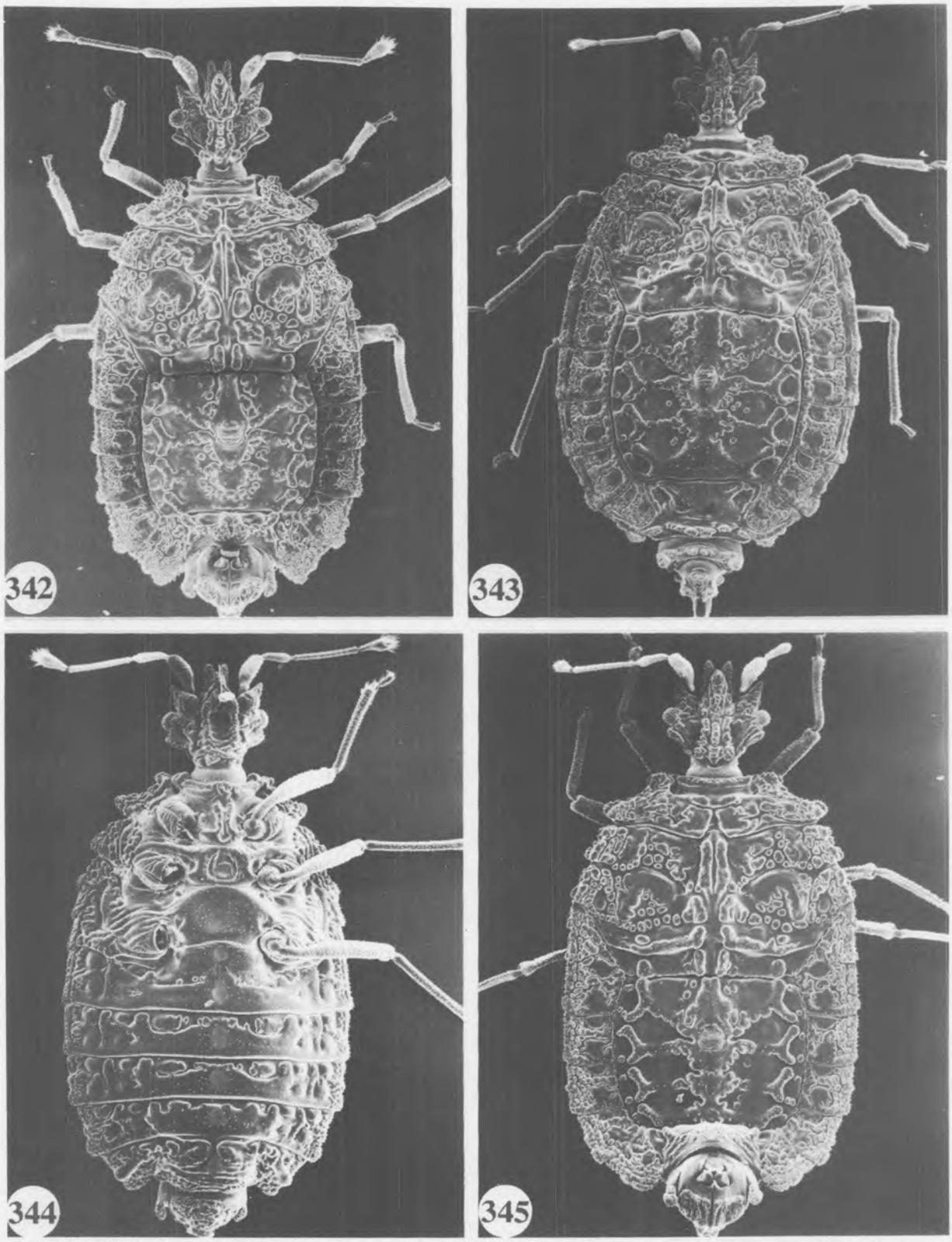
Figs 318-325. Scanning electron photomicrographs of *Dundocoris stuckenbergi stuckenbergi* Heiss & Jacobs. 318-319. Male paratype. 318. Dorsal aspect. 319. Ventral aspect. 320-323. Different aspects of the left paramere (scale bar = 50 μm). 324-325. Pygophore. 324. Caudal aspect. 325. Dorsal aspect.



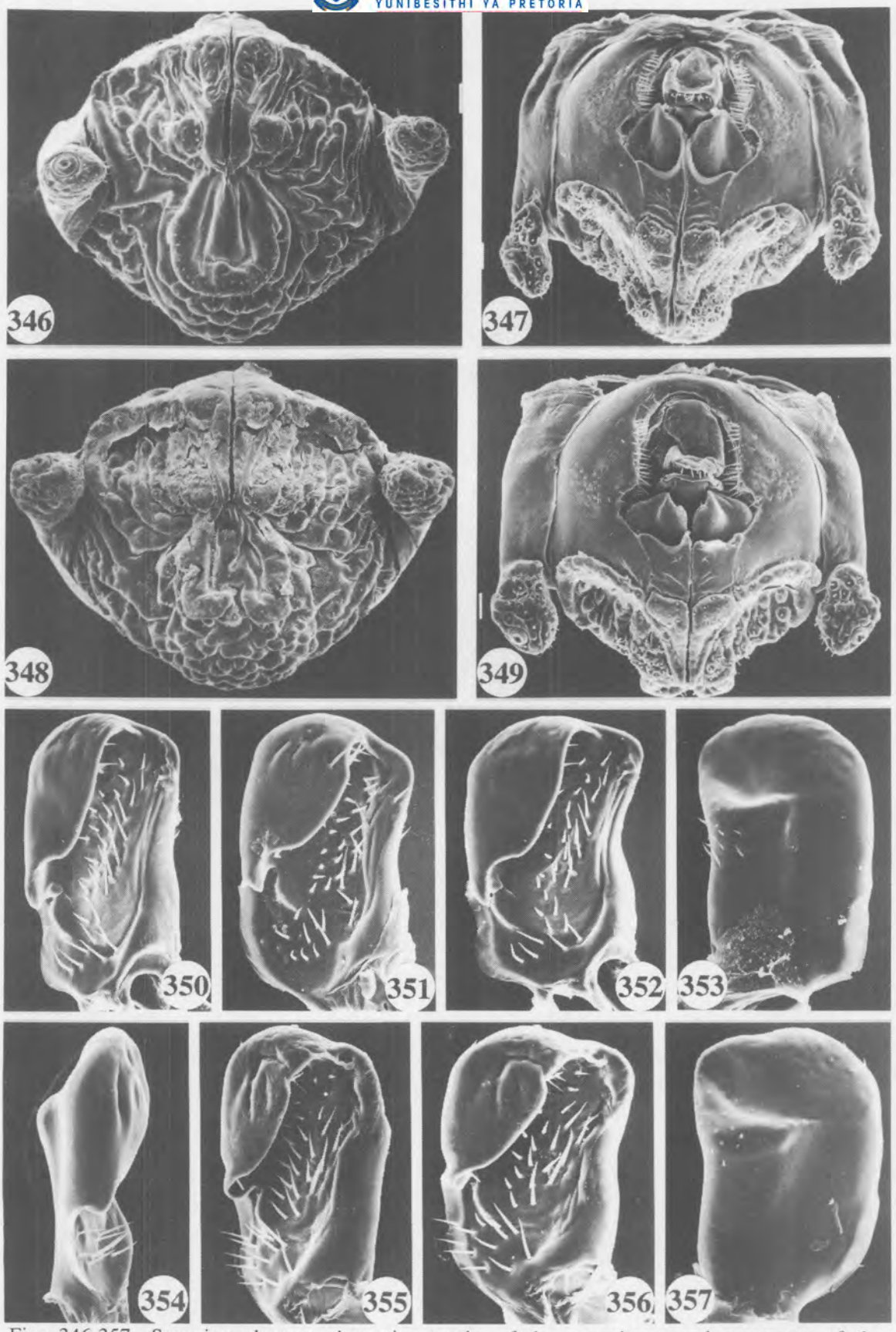
Figs 326-333. Scanning electron photomicrographs of *Dundocoris stuckenbergi ngomensis* **subspec. nov.** 326. Male paratype, dorsal aspect. 327. Female paratype, dorsal aspect. 328-331. Different aspects of the left paramere (scale bar = 50 μm). 332-333. Pygophore. 332. Caudal aspect. 333. Dorsal aspect (scale bar = 50 μm).



Figs 334-341. Scanning electron photomicrographs of *Dundocoris nigromaculatus* Heiss & Jacobs. 334. Male paratype, dorsal aspect. 335. Female paratype, dorsal aspect. 336-339. Different aspects of the left paramere (scale bar = 50 μm). 340-341. Pygophore. 340. Caudal aspect. 341. Dorsal aspect (scale bar = 50 μm).



Figs 342-345. Scanning electron photomicrographs of the subspecies of *Dundocoris flavilineatus* **spec. nov.** 342-344. *D. flavilineatus flavilineatus* **spec. nov.** 342. Dorsal aspect of male paratype. 343. Dorsal aspect of female paratype. 344. Ventral aspect of male paratype. 345. *D. flavilineatus ndabeniensis* **spec. et subspec. nov.**, dorsal aspect of male paratype.



Figs 346-357. Scanning electron photomicrographs of the pygophores and parameres of the subspecies of *Dundocoris flavilineatus* **spec. nov.** 346-349. Pygophores. 346-347. *D. flavilineatus flavilineatus* **spec. nov.** 346. Caudal aspect. 347. Dorsal aspect (scale bar = 50 μm). 348-349. *D. flavilineatus ndabeniensis* **spec. et subspec. nov.** 348. Caudal aspect. 349. Dorsal aspect (scale bar = 50 μm). 350-357. Different aspects of the left paramere. 350-354. *D. flavilineatus flavilineatus* **spec. nov.** 355-357. *D. flavilineatus ndabeniensis* **spec. et subspec. nov.**

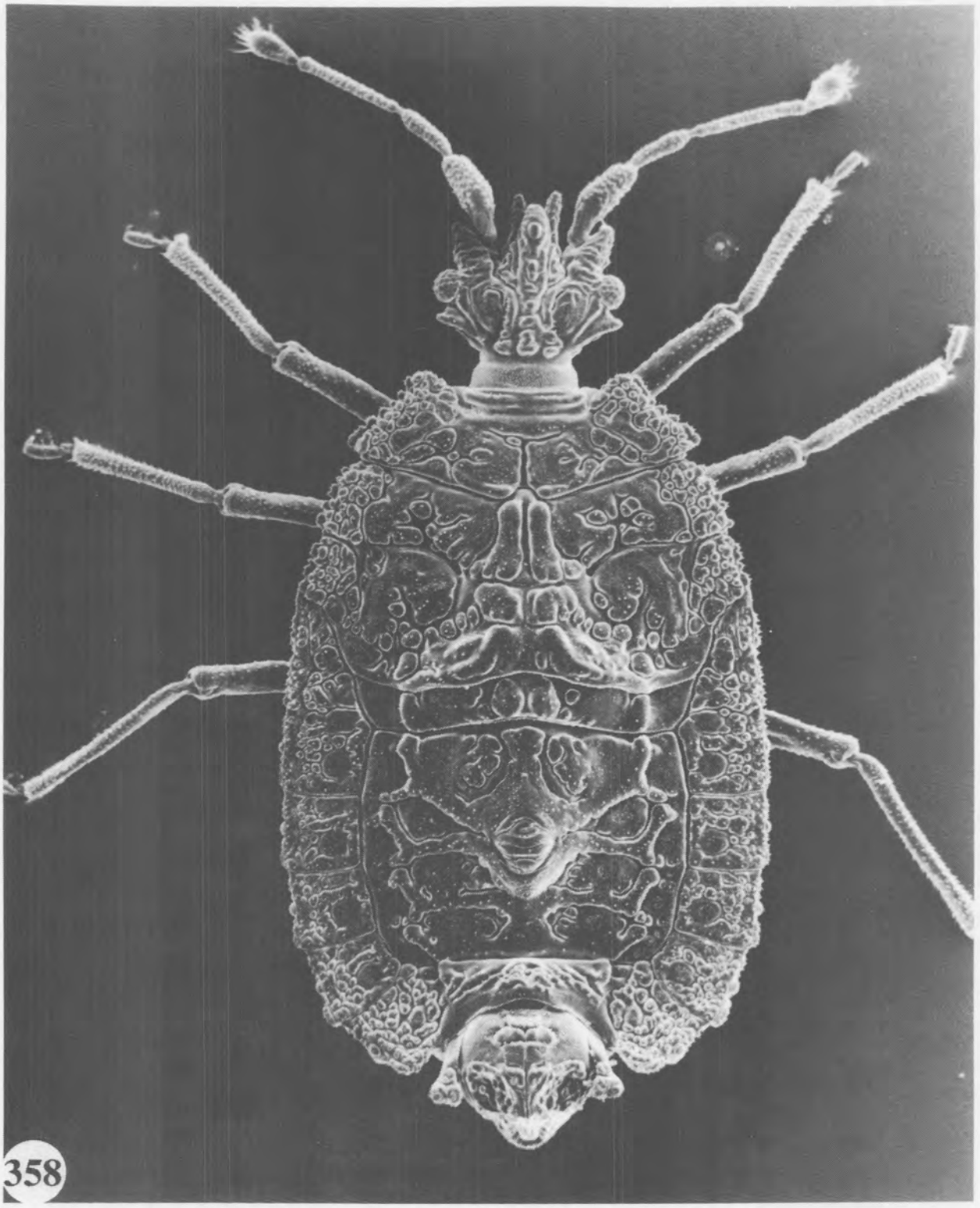
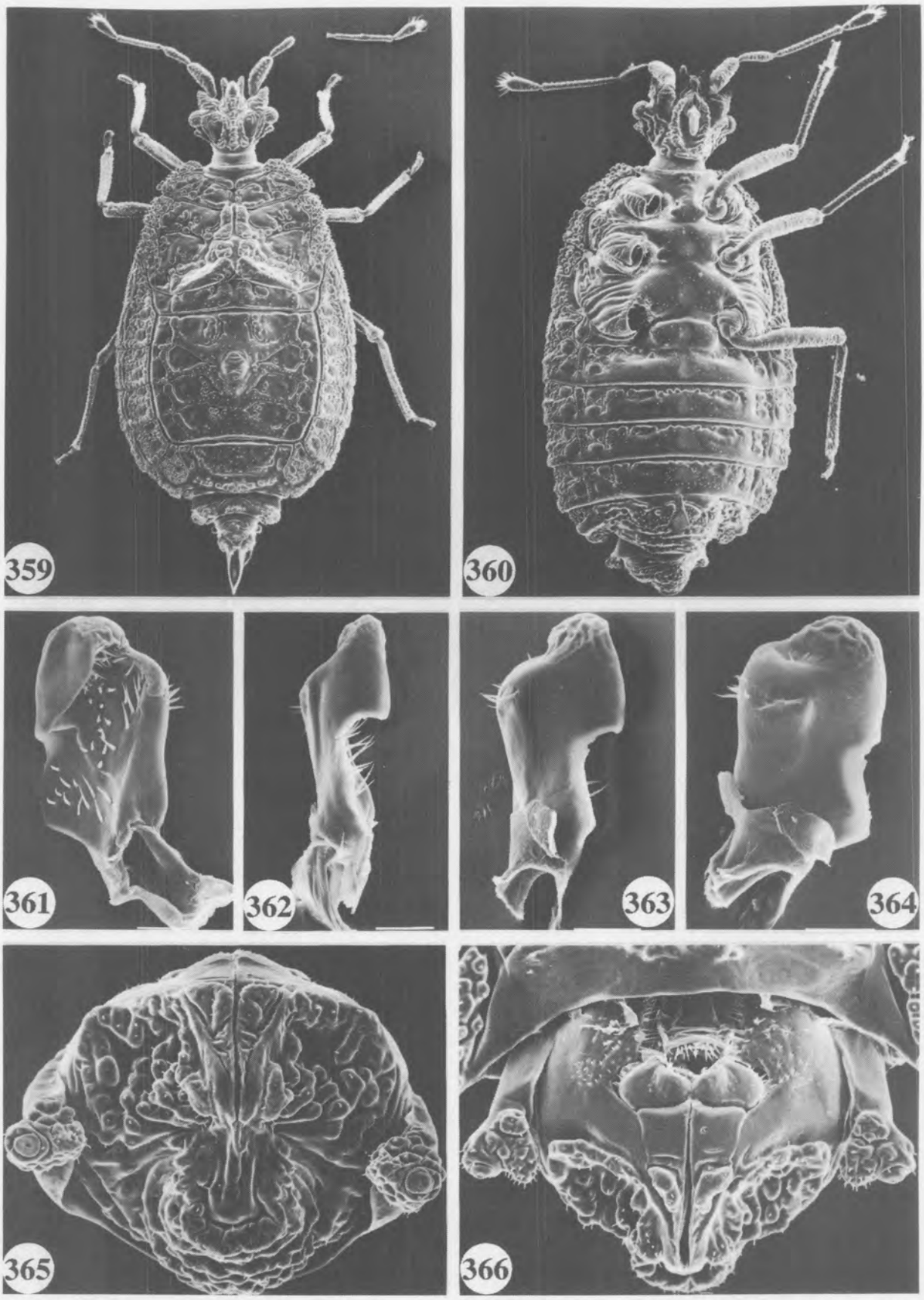
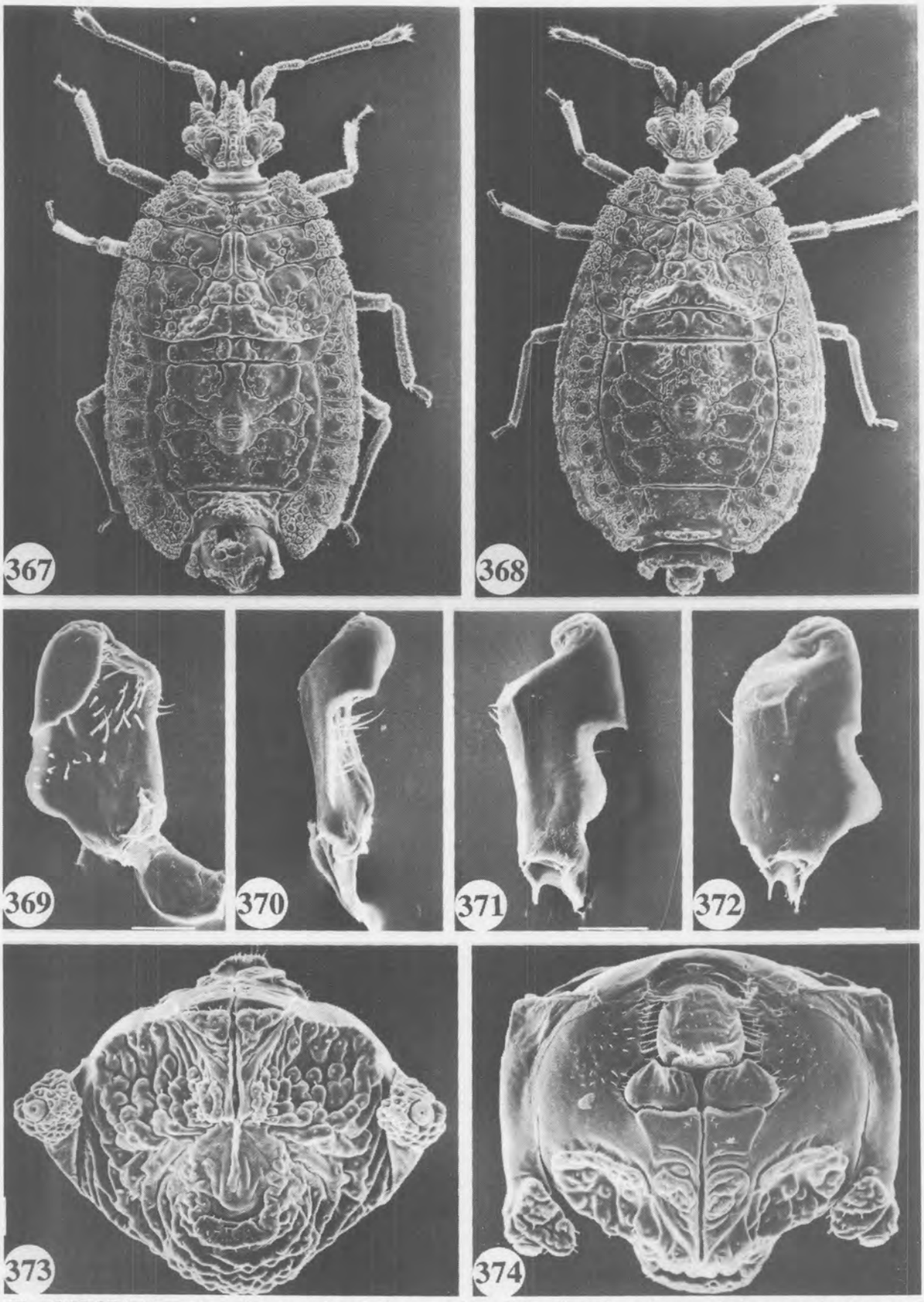


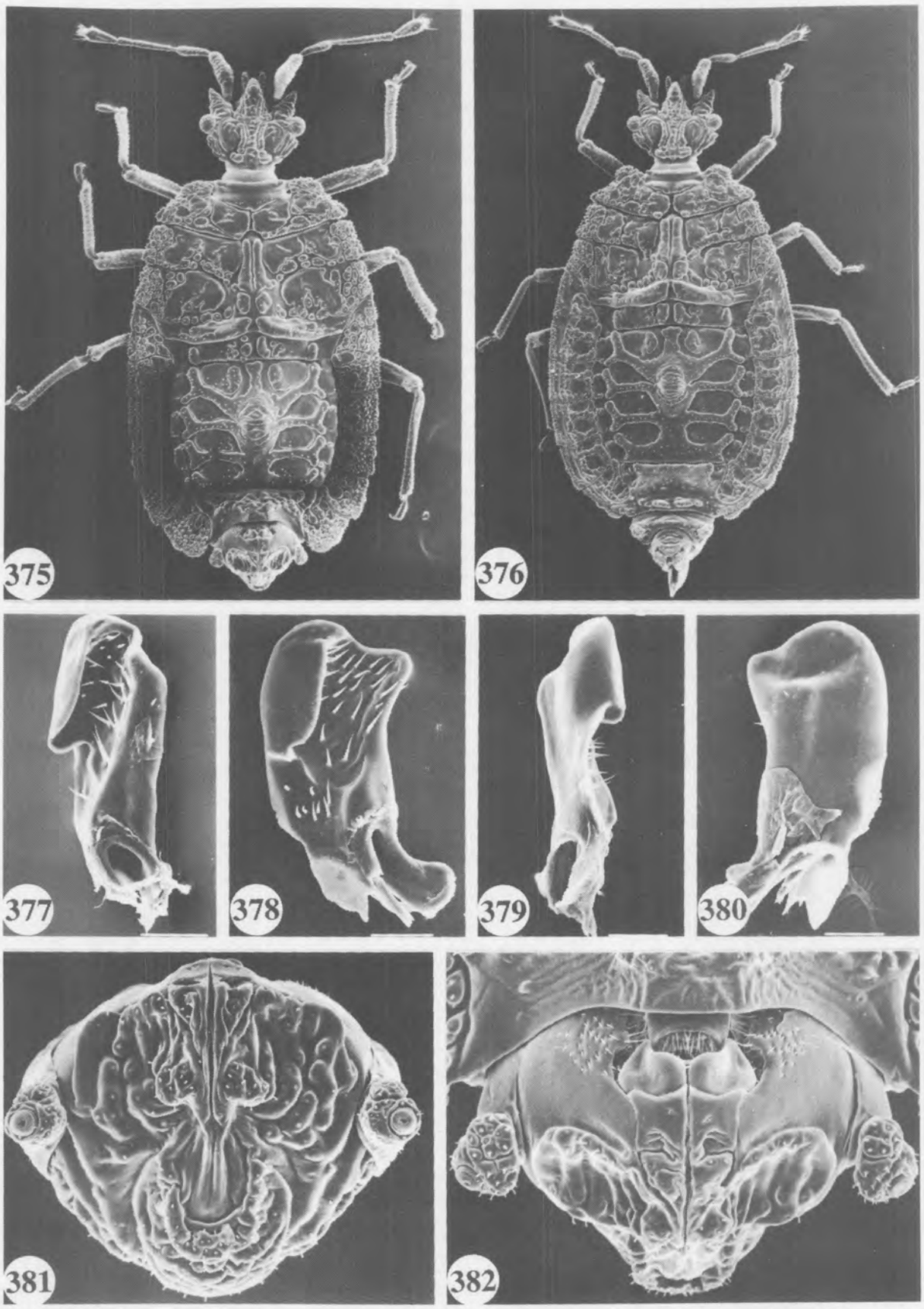
Fig. 358. Scanning electron photomicrograph of *Dundocoris schoemani schoemani* **spec. nov.**, dorsal aspect of male paratype.



Figs 359-366. Scanning electron photomicrographs of *Dundocoris schoemani schoemani* **spec. nov.** 359. Female paratype, dorsal aspect. 360. Male paratype, ventral aspect. 361-364. Different aspects of the left paramere (scale bar = 50 μm). 365-366. Pygophore. 365. Caudal aspect. 366. Dorsal aspect.



Figs 367-374. Scanning electron photomicrographs of *Dundocoris schoemani dwesaensis* **spec. et subspec. nov.** 367. Male paratype, dorsal aspect. 368. Female paratype, dorsal aspect. 369-372. Different aspects of the left paramere (scale bar = 50 μm). 373-374. Pygophore. 373. Caudal aspect (scale bar = 50 μm). 374. Dorsal aspect.



Figs 375-382. Scanning electron photomicrographs of *Dundocoris scholtzi* **spec. nov.** 375. Male paratype, dorsal aspect. 376. Female paratype, dorsal aspect. 377-380. Different aspects of the left paramere (scale bar = 50 μm). 381-382. Pygophore. 381. Caudal aspect. 382. Dorsal aspect.

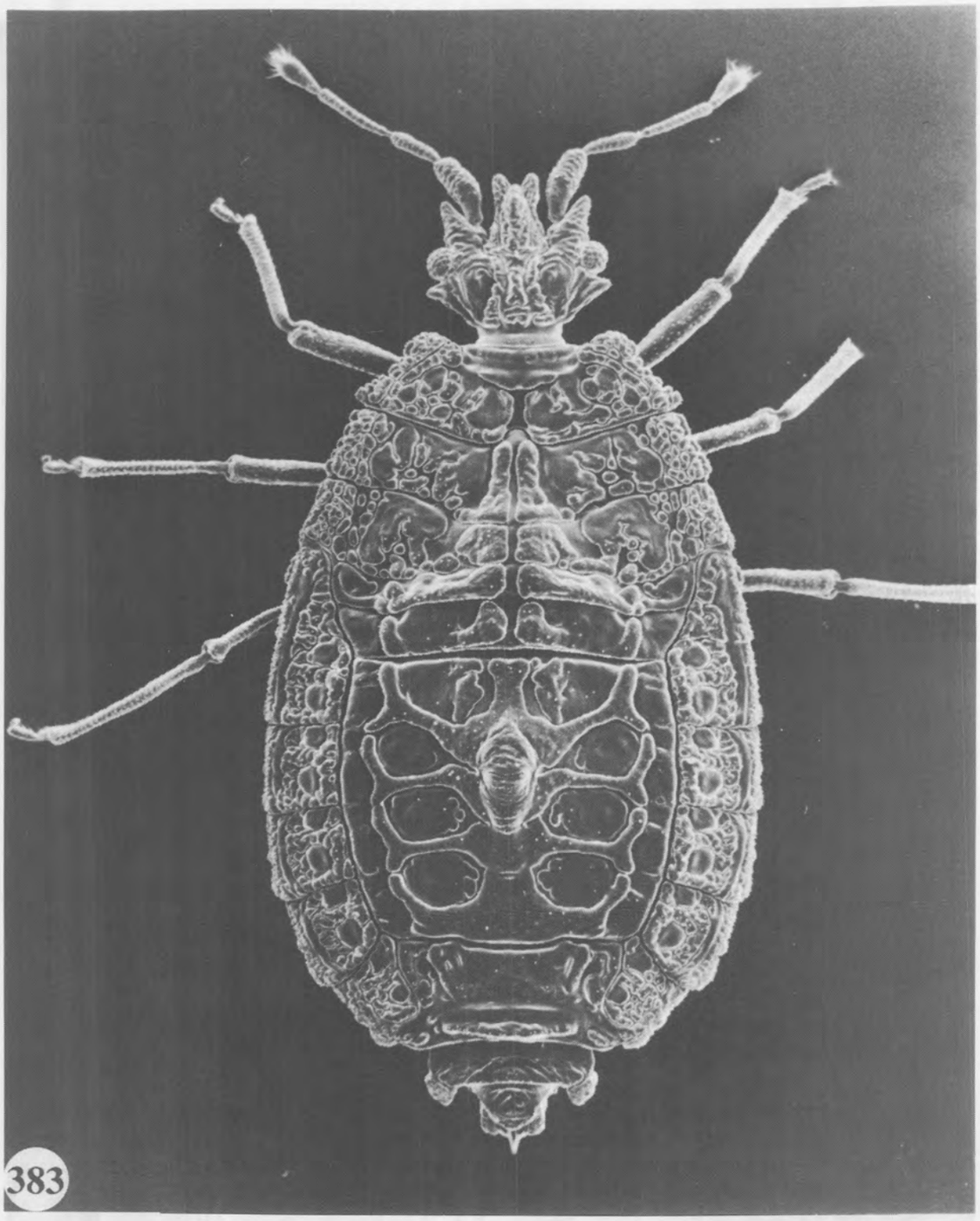
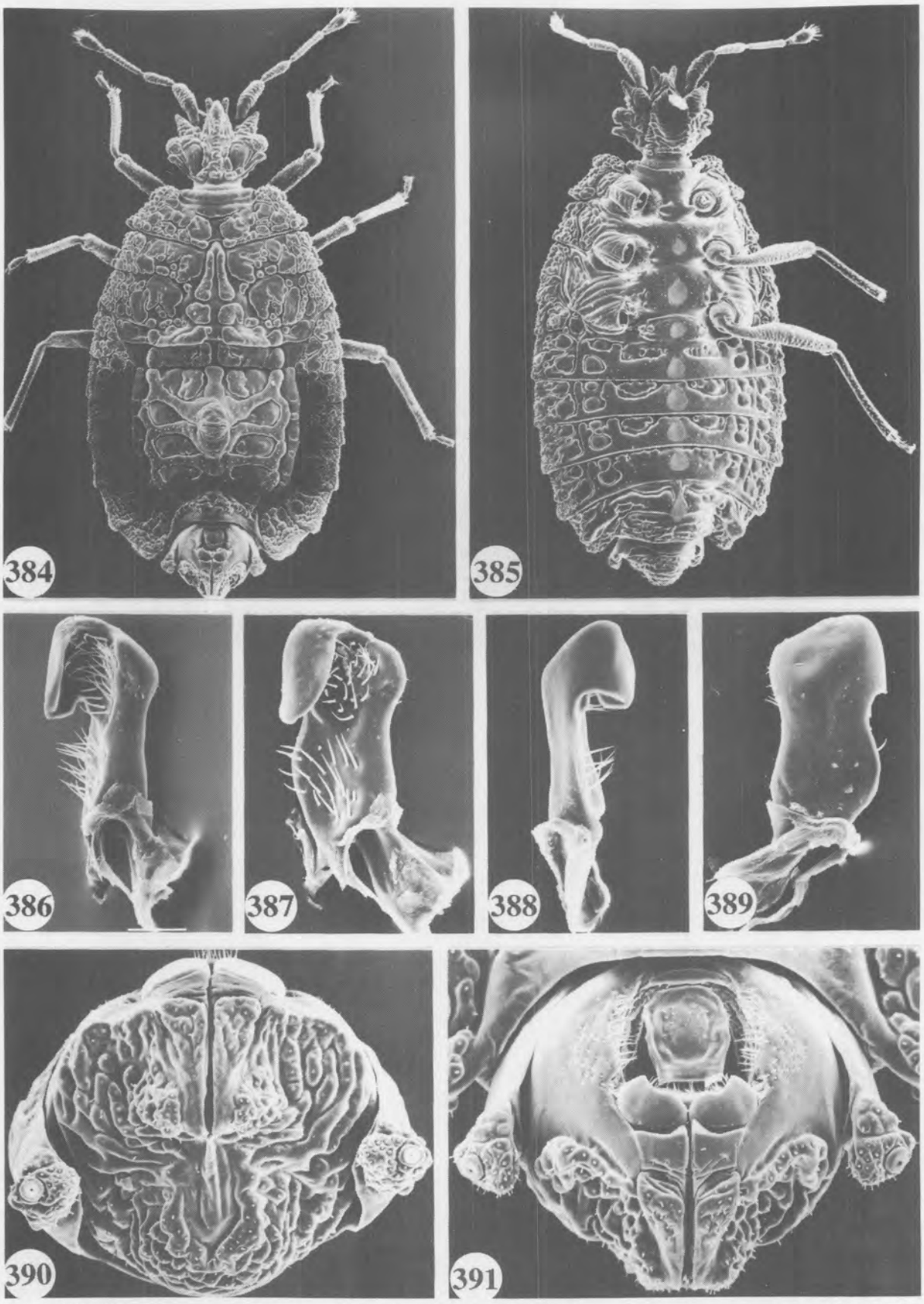
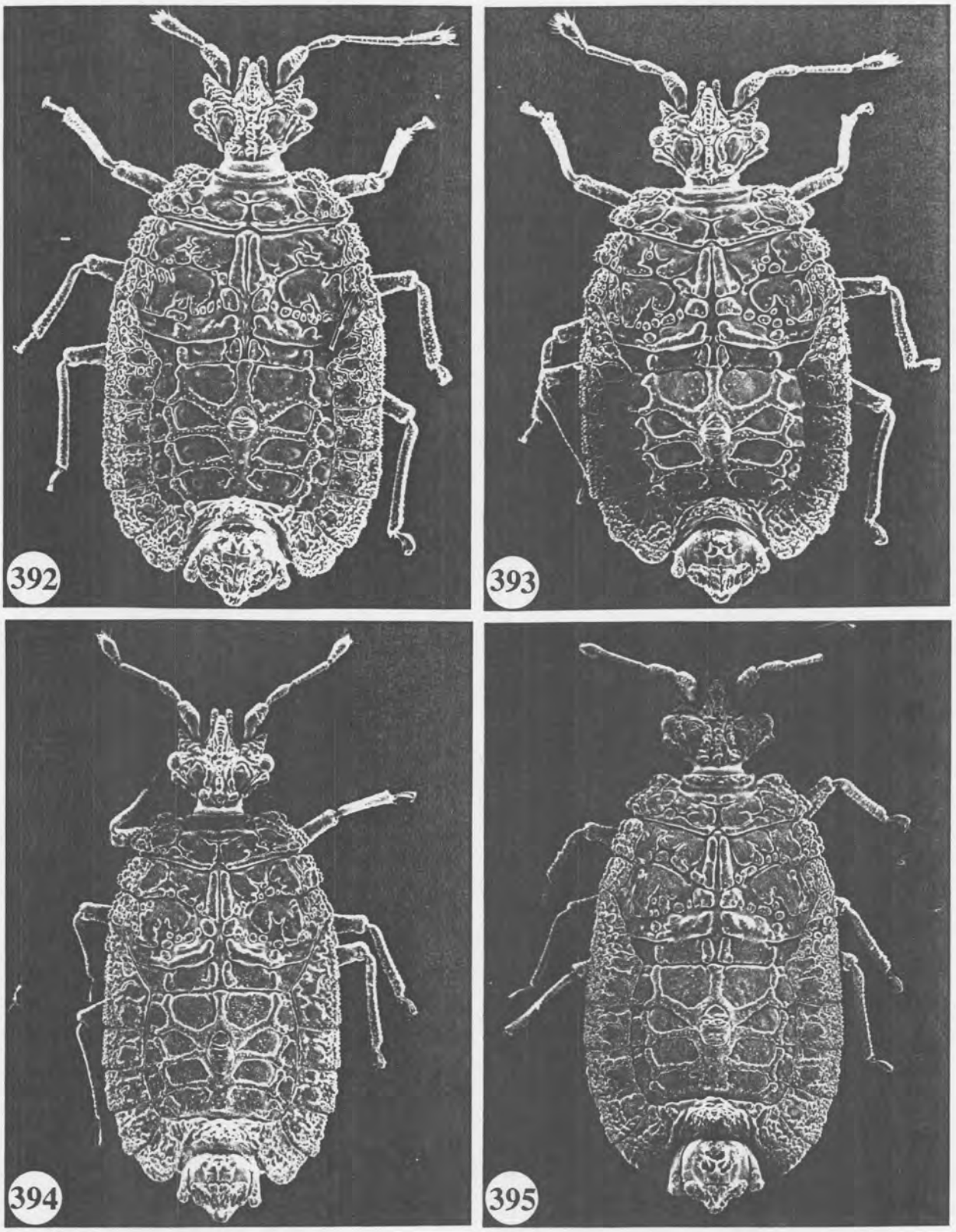


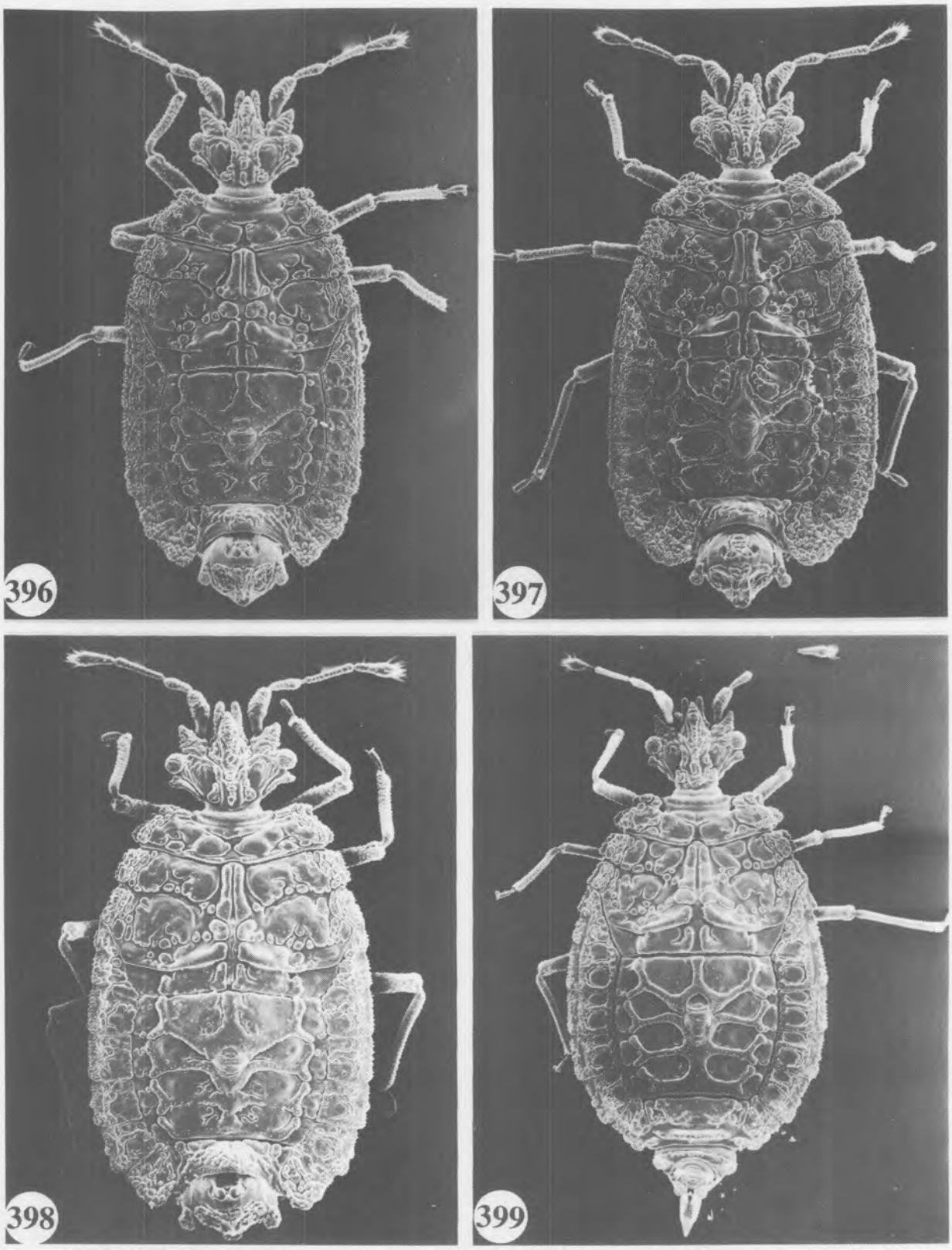
Fig. 383. Scanning electron photomicrograph of *Dundocoris fuscus* **spec. nov.**, dorsal aspect of female paratype.



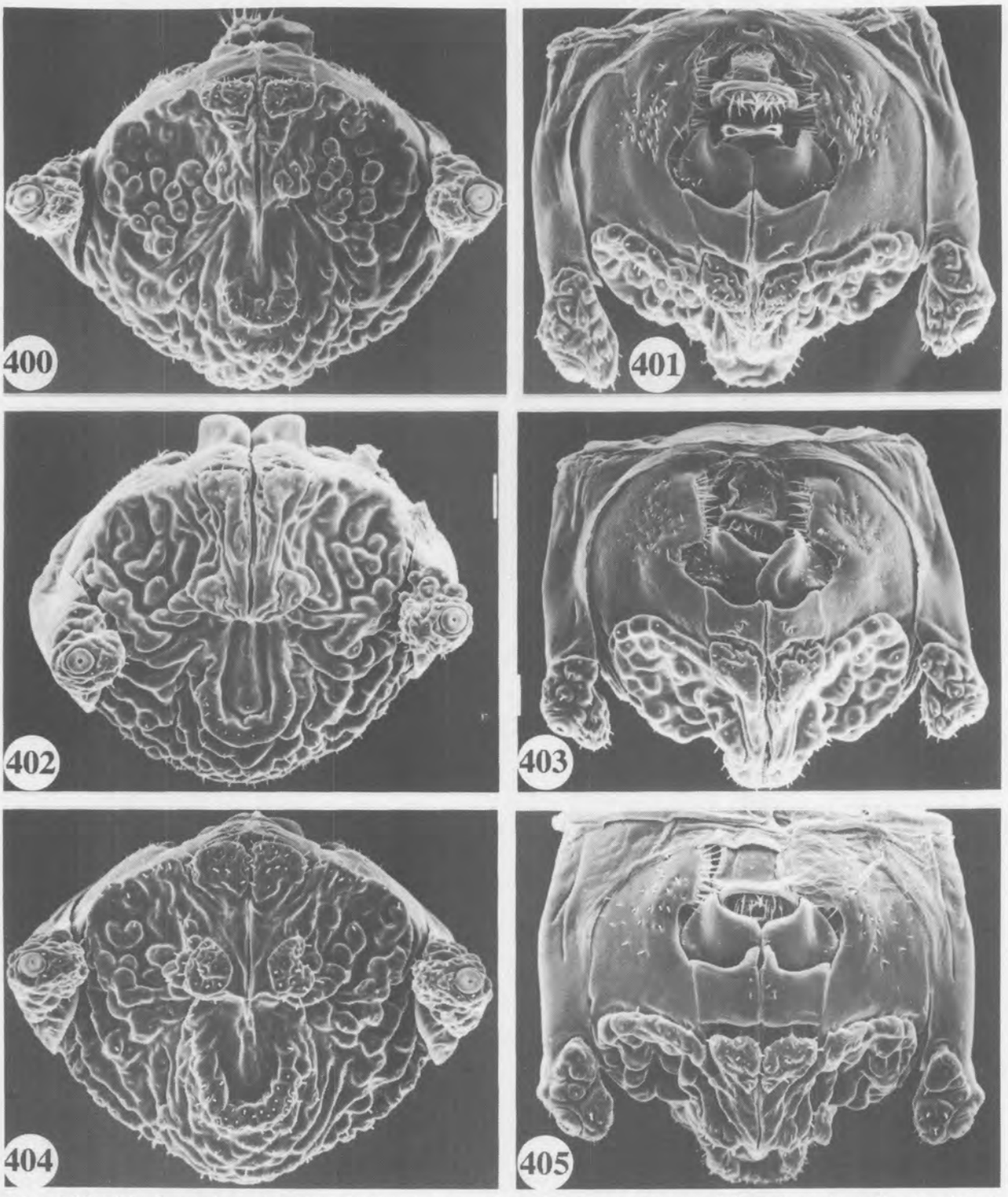
Figs 384-391. Scanning electron photomicrographs of *Dundocoris fuscus* **spec. nov.**. 384-385. Male paratype. 384. Dorsal aspect. 385. Ventral aspect. 386-389. Different aspects of the left paramere (scale bar = 50 μm). 390-391. Pygophore. 390. Caudal aspect. 391. Dorsal aspect.



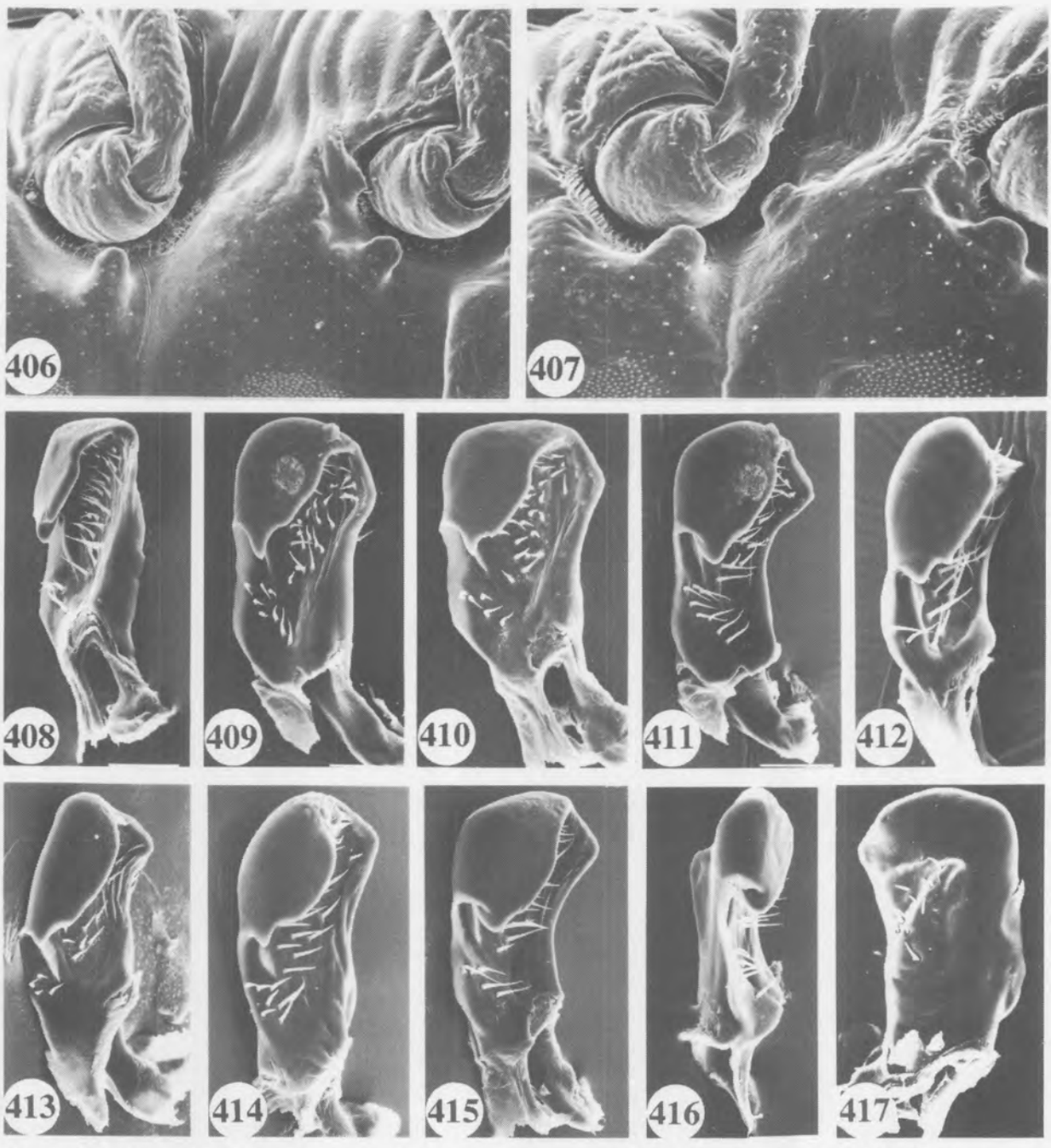
Figs 392-395. Scanning electron photomicrographs of *Dundocoris callani callani Hoberlandt*. 392. Dorsal aspect of male from Scottburgh. 393-394. Dorsal aspects of males from Ngoye Forest. 395. Dorsal aspect of male from Stainbank Nature Reserve.



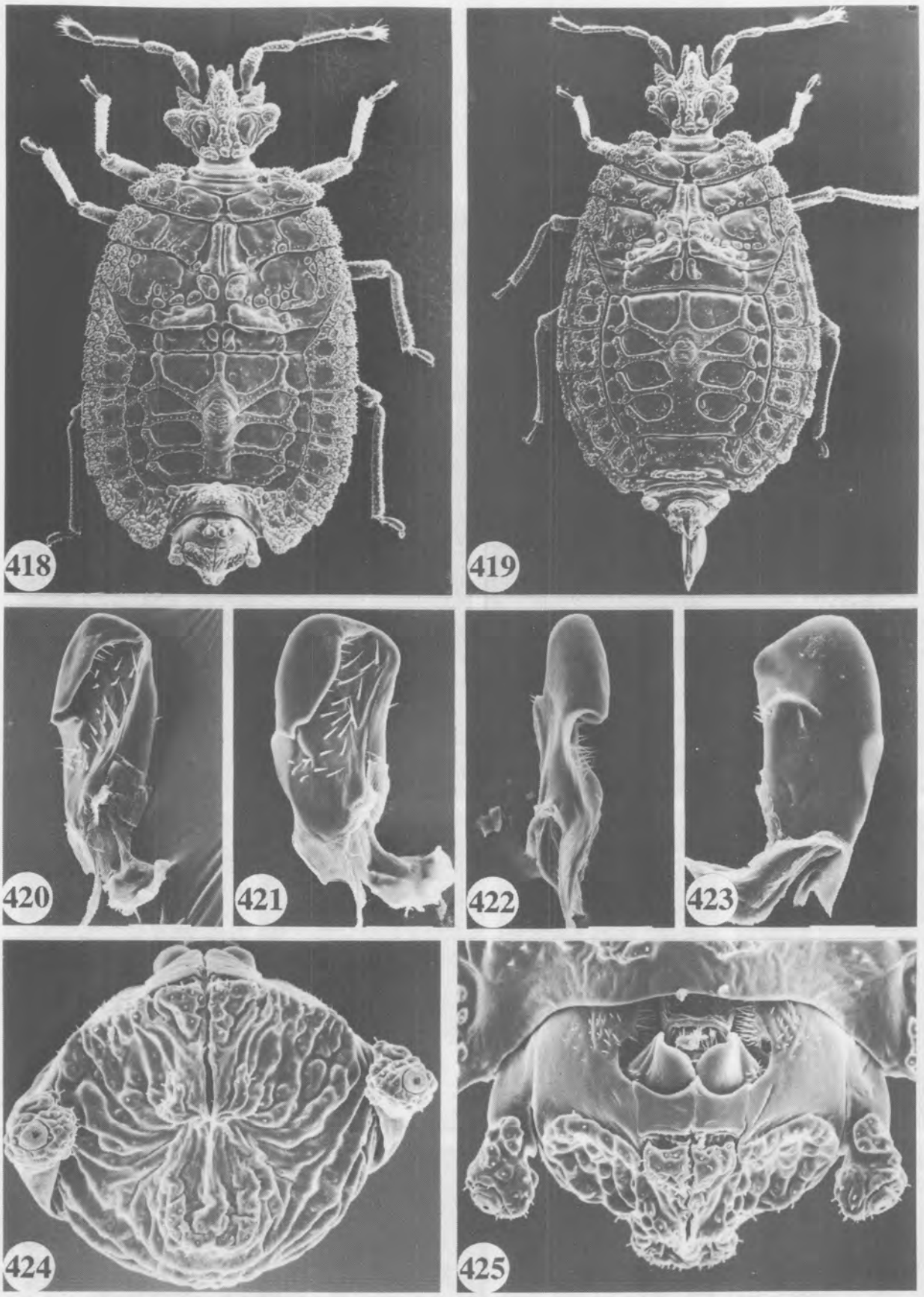
Figs 396-399. Scanning electron photomicrographs of *Dundocoris callani callani* Hoberlandt. 396. Dorsal aspect of male from Port St. Johns. 397. Dorsal aspect of male from Nquaba forest. 398. Dorsal aspect of male from Alexandria forest. 399. Dorsal aspect of female from Ngoye forest.



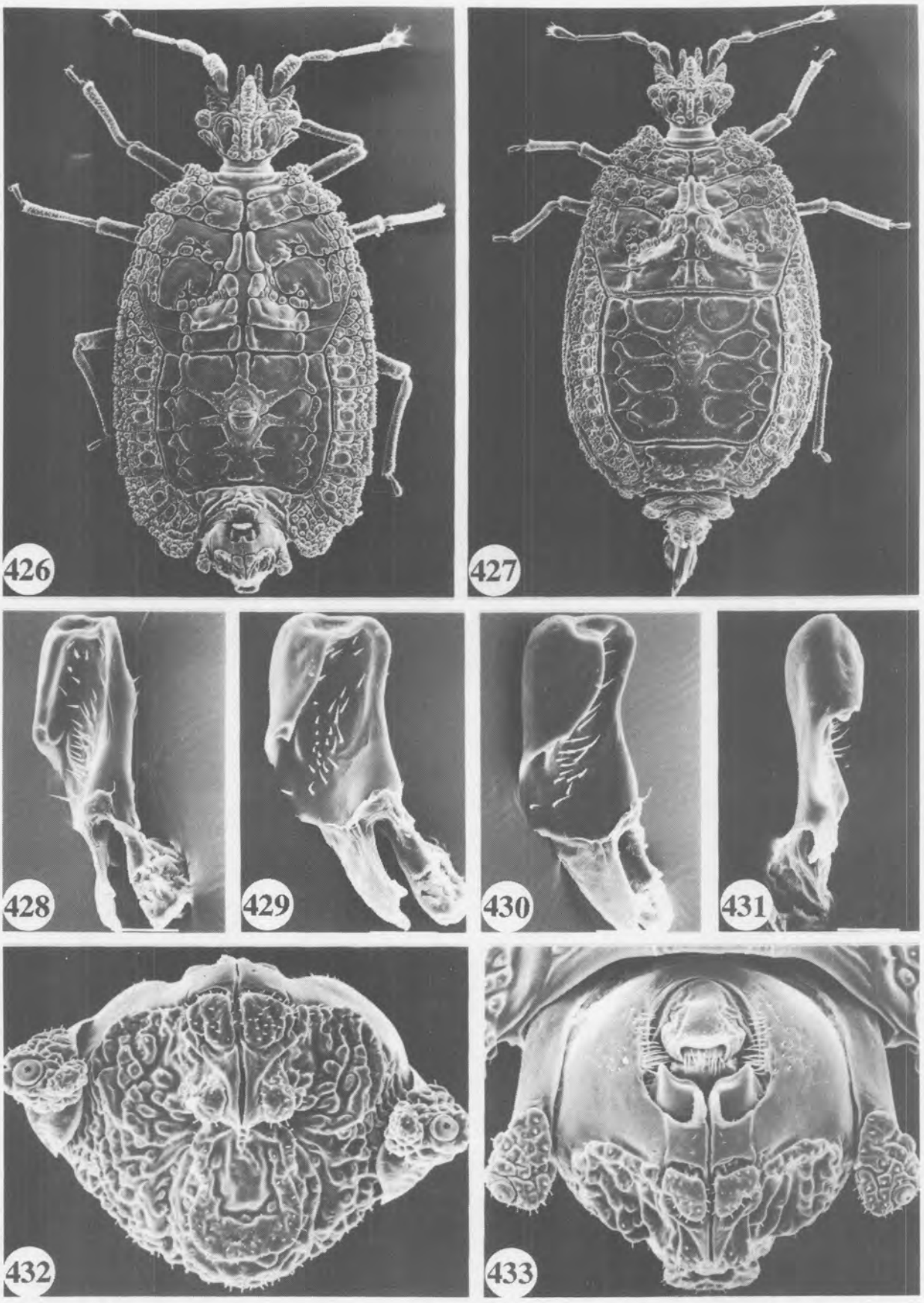
Figs 400-405. Scanning electron photomicrographs of the pygophore of *Dundocoris callani callani* Hoberlandt from different localities. 400-401. From Dwesa forest. 400. Caudal aspect. 401. Dorsal aspect. 402-403. From Scottburgh. 402. Caudal aspect (scale bar = 50 μm). 403. Dorsal aspect (scale bar = 50 μm). 404-405. From Ngoye forest. 404. Caudal aspect. 405. Dorsal aspect.



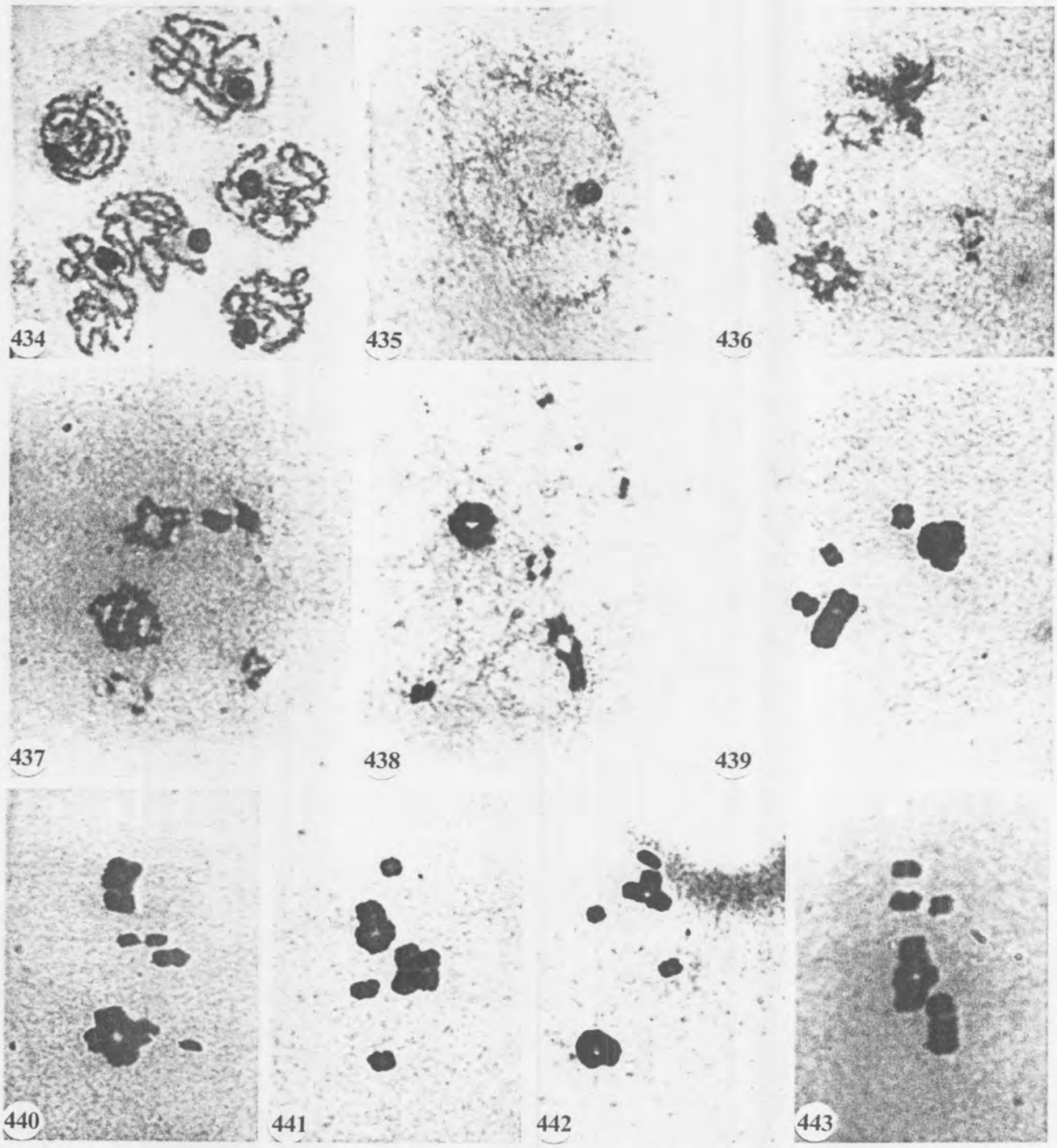
Figs 406-417. Scanning electron photomicrographs of *Dundocoris natalensis* Kormilev and *Dundocoris callani callani* Hoberlandt. 406. Ventral aspect of the metasternum of *D. natalensis* Kormilev showing the absence of the anterolateral tubercle. 407. Same of *D. callani* illustrating the presence of the anterolateral tubercle (arrow). 408-417. Different aspects of the parameres of *Dundocoris callani callani* Hoberlandt from various localities. 408, 410 & 415-417. Scottburgh. 409 & 411. Umdoni Park. 412. Alexandria forest. 413. Ngoye forest. 414. Nquaba forest.



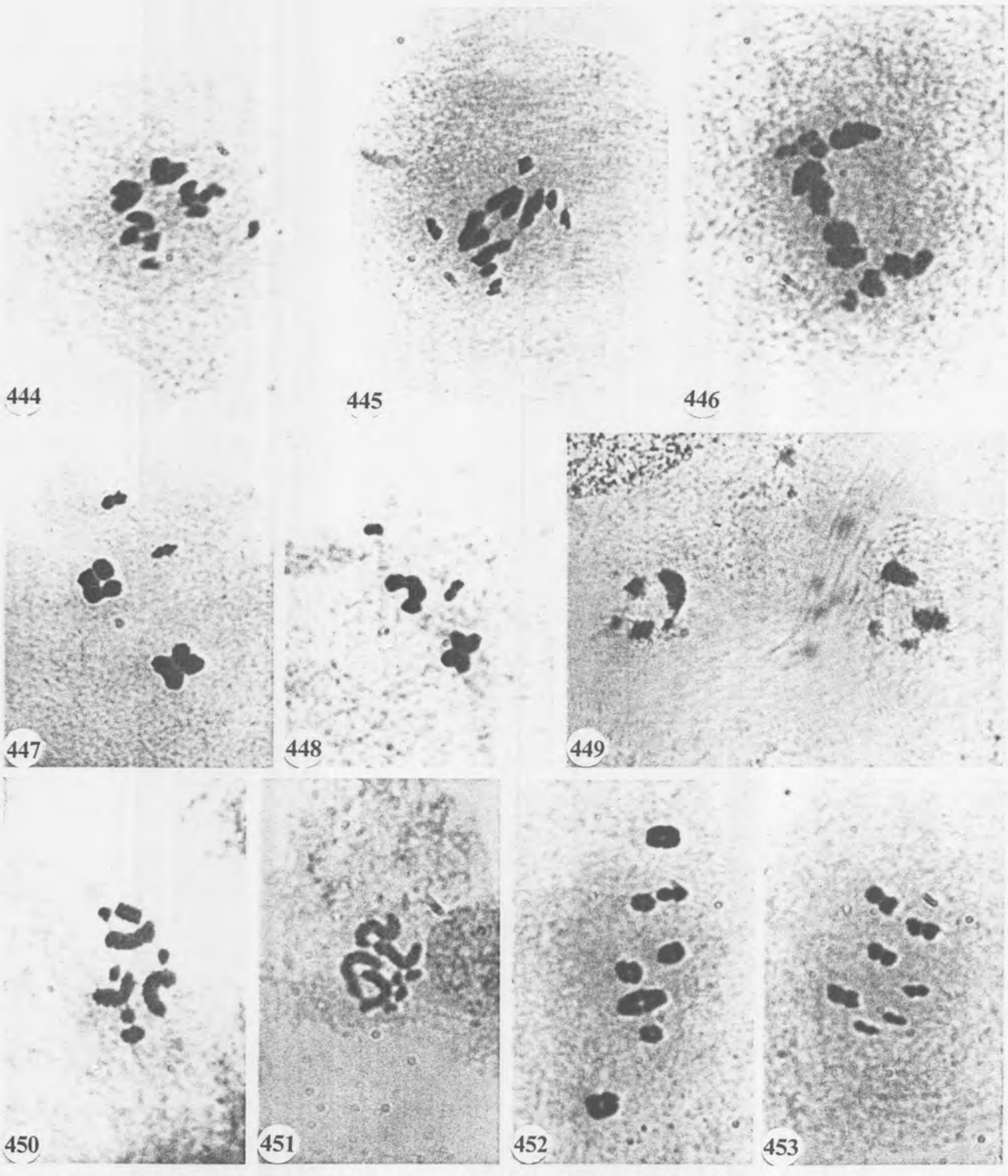
Figs 418-425. Scanning electron photomicrographs of *Dundocoris callani noduliclypeatus* **subspec. nov.** 418. Male paratype, dorsal aspect. 419. Female paratype, dorsal aspect. 420-423. Different aspects of the left paramere (scale bar = 50 μm). 424-425. Pygophore. 424. Caudal aspect. 425. Dorsal aspect.



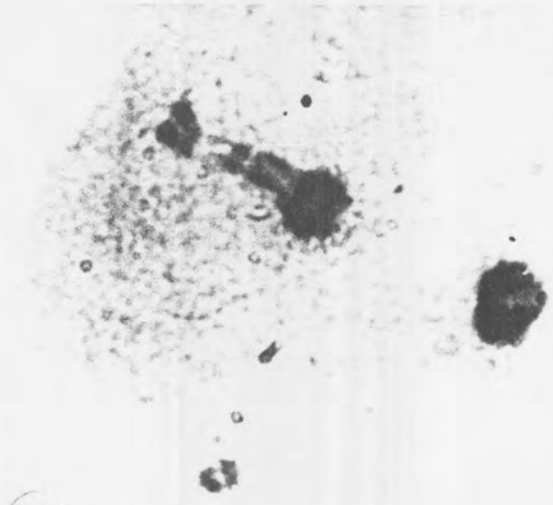
Figs 426-433. Scanning electron photomicrographs of *Dundocoris natalensis* Kormilev. 426. Dorsal aspect of male. 427. Dorsal aspect of female. 428-431. Different aspects of the left paramere (scale bar = 50 μm). 432-433. Pygophore. 432. Caudal aspect. 433. Dorsal aspect.



Figs 434-443. Meiotic stages in *Dundocoris nodulicarinus novenus*. 434. Pachytene. 435. Diffuse stage. 436-437. Diplotene. 438. Diakinesis. 439-443. Metaphase I showing different configurations of the neo-X-Y 'bivalent' and the large autosome.



Figs 444-453. Meiotic stages in *Dundocoris nodulicarinus*. 444-451. *D. nodulicarinus novenus*. 444-446. Anaphase I showing different modes of segregation of the large autosome. 447-448. Metaphase II. 449. Late Anaphase II/Telophase II. 450. Spermatogonial Metaphase. 451. Oogonial Metaphase. 452-453. *D. nodulicarinus nodulicarinus*. 452. Metaphase I. 453. Metaphase II.



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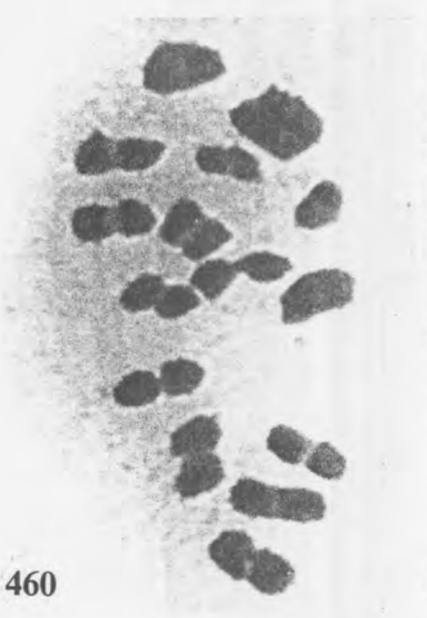
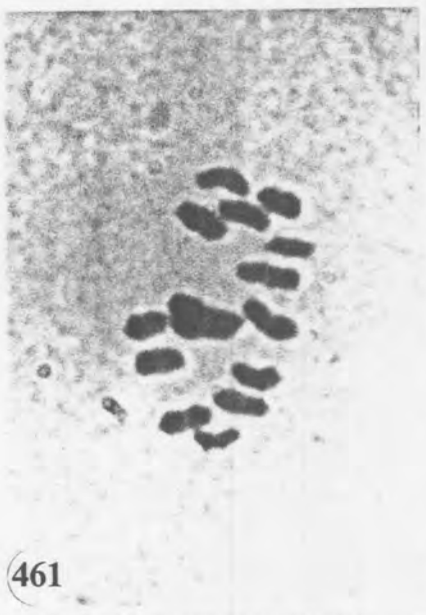
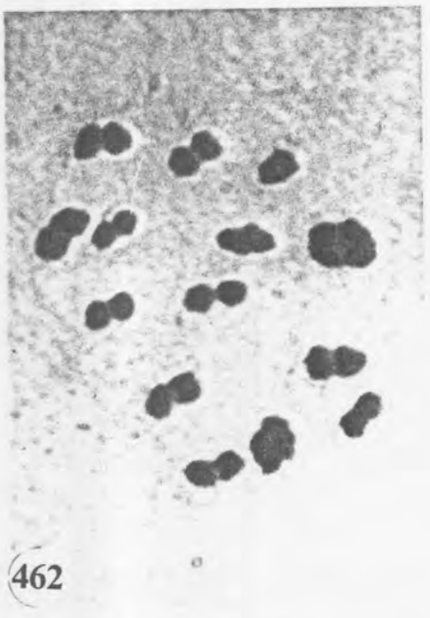
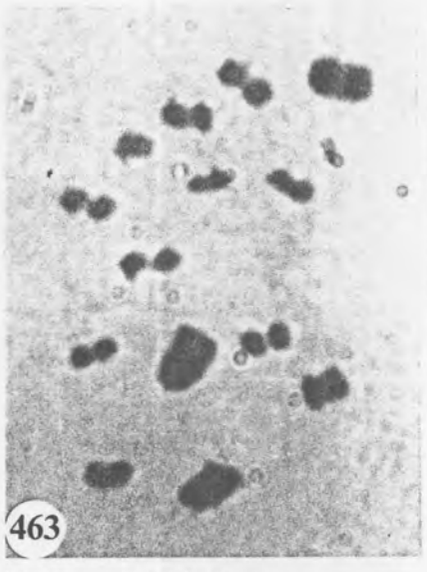
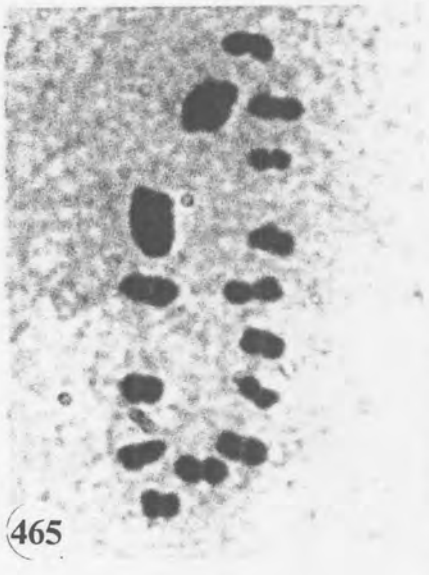
Figs 454-459. Meiotic stages in *Dundocoris nodulicarinus septeni*. 454. Diakinesis showing double crossover in neo-X-Y 'bivalent' and the fusion of the small autosomal pair to the original X- and Y-chromosomes respectively. 455-456. Metaphase I. 457. Metaphase II. 458. Spermatogonial mitosis. 459. Mitosis in female embryo.

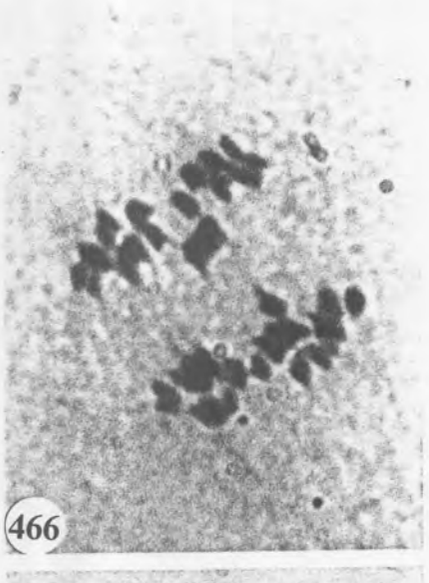


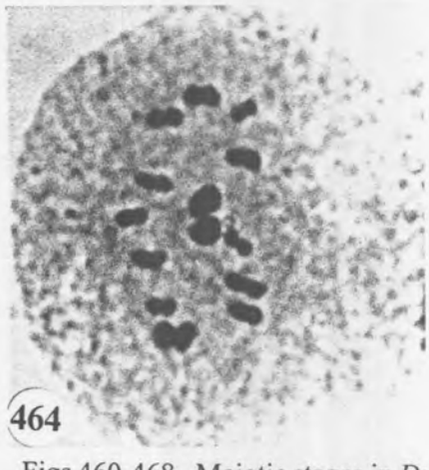


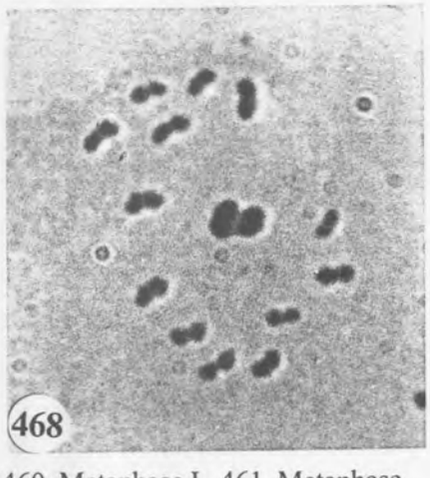




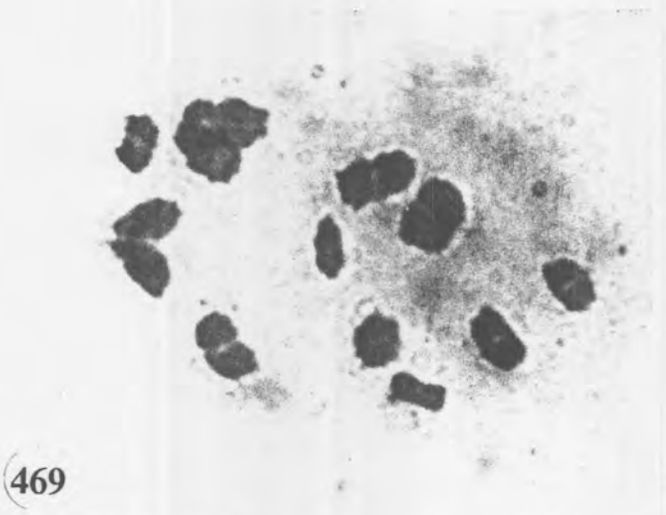


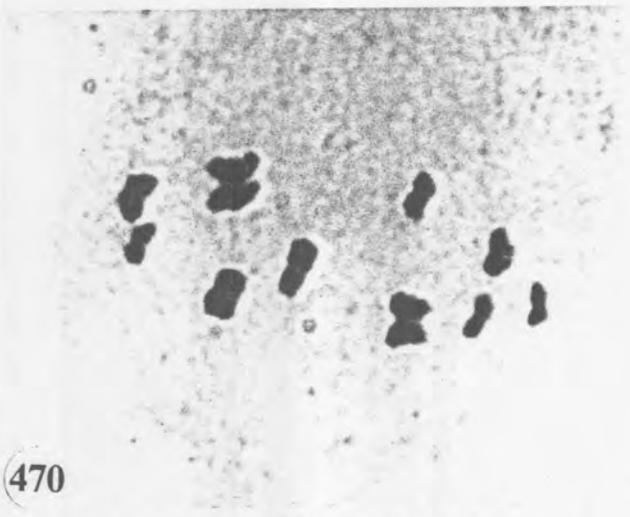


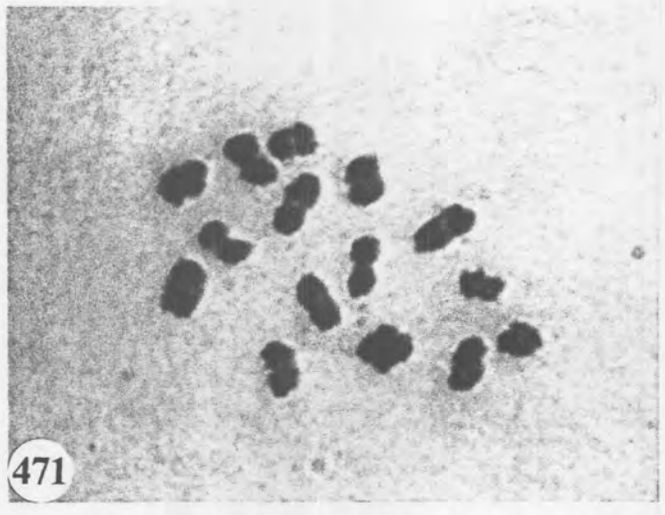


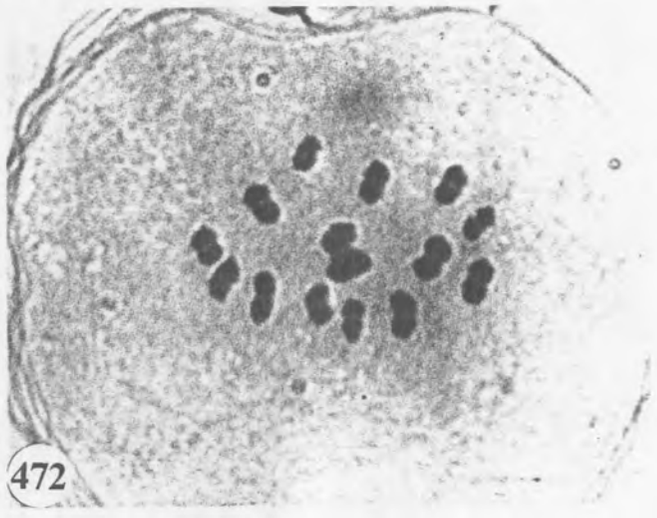


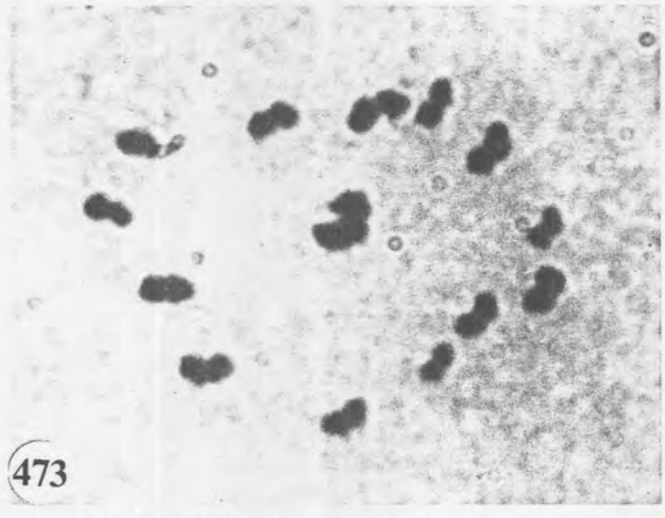
Figs 460-468. Meiotic stages in *Dundocoris* taxa. 460-461. *D. marieps*. 460. Metaphase I. 461. Metaphase II. 462. *D. begemanni*, Metaphase I. 463-464. *D. stuckenbergi stuckenbergi*. 463. Metaphase I. 464. Metaphase II. 465-467. *D. stuckenbergi ngomensis*. 465. Metaphase I. 466. Anaphase I. Note the broadsided movement of the sex chromosomes. 467. Metaphase II. 468. Metaphase II in an undescribed subspecies of *D. stuckenbergi* from Ngoye Forest.

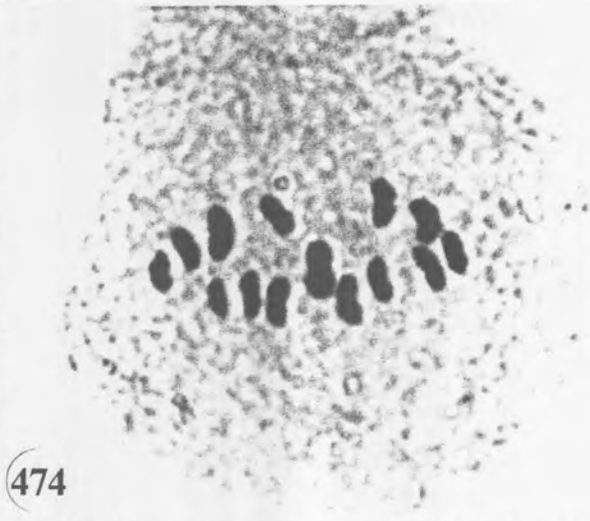




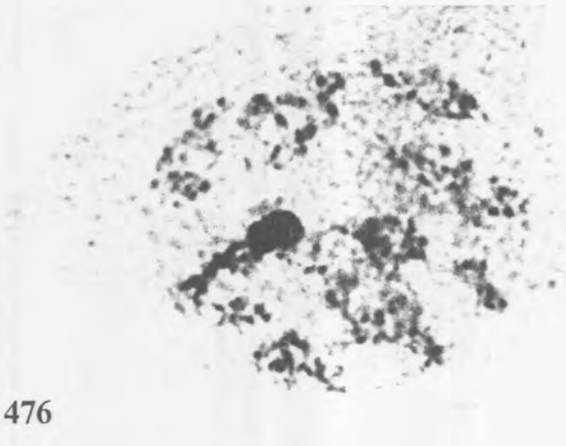


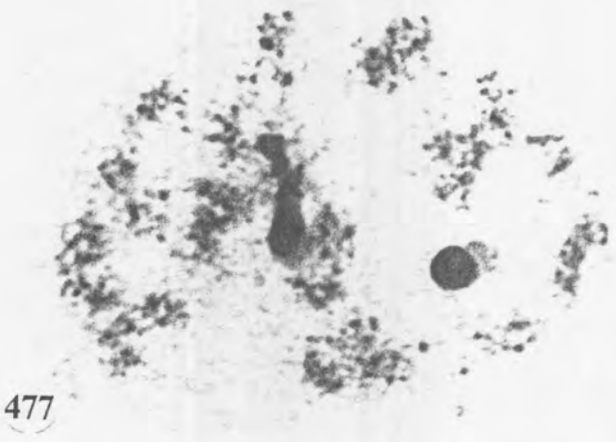


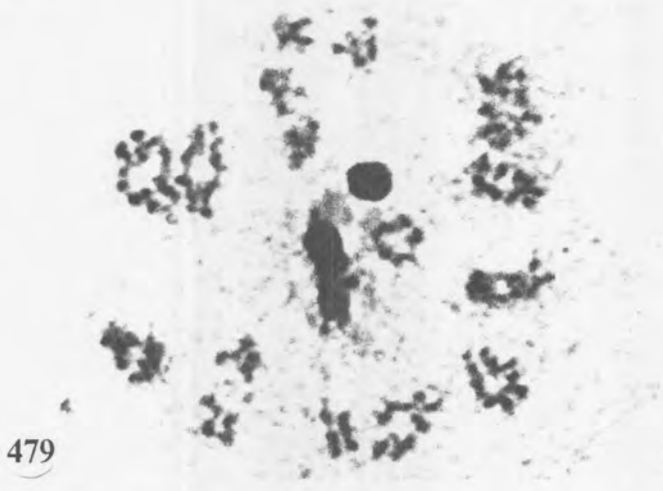




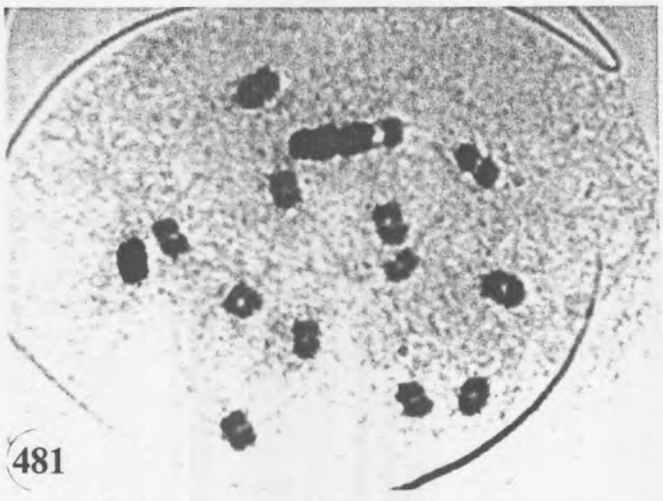
Figs 469-474. Meiotic stages in *Dundocoris* species. 469-470. *D. nigromaculatus*. 469. Metaphase I. 470. Metaphase II. 471-474. *D. flavilineatus flavilineatus*. 471. Metaphase I in a specimen of Ngoye Forest. 472-474. Metaphase II in specimens from different localities. 472. Ngoye Forest. 473. Scottburgh. 474. Mpsheni Forest.

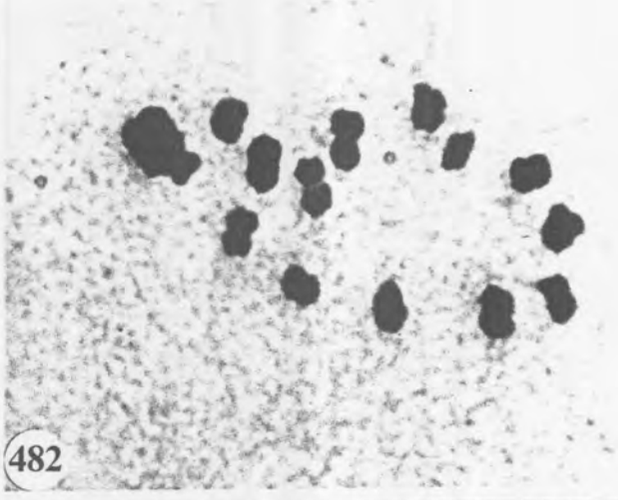


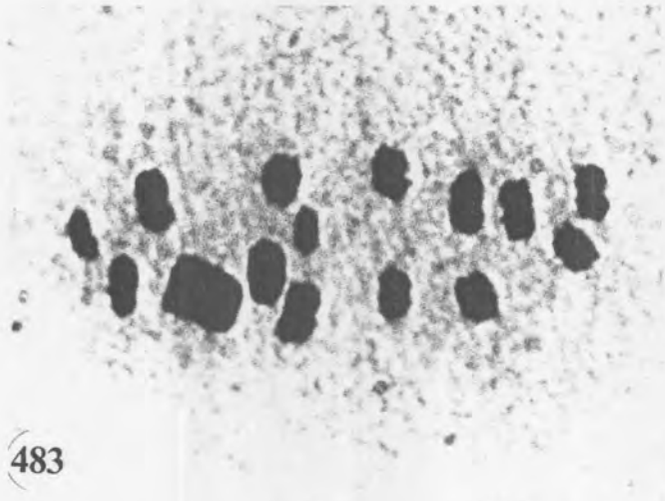


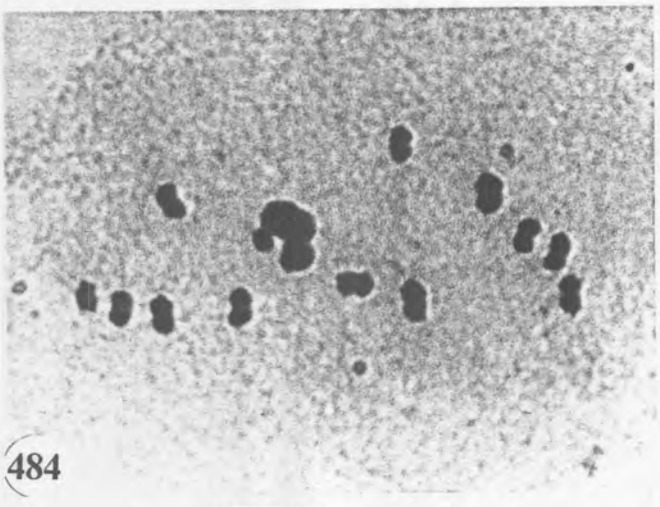


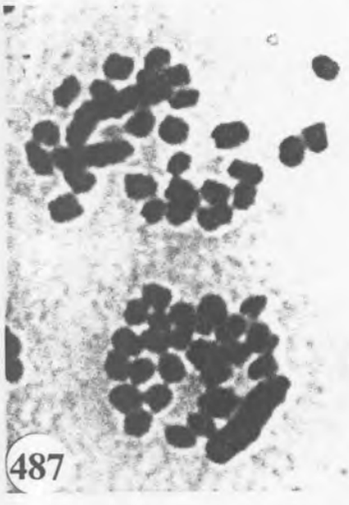
Figs 475-480. Meiotic stages in *Dundocoris flavilineatus ndabeniensis*. 475. Pachytene. 476-478. Diffuse stage. 476. Note the heterochromatic nodulate filametous neo-Y. 477. Note the nucleoli associated with both the original X- and Y-chromosomes. 478. Note the thin filaments connecting the heterochromatic neo-Y and euchromatic neo-X_2. 479-480. Diplotene. 480. Note the autosomal bivalents with interstitial chiasmata.



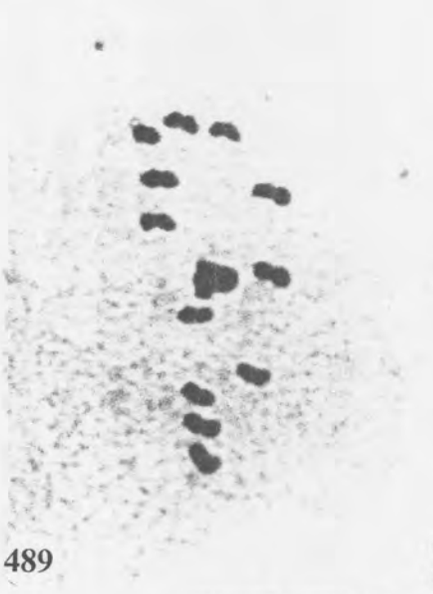


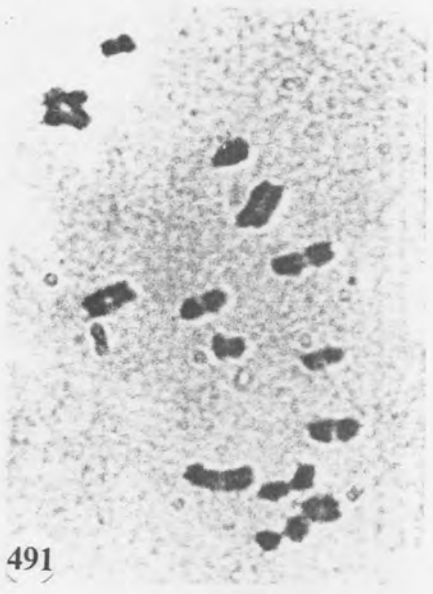


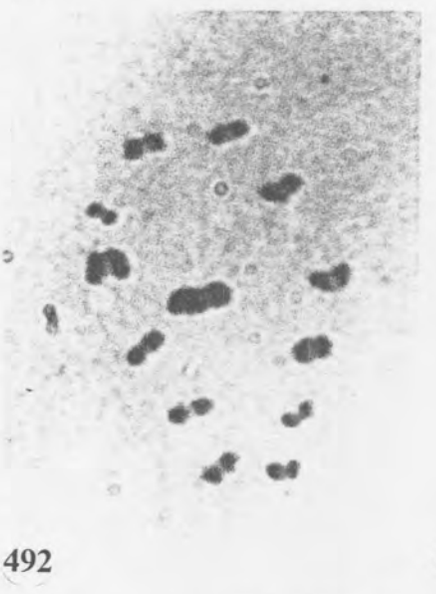


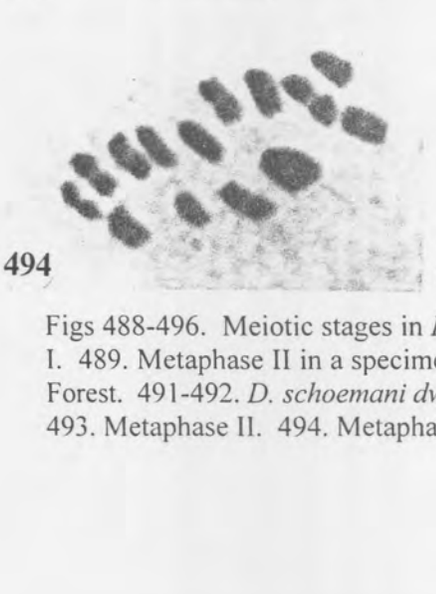


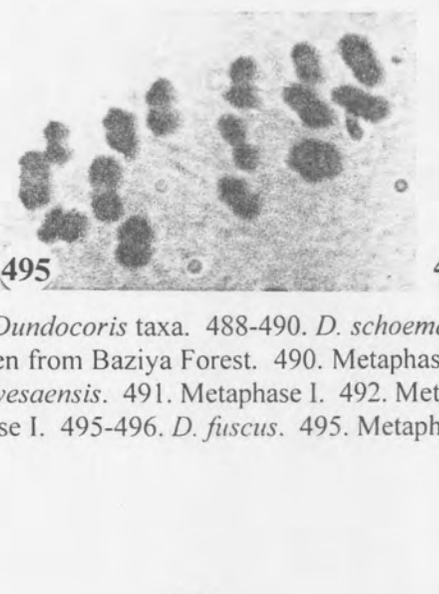
Figs 481-487. Meiotic stages in *Dundocoris flavilineatus ndabeniensis*. 481. Diakinesis. Note the tripartite structure of the neo-Y-X_2 'bivalent'. 482-483. Metaphase I. 482. X_2 attached to neo-Y. 483. X_2 separate from neo-Y. 484. Metaphase II. 485. Tetraploid Metaphase II. 486-487. Spermatogonial mitosis.

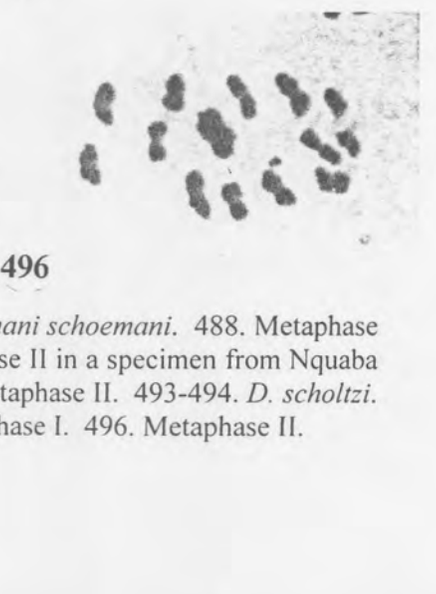












Figs 488-496. Meiotic stages in *Dundocoris* taxa. 488-490. *D. schoemani schoemani*. 488. Metaphase I. 489. Metaphase II in a specimen from Baziya Forest. 490. Metaphase II in a specimen from Nquaba Forest. 491-492. *D. schoemani dwesaensis*. 491. Metaphase I. 492. Metaphase II. 493-494. *D. scholtzi*. 493. Metaphase II. 494. Metaphase I. 495-496. *D. fuscus*. 495. Metaphase I. 496. Metaphase II.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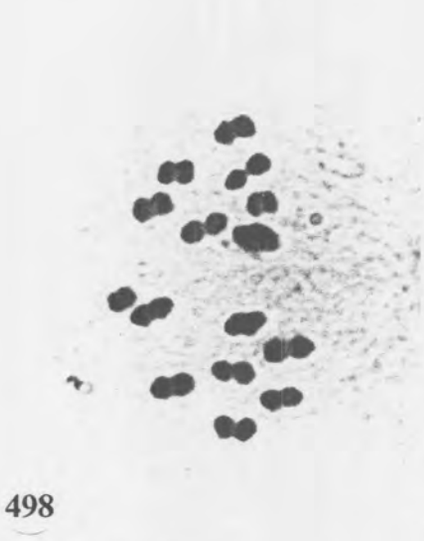
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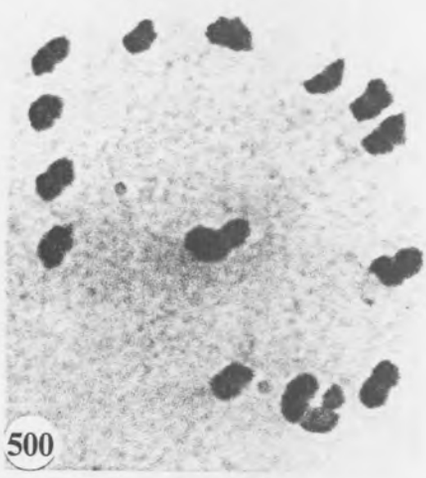
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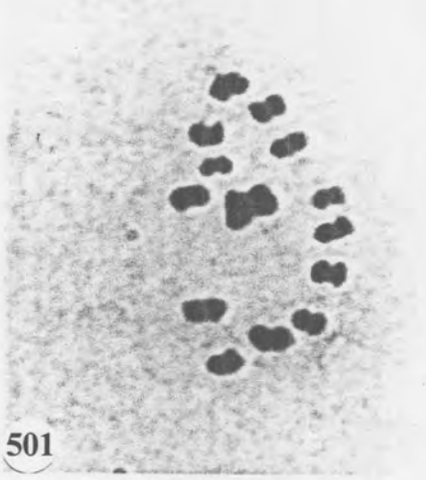
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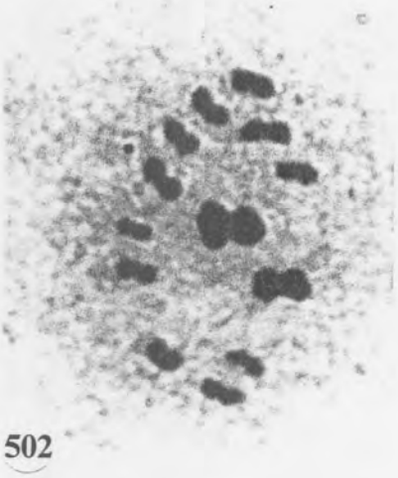
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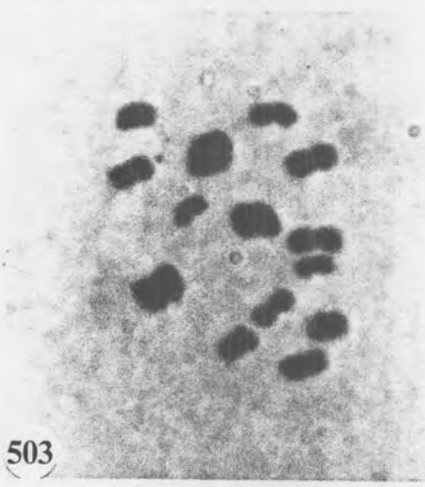
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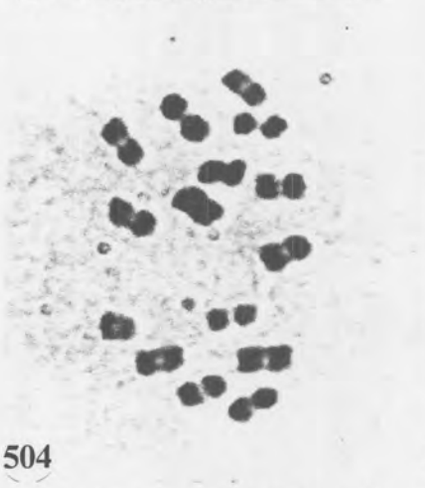
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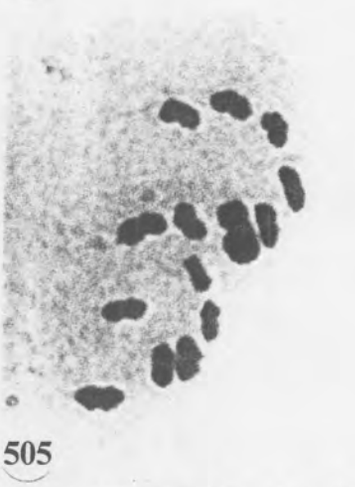
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Figs 497-505. Meiotic stages in *Dundocoris* taxa. 497-501. *D. callani callani*. 497-498. Metaphase I in specimens from different localities. 497. Ngoye Forest. 498. Scottburgh. 499-501. Metaphase II in specimens from different localities. 499. Ngoye Forest. 500. Nquaba Forest. 501. Scottburgh. 502-503. *D. callani noduliclypeatus*. 502. Metaphase II. 503. Metaphase I. 504-505. *D. natalensis*. 504. Metaphase I. 505. Metaphase II.

Chapter 10

GENUS *SPICULANOTUS* GEN. NOV.

10.1 *Spiculanotus* gen. nov. (Figs 508-516).

Type species: *Spiculanotus montanus* spec. nov.

Etymology: Spiculum (L) = arrow point referring to the thin but prominent bar medially on MTg 1 and 2.

Apterous. Body oval, incrustate, shining and granular beneath incrustation. The following description is based on specimens with the incrustation removed.

Head: Slightly longer (not including neck) than wide (across eyes). Genae produced beyond apex of clypeus. Antenniferous lobes prominent, diverging anteriorly. Ocelli absent. Postocular tubercles present. Jugae small, triangular. Vertex with three irregular nodose median ridges; the lateral two curving laterad to follow outline of the oval interocular callosities; the median broader ridge extending nearly to tip of clypeus where it ends in a prominent subapical tubercle. Antennae 4-segmented, more than 1,5x as long as width across eyes, first segment thickest, slightly curved, tapering towards base and slightly towards apex, extending beyond apex of genae; second segment shorter and thinner than segment one, slightly curved basally, gradually thickening towards apex; third segment slender, longest, thinnest, pedicellate, slightly and evenly thickened towards apex; fourth segment fusiform, thicker than segment 2 and 3, conical apex pilose. Labium shorter than head, 3-segmented, only apical 2 segments visible exteriorly, leaving the head through a slit-like atrium. Labrum not discernable. Rostral groove well developed, closed posteriorly. Neck slightly constricted just behind head.

Thorax: **Dorsum**. Pronotum more than 3x as wide as long. Collar prominent with 2(1+1) large tubercles laterally and 2(1+1) smaller tubercles dorsolaterally. Pronotum constricted behind the collar. Lateral lobes granulate, elevated and reflexed so that lobulate propleural margin is visible from above. Disk formed by 2(1+1) irregular excavated shining plates, medially separated by a longitudinal furrow. Pronotum separated from mesonotal by a deep transverse sulcus, posterior margin cut out medially for the reception of the mesonotal median ridge.

Mesonotum shorter and wider than pronotum comprising 2(1+1) transverse rectangular plates separated by a median ridge. The median ridge consist of 2(1+1) longitudinal elevations split by a median suture. The elevations converge and merge posteriorly where they wedge in between the elevations of the metanotal median ridge and forms a thin but prominent bar that reaches posteriorly to the posterior margin of MTg 2. Although this bar appears solid a indication of a transverse suture is present between the metanotum and MTg 1. Lateral lobes granulate, slightly reflexed so that mesopleural margins visible from above. Disk irregularly nodulate, except for thin glabrous areas anteriorly, sublaterally and adjacent to median ridge.

Metanotum medially shorter but sublaterally much longer than mesonotum, laterally well delimited from mesonotum by a sulcus but fused to it on median ridge. Median ridge formed by 2(1+1) suboval or reniform elevations which is separated medially by a depression with the extended bar of the mesonotal elevations in the centre of it. The metanotal ridge slopes laterad and is not well separated from disk. Disk with 2(1+1) fairly narrow glabrous areas, rest irregularly nodulated. Lateral lobes granular, not well delimited from disk. Metanotum fused to MTg 1 although a ill defined, irregular suture may be present laterally and some irregular nodules on posterior margin may indicate the border submesally.

MTg 1 with transverse nodulate, anteriorly sloping ridge on posterior margin for submesal two-thirds; lateral of this it is on about the same level as the metanotum; mesally the ridge ends adjacent to median furrow containing the longitudinal bar. MTg 1 transverse and more or less of constant length.

MTg 2 slightly longer or subequal in length to MTg 1, fused to it although a irregular ill defined suture is usually present laterally; MTg 2 for most part on a lower level than MTg 1; comprising 2(1+1) submedian longitudinal ridges (adjacent to median depression with bar) and 2(1+1) sublateral longitudinal elevations with an uneven surface between them.

Venter. Prosternum with a inverted T-shaped elevation. Meso- and metasterna smooth, each with a median, finely rastrate, slightly depressed oval or circular area.

Legs: Slender, covered with setiferous tubercles. Trochanters fused with femora but line of fusion usually 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**. MTg 3-6 fused to form tergal disk which is only slightly elevated along median line. Carinae separating glabrous impressions well developed, reaching lateral margins of tergal disk. DELTg 1-3 fused. Dorsal hem absent in both sexes and DELTg's unicolorous. DELTg 5-7 increasingly protruding. MTg 7 of males raised medially for the reception of the pygophore; paratergites 8 of males short, conical, not reaching apex of pygophore. MTg 7 of females with a prominent transverse ridge near posterior margin, paratergites 8 produced posteriorly as 2(1+1) semi-acute lobes that nearly reach to level of apex of tergite 9.

Venter. Sternites 1-3 fused; 1+2, 3-6 with slightly depressed, finally rastrate oval areas medially. Intersegmental sutures 3/4, 4/5, 5/6 and 6/7 well developed, reaching lateral margins of body; 6/7 medially produced anteriad in females to accommodate genitalia. VLTg 3-6 delimited by prominent longitudinal sulci. Ventral hem absent in both sexes. Spiracle 2 ventral; 3-4 sublateral, not visible from above; 5-7 lateral and visible from above, 8 subterminal on paratergites.

Genitalia: Visible part of pygophore pyriform, with rugose surface, dorsally with 2(1+1) transverse triangular elevations separated by a cleft which ends slightly above level of paratergites 8; ventral of this a small pit, formed by carinate ridges is usually present. In dorsal view (of part usually obscured by MTg 7) 2(1+1) transverse rectangular pseudophallic styli are present just posteriad of the dorsal visible parts of the parameres. The latter (in dorsal view) placed transversely. Female genitalia similar to those of most Carventinae.

Discussion: *Spiculanotus* is characterized by the medial bar-like elevation on the nota which extends from the posterior margin of the mesonotum to the posterior margin of MTg 2.

It is closely related to *Dundocoris* from which it can be distinguished by the presence of the median bar on the thorax, the carinae on the tergal disk that reaches its lateral margin and are not Y-shaped, the absence of the dorsal hems in females as well as the unicolorous DELTg's and the different appearance of the parameres in dorsal view.

Spiculanotus is also related to *Silvacoris* which also have the median bar on MTg 1 and 2 but can be distinguished from it by its more elongate oval and flatter body form, the different shape and fusion of MTg 1 and 2, the absence of a prominent suture between the metanotum and MTg 1, the smooth mesonotal median ridge and the different shape of the parameres in dorsal view.

10.1.1 *Spiculanotus montanus* spec. nov. Figs 508-516.

Length: ♂ 4,5 - 4,8 mm; ♀ 5,1 - 5,8 mm;

Width: ♂ 2,0 - 2,3 mm; ♀ 2,5 -2,9 mm.

Diagnostic measurements are given in Table 10.1.

Table 10.1. Measurements (in mm) of *Spiculanotus montanus* spec. nov.

STRUCTURE		MALES					FEMALES				
		HT*	N♂	Mean	SD	Range	AT#	N♀	Mean	SD	Range
Total	length	4.69	5	4.65	0.095	4.52-4.78	5.62	5	5.49	0.215	5.18-5.74
	width	2.21	5	2.16	0.074	2.05-2.26	2.75	5	2.70	0.100	2.59-2.86
Head	length	0.90	5	0.88	0.016	0.85-0.90	0.96	5	0.96	0.024	0.94-1.01
	width	0.88	5	0.87	0.016	0.85-0.90	0.94	5	0.93	0.029	0.89-0.97
Pronotum	length	0.48	5	0.48	0.012	0.46-0.51	0.53	5	0.53	0.006	0.52-0.54
	width	1.56	5	1.59	0.045	1.54-1.66	1.76	5	1.75	0.047	1.68-1.82
Tergal disk	length	1.22	5	1.22	0.036	1.16-1.27	1.70	5	1.68	0.047	1.63-1.75
	width	1.42	5	1.40	0.039	1.34-1.44	1.72	5	1.70	0.055	1.61-1.77
Antennal segments	I	0.40	5	0.39	0.006	0.38-0.40	0.42	5	0.42	0.007	0.40-0.43
	II	0.28	5	0.27	0.011	0.25-0.28	0.29	5	0.29	0.008	0.28-0.31
	III	0.45	5	0.45	0.013	0.42-0.46	0.53	5	0.50	0.033	0.44-0.54
	IV	0.28	5	0.28	0.006	0.27-0.30	0.31	5	0.30	0.016	0.28-0.32

* HT = holotype. # AT = allotype.
♦ 4♂♂ 4♀♀ from Bridal Veil Falls and 1♂ 1♀ Grootkloof forest.

Apterous. Male oval, female ovate. Body coated with a yellowish brown incrustation resulting in a greyish-brown appearance of specimens. The following description is based on specimens with the incrustation removed.

Head: Slightly (less than 1,05x) longer (not including neck) than width across eyes. Genae straight. Antenniferous lobes prominent, diverging anteriorly. Postocular lobes small, usually not

reaching level of outer margins of eyes. Subapical tubercle on clypeus very prominent. Antennae about 1,6x as long as width across eyes; first segment extending beyond apex of genae by about two-fifths of its length; relative lengths of segments: 14,6:10:17:10,5.

Thorax: **Dorsum**. Pronotum about 3,3x as wide as long. Lateral lobes coarsely granulate except for a small elevated, reniform glabrous area; lateral margin concave, anterolateral angles rectangularly produced anteriorly to level of anterior margin of collar or little beyond; posterolateral angles produced laterally. Disk irregularly excavated.

Mesonotal median ridge narrow, comprising 2(1+1) parallel longitudinal elevations separated by a narrow median furrow which may be partly obliterated in some specimens; elevations converge and fused posteriorly where they wedge in between elevations of metanotal median ridge, forming a median bar-like elevation that reaches posteriorly to the posterior margin of MTg 2. Disk with narrow glabrous areas adjacent to median ridge as well as anteriorly and sublaterally, the latter ones elevated; rest irregularly excavated and nodulate with a ill defined row of nodules on its posterior margin which may merge with elevations of median ridge. Lateral lobes densely granulate.

Metanotal median ridge comprising 2(1+1) suboval or reniform elevations separated by a median depression containing above-mentioned bar. Disk with glabrous area anteromedially, continuing posteriad sublaterally to form a roughly comma-shaped area, the sublateral longitudinal part is elevated forming a ridge clearly visible in uncleaned specimens; rest of disk irregularly nodulate with an irregular, widely spaced row of tubercles on posterior margin. Lateral lobes granulate.

MTg 1 with 2(1+1) transverse ridges for mesal two-thirds on posterior margin separated by median depression containing the bar; the ridge is usually nodulate but in some specimens the nodulations are fused to form a continuous but uneven surface; lateral third on lower level than metanotum, with uneven surface and irregular nodules. MTg 1 fused with metanotum but an ill defined suture usually present laterally.

MTg 2 usually slightly longer than MTg 1, laterally separated from it by an ill defined suture, medially fused although on a slightly lower level (no abrupt decline usually present); bearing 2(1+1) submedian and 2(1+1) sublateral longitudinal elevations, the former separated by depression containing bar; rest of surface glabrous but uneven.

Venter and legs: As for genus.

Abdomen: **Dorsum**. Tergal disk about 1,15x as wide as long in males and 1,01x in females, only slightly elevated along mid-line. Carinae separating glabrous impressions well developed, sometimes somewhat nodulate near mid-line; reaching lateral border of tergal disk. Surface between carinae and impressions uneven along margins of carinae. Dorsal hem absent in females. Posteroexterior angles of DELTg 5-7 increasingly protruding.

Venter: Spiracle 2 ventral; 3-4 sublateral, 3 about 1½ spiracle widths from lateral margin in males and 2 spiracle widths in females, 4 about a spiracle width from lateral margin in males and about 1½ spiracle widths in females; 5-7 lateral and visible from above; 8 subterminal on paratergites.

Genitalia: Pygophore as in Figs 515-516. Removed parameres as in Figs 511-514.

Chromosome number: 2n (♂) = 16XY.

Habitat and distribution: Evergreen montane forests in the Mpumalanga. The known distribution is shown in Fig. 506.

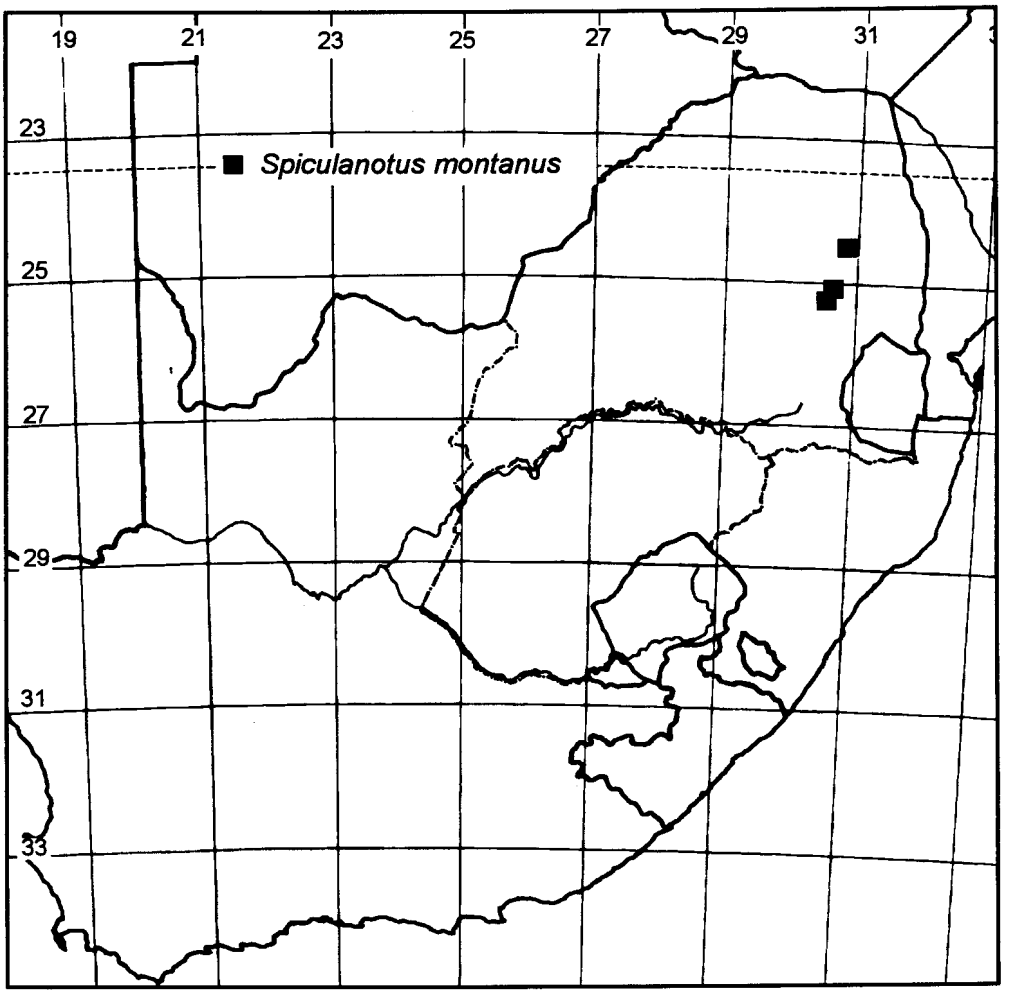


Figure 506. Distribution of *Spiculanotus montanus* gen. et spec. nov.

Etymology: Montanus (L) = from the mountains, referring to its habitat in montane forests.

Discussion: This species is easily distinguishable from all other carventine species as discussed under the genus.

MATERIAL EXAMINED: **SOUTH AFRICA, Mpumalanga**. ♂ Holotype: Bridal Veil Falls, nr. Sabie, 25°05′S 30°43′E, 5.xi.1988, D.H. Jacobs (TMSA); ♀ allotype: ditto (TMSA); 15 paratypes as follows: 2♀♀: Mariepskop forest, nr. Hoedspruit, 24°33′S 30°54′E, 6.x.1981, Liebenberg & Jacobs (DHJS); 1♂: Blyderivierspoort Nature Reserve, nr. Bourke's Luck, 24°39′S 30°52′E, 28.i.1989, D.H. Jacobs (DHJS); 4♂♂ 4♀♀: Same data as holotype (DHJS, TMSA); 1♂: S. Afr, Tvl, Uitsoek, Grootkloof indigenous forest, 25°15′S 30°33′E, 28.ix.1986, E-Y:2294, intercept trap 28d, leg. Endrödy-Younga (TMSA); 1♀: ditto E-Y: 2295, ground-traps, 28 days (TMSA); 1♂: ditto 26.x.1986, E-Y: 2320, sifted forest litter (TMSA); 1♀: ditto, 6.ii.1987, E-Y: 2425, beating in forest (TMSA).

10.2. Cytogenetics of the genus *Spiculanotus*.

At this stage *Spiculanotus* is a monotypic genus with *S. montanus* as its only species, but I am aware of a second, closely related and very similar species that Prof. Dr. Ernst Heiss has collected in Rwanda in central Africa.

10.2.1. *Spiculanotus montanus*. (Figs 507, 517-522).

The chromosome number *S. montanus* is 2n(♂) = 16XY. The localities and numbers of individuals that were cytogenetically studied are presented in Table 10.2. The true and relative chromosome areas for *S. montanus* are presented in Table 10.3 and an idiogram in Fig 507.

Table 10.2. Localities and numbers of individuals of *Spiculanotus montanus* cytogenetically studied.

Locality	Co-ordinates	Date collected	No. of individuals cytogenetically studied
Spiculanotus montanus			
Mariepskop forest, nr. Hoedspruit	**24°33'S 30°54'E**	**4-8/x/1981**	**1**
Bridal Veil Falls, nr. Sabie	**20°05'S 30°43'E**	**5/xi/1988**	**2**

Table 10.3. True and relative chromosome areas of *S. montanus*.

True chromosome areas (μm²) and standard deviation.		Relative chromosome areas (% of total area of autosomes) and standard deviation.
Chromosome	**Mariepskop forest**	**Mariepskop forest**
Individuals	**1**	**1**
Cells	**5**	**5**
A1	**4.40(±0.38)**	**19.17(±1.20)**
A2	**3.74(±0.60)**	**16.16(±0.51)**
A3	**3.58(±0.57)**	**15.49(±0.33)**
A4	**3.40(±0.54)**	**14.72(±0.38)**
A5	**3.13(±0.60)**	**13.47(±0.53)**
A6	**2.54(±0.53)**	**10.93(±0.55)**
A7	**2.32(±0.34)**	**10.05(±0.14)**
X	**2.76(±0.44)**	**11.98(±1.22)**
Y	**1.35(±0.33)**	**5.81(±0.93)**
Autosomes	**23.10(±3.52)**	
All chromosomes	**27.21(±4.18)**	

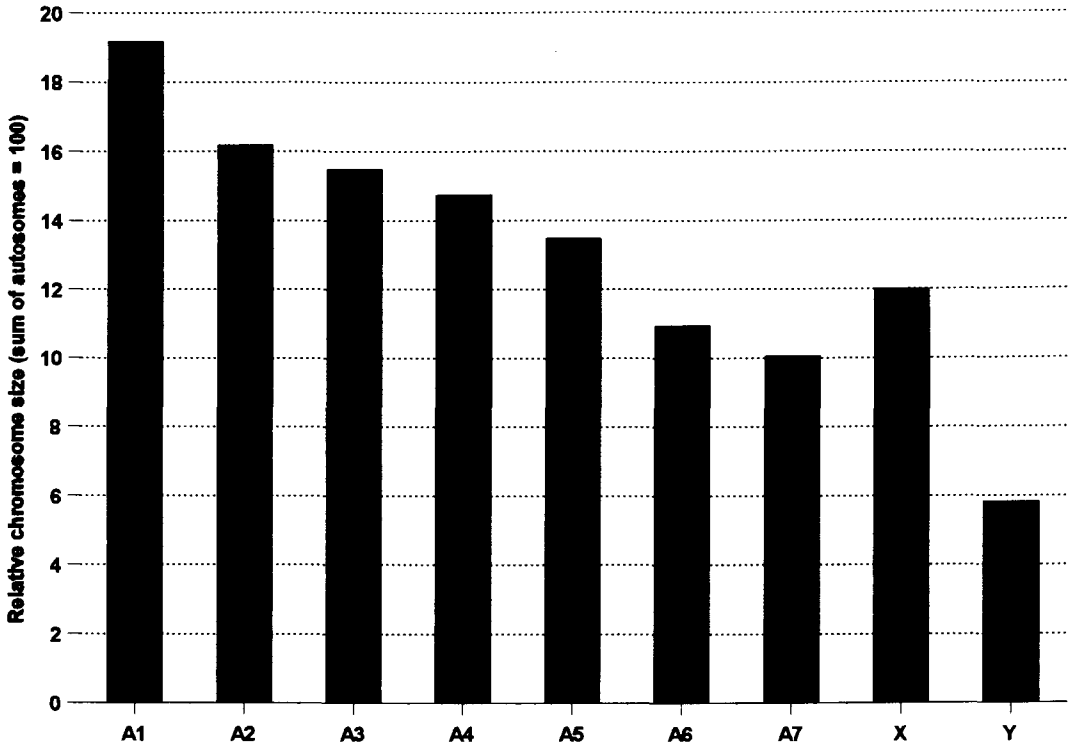


Figure 507. Idiogram of *Spiculanotus montanus*.

The largest autosome (A1) is distinctly larger than A2; A2-A5 form a more or less gradual series, while A6 and A7, which are subequal in size, are markedly smaller than A5. The sex chromosomes are small: the X-chromosome is between A5 and A6 in size while the Y-chromosome is by far the smallest chromosome in the complement, being less than half the size of the smallest autosome.

The course of meiosis is of the regular Carventine type as described for *Adamanotus uncotibialis*. A true diffuse stage is present and at both MI and MII the sex chromosomes lie in the centre of the peripheral ring of autosomes.

S. montanus probably originated from a 14XY ancestor by the fragmentation of one of the autosomes. From the pattern of its karyotype it seems likely that A2 of the ancestor has fragmented to form A6 and A7 of *S. montanus*. The sizes of the latter two chromosomes, however, do not support this hypothesis, but from prophase cells (Fig. 518) it is evident that much heterochromatin is present in its genome and this might have obscured the original size differences. From the results of various workers (Papeschi 1991, Panzera et al. 1995, Panzera et al. 1997) it is evident that if heterochromatic blocks occur in a species (or population), they often tend to be present on all or most of the chromosomes in similar positions, resulting in the general pattern of the karyotype staying the same, but only the sizes of the chromosomes differing.

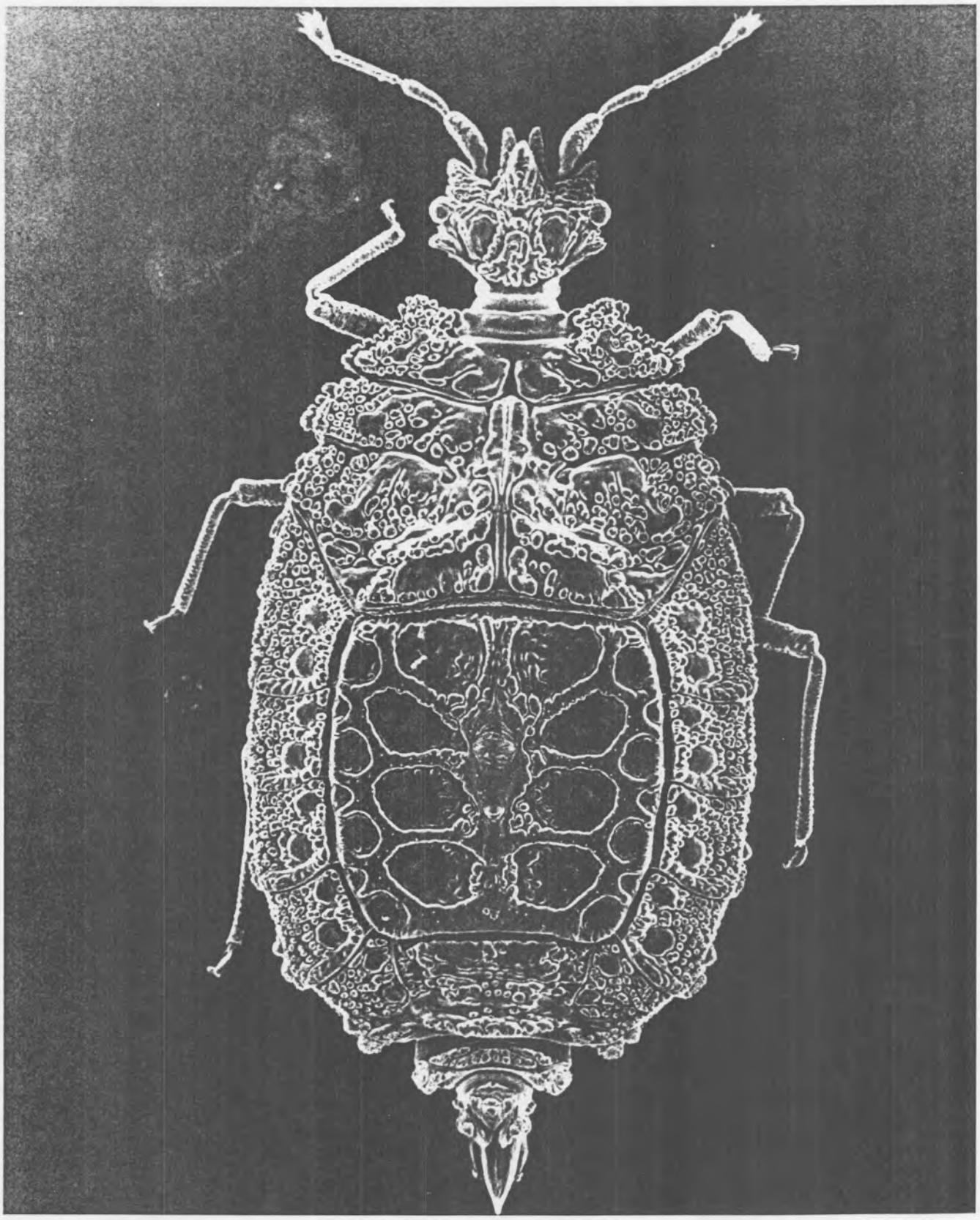
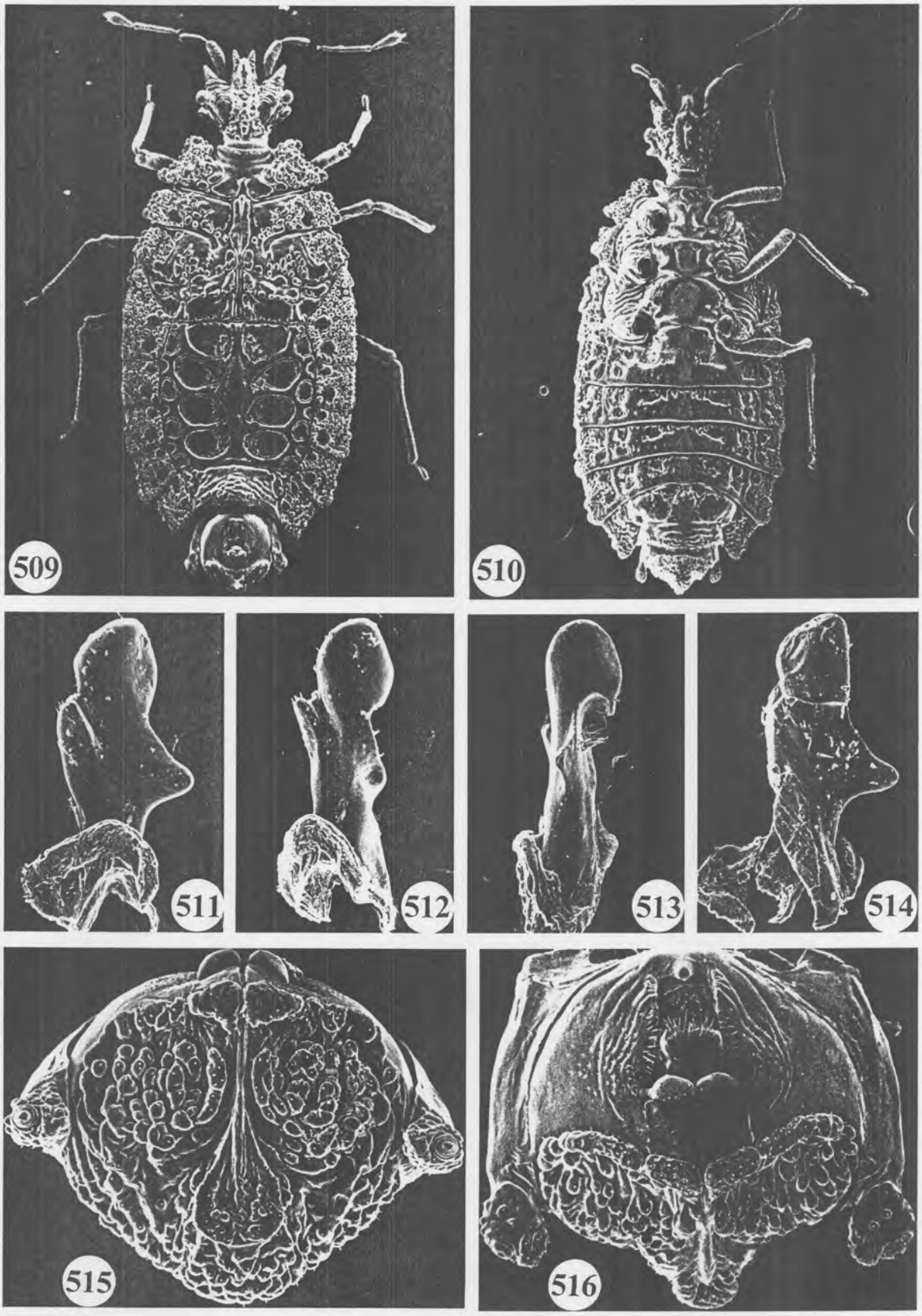
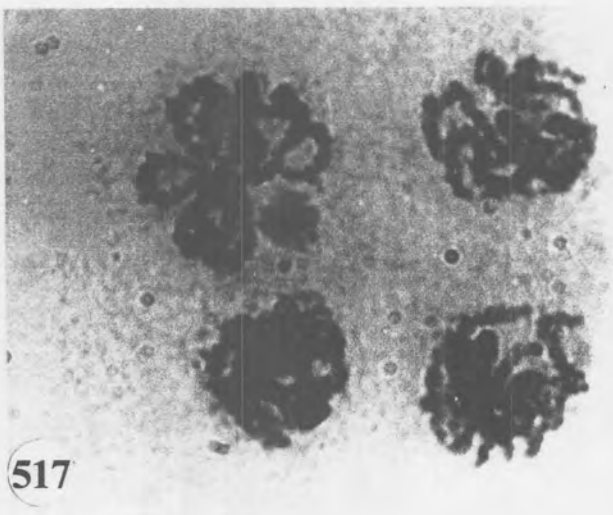


Fig. 508. Scanning electron photomicrograph of *Spiculanotus montanus* **gen. et spec. nov.**, dorsal aspect of female paratype.



Figs 509-516. Scanning electron photomicrographs of *Spiculanotus montanus* **gen. et spec. nov.** 509. Male paratype, dorsal aspect. 510. Male paratype, ventral aspect. 511-513. Different aspects of the left paramere. 514. Mesal aspect of the right paramere. 515-516. Pygophore. 515. Caudal aspect. 516. Dorsal aspect.



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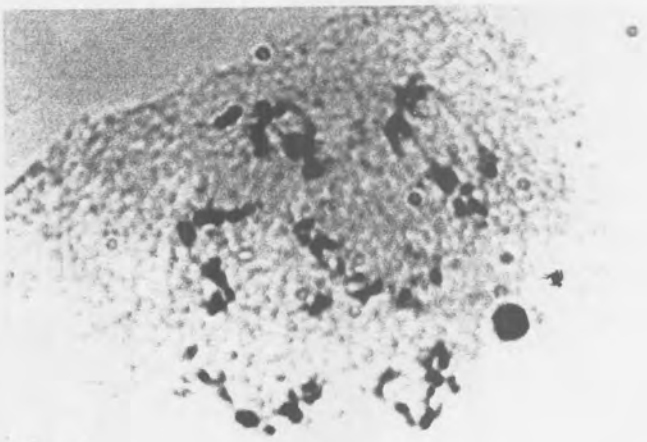

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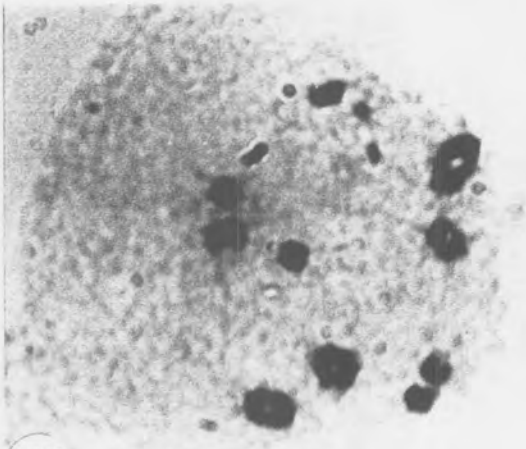

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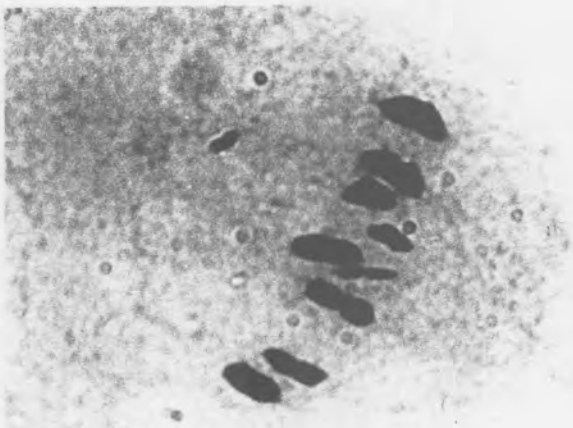

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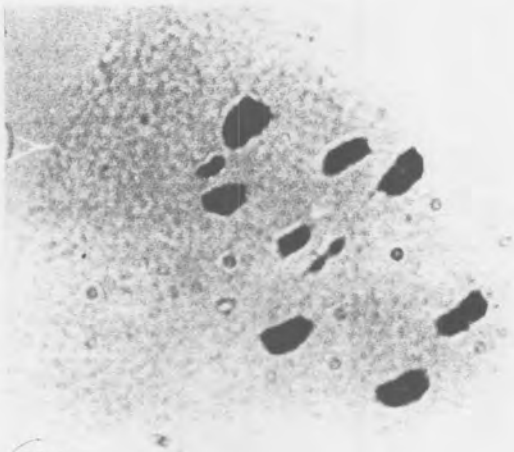

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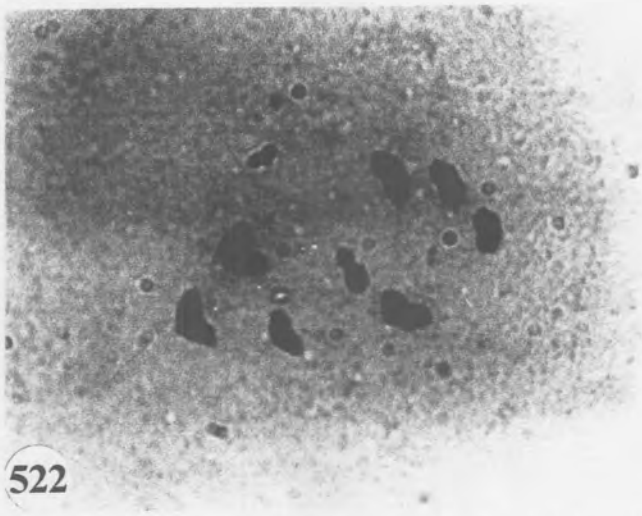

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Figs 517-522. Meiotic stages in *Spiculanotus montanus*. 517. Pachytene. 518. Diffuse stage. 519. Diakinesis. 520-521. Metaphase I. 522. Metaphase II.

Chapter 11

OVERVIEW OF THE CYTOGENETICS OF THE OTHER ARADIDAE SUBFAMILIES

It is evident that karyotype evolution was pronounced in the Carventinae. One is tempted to ascribe this to their flightlessness and accompanying extremely low vagility for it is known that katyotype evolution has been extensive in many such groups in the animal kingdom. White (1978) has also based his concept of stasipatric evolution on the restricted vagility of organisms. It is therefore appropriate to ascertain if the same tendencies also occur in the winged subfamilies of the Aradidae. Chromosome numbers of species representing six of the eight subfamilies are known, only for the Chinamyersinae and Prosympiestinae no data exists. From Table 11.1 it is evident that the chromosome numbers in the other subfamilies also vary considerably.

Table 11.1. Chromosome numbers in the Aradidae subfamilies (except the Carventinae)

Taxon	2n chromosome number and sex chromosome system	Reference
ANEURINAE		
Aneurillus foliaceus	24XY	Jacobs 1986
Aneurus avenius	$27X_1X_2Y$	Grozeva 1997
Breviscutaneurus breviscutatus	16XY	Jacobs 1986
B. helenae	22XY	Jacobs 1986
B. medioscutatus	24XY	Jacobs 1986
Paraneurus brincki brincki	$27X_1X_2Y$	Jacobs 1986
P. brincki marieps	26XY	Jacobs 1986
P. congolensis	$40X_1X_2X_3Y$	Jacobs 1986
P. nodosus	$27X_1X_2Y$	Jacobs 1986
P. ruandae multifarius	32XY	Jacobs 1986
ARADINAE		
Aradus cinnamomeus	$35X_1X_2Y$	Grozeva 1997
A. corticalis corticalis	28XY	Grozeva 1997
A. conspiculus	28XY	Grozeva 1997
CALISIINAE		
Calisius africanus	14XY	Jacobs (unpublished)
ISODERMINAE		
Isodermus gayi	$23X_1X_2Y$	Ueshima 1963

Taxon	2n chromosome number and sex chromosome system	Reference
MEZIRINAE		
Brachyrhynchus sp. nr. *furcatus*	$45X_1X_2X_3X_4Y$	Jacobs (unpublished)
B. germari	26XY	Jacobs (unpublished)
B. sp. 1	14XY	Jacobs (unpublished)
B. sp. 2	22XY	Jacobs (unpublished)
B. sp. 3	24XY	Jacobs (unpublished)
B. sp. 4 (from Hawaii)	24XY	Jacobs (unpublished)
B. sp. 5	$27X_1X_2Y$	Jacobs (unpublished)
B. sp. 6	48XY	Jacobs (unpublished)
Dysodius lunatus	$31X_1X_2Y$	Schrader 1947
Mezira pacifica	$27X_1X_2Y$	Ueshima 1963
Neuroctenus caffer	18XY	Jacobs (unpublished)
N. sp. 1	20XY	Jacobs (unpublished)
N. sp. 2	24XY	Jacobs (unpublished)
Stelgidocoris minutus	24XY	Jacobs (unpublished)
Strigocoris pubescens	36XY	Jacobs (unpublished)

11.1 **Aneurinae.** (Figs 523-532).

The Aneurinae is a cosmopolitan subfamily that contains about 150 described species. The chromosome numbers of most of the South African species and one European species are known and they vary between 16XY and $40X_1X_2X_3Y$. The ten taxa that were studied belong to nine species and four (or three as I suspect that *Aneurus avenius* may belong to *Paraneurus*) genera. No real pattern emerges but three taxa have $2n = 27X_1X_2Y$ and one 2n = 26XY. If we assume that 14XY is the ancestral number for the Aneurinae, then they could have arisen by chromosome doubling as was also postulated for some genera of the Carventinae (refer to 12.1.2 for a more detailed discussion).

Paraneurus congolensis with $2n = 40X_1X_2X_3Y$ is of particular interest. The Y-chromosome is by far the largest chromosome in the complement, while the three X-chromosomes collectively are about the same size. At MI the Y-chromosome orientates perpendicular to the spindle axis and at AI it moves broadsided to the poles (Fig. 528). During MII it also orientates perpendicular to the spindle axis with the three X-chromosomes in a row along its long axis (Fig. 527). *P. congolensis* could have originated from a 14XY ancestor by means of chromosome tripling, but if it happened by means of 'chromatid autonomy' (Schrader & Hughes-Schrader 1958) it means that each chromatid must have been at least

trineme and not unineme as generally accepted (refer to discussion at 12.1.2.2). The other possibilities are that it happened by fragmentation of chromosomes or by polyploidy as Thomas (1996) proposed.

All the taxa of *Paraneurus* have high chromosome numbers (26XY - $40X_1X_2X_3Y$) while the three *Breviscutaneurus* species have lower numbers (16XY - 24XY).

11.2 **Aradinae**

The Aradinae is a cosmopolitan subfamily, but more than 75% of its 220 described species occur in the Holarctic region. More than 90% of the species belong to the genus *Aradus*. The chromosome numbers of only three species of Aradinae, all belonging to *Aradus*, are known. Two of them have 2n = 28XY (*A. corticalis* and *A. conspiculus*)and the third 2n = $35X_1X_2Y$ (*A. cinnamomeus*). From the figures in Grozeva (1997) it seems as if the autosomes of *A. cinnamomeus* form a gradual size series, while some of the autosomes are distinctly larger than the others in *A. corticalis* and *A. conspiculus*. Both sex chromosomes in *A. conspiculus* and the Y-chromosome in *A. cinnamomeus* seem to be larger than all the autosomes, but in *A. corticalis* both the sex chromosomes seem to be of the same size as the second or third largest autosome. When Grozeva (1997) states about *A. corticalis*: "The sex chromosomes are nearly the smallest autosomal bivalents" (sic) she obviously did not take into account that they are monovalents, while the autosomes are bivalents at MI or chromatids and not chromosomes at MII.

Too little data is available and too few species have been studied to draw any conclusions about the ancestral chromosome number and karyotype evolution of the Aradinae.

11.3 **Calisiinae**

The Calisiinae is a cosmopolitan subfamily that contains six genera and about 100 described species that are predominantly of Australian distribution (about 55 species). About 90% of the described species belong to the genus *Calisius*. The chromosome number of only *Calisius africanus* is known and is 2n = 14XY. This karyotype could present the ancestral karyotype of the Aradidae and of the Pentatomorpha. The six autosomes gradually decrease in size, although the smallest autosome is set apart by a small step in the series. The sex chromosomes are subequal in size, slightly larger than the largest autosome.

11.4 **Isoderminae**

The Isoderminae is a small subfamily that includes a single genus with six species. Five of them occur in Australia and New Zealand and one in Chile. The chromosome number of only *Isodermus gayi*, the South American species is known: 2n = $23X_1X_2Y$.

11.5 **Mezirinae** (Figs 533-541).

The Mezirinae is the subfamily with by far the largest number of species: about 1100 species belonging to about 130 genera. It is cosmopolitan, but the Holarctic region is poorly represented (only about 35 species). The chromosome number of 15 species belonging to six genera is known. The chromosome numbers range from 2n = 14XY to 48XY.

The genus *Brachyrhynchus* (eight species studied) exhibits the widest range of chromosome numbers for a single genus in the Aradidae, having diploid numbers from 2n = 14XY to 48XY. Furthermore it has a species with a $X_1X_2X_3X_4Y$ sex chromosome system - the most X-chromosomes thus far in the Aradidae. Various authors (Usinger & Matsuda 1959, Kormilev 1971, Monteith 1997) have stressed the need for a critical review of the *Mezira* - *Brachyrhynchus* complex on a world basis, as it is certainly composite and should be divided in several genera. It is thus possible that the variation in chromosome numbers actually reflects the heterogeneous nature of the genus.

The 14XY species exhibit the typical hypothetical ancestral karyotype with the autosomes forming a gradual size series and the sex chromosomes being smaller than the largest autosome. The existence of this chromosome number and karyotype in the Mezirinae supports the idea that 14XY is also the ancestral number for the subfamily.

In *B. germari* (26XY)(Fig. 535) the autosomes form a gradual size series, while both sex chromosomes are larger than the largest autosome. In the $27X_1X_2Y$ species (Fig. 536) the autosomes also form a gradual size series, while all three sex chromosome are smaller than the largest autosome. In the South African 24XY species (Fig. 534) the largest autosome is distinctly larger than A2, indicating that it may be the fusion product of two autosomes, while the sex chromosomes are subequal in size to the large autosome. In the Hawaiian 24XY species the autosomes form a gradual size series and the X-chromosome is larger than the largest autosome, while the Y-chromosome is subequal in size to it. In the 22XY species (Fig. 533) one autosome is much larger than the other autosomes that form a gradual size series. Both sex chromosomes are much larger than the latter autosomes, but smaller than the large autosome. The large autosome is probably the product of the fusion of three autosomes. In the $45X_1X_2X_3X_4Y$ species (Fig. 537) three or four of the autosomes are markedly larger than the others, the Y-chromosome is about the size of the largest autosome, and all four X-chromosomes are smaller than the smallest autosome. In the 48XY species (Fig. 538) both sex chromosomes are very large, about three times as large as the largest autosome.

The three *Neuroctenus* species are interesting considering that the 24XY species (Fig. 541) have one autosome, the 20XY species (Fig. 520) have three and the 18XY species (*N. caffer* - Fig. 539) have four autosomes that are distinctly larger than the rest of the autosomes. In all three species the X- and Y-chromosomes are subequal in size and smaller than the large autosomes, but larger than the small autosomes. The karyotypes of these species could have arisen by the repeated fragmentation of

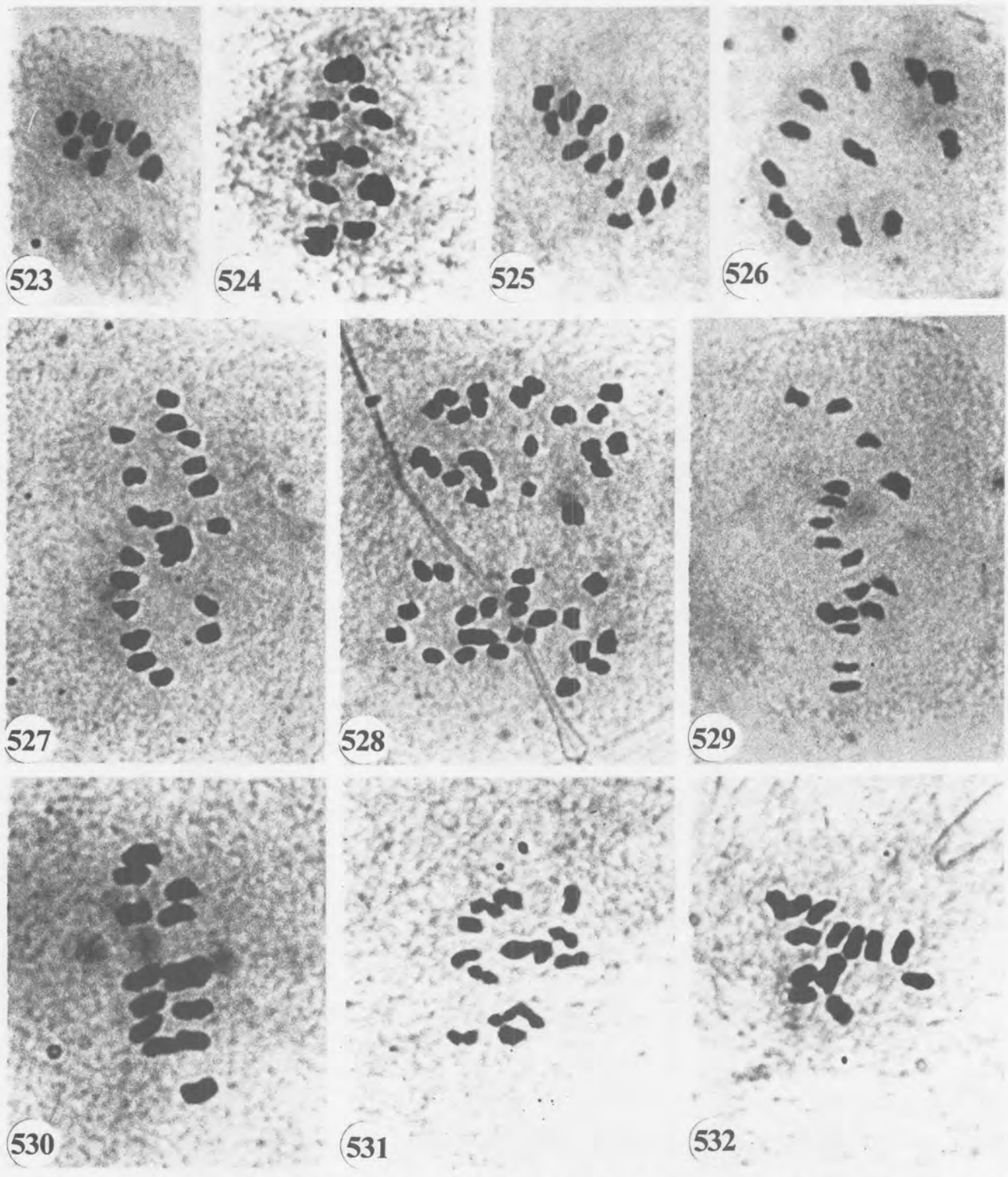
autosomes of a 14XY ancestor or by the repeated fusion of autosomes of a 26XY ancestor. I prefer the latter option because fusions seem to be predominant in the Aradidae and in the case of the 22XY *Brachyrhynchus* species it is clear that it originated by fusion from a 26XY ancestor.

11.6 **Discussion**

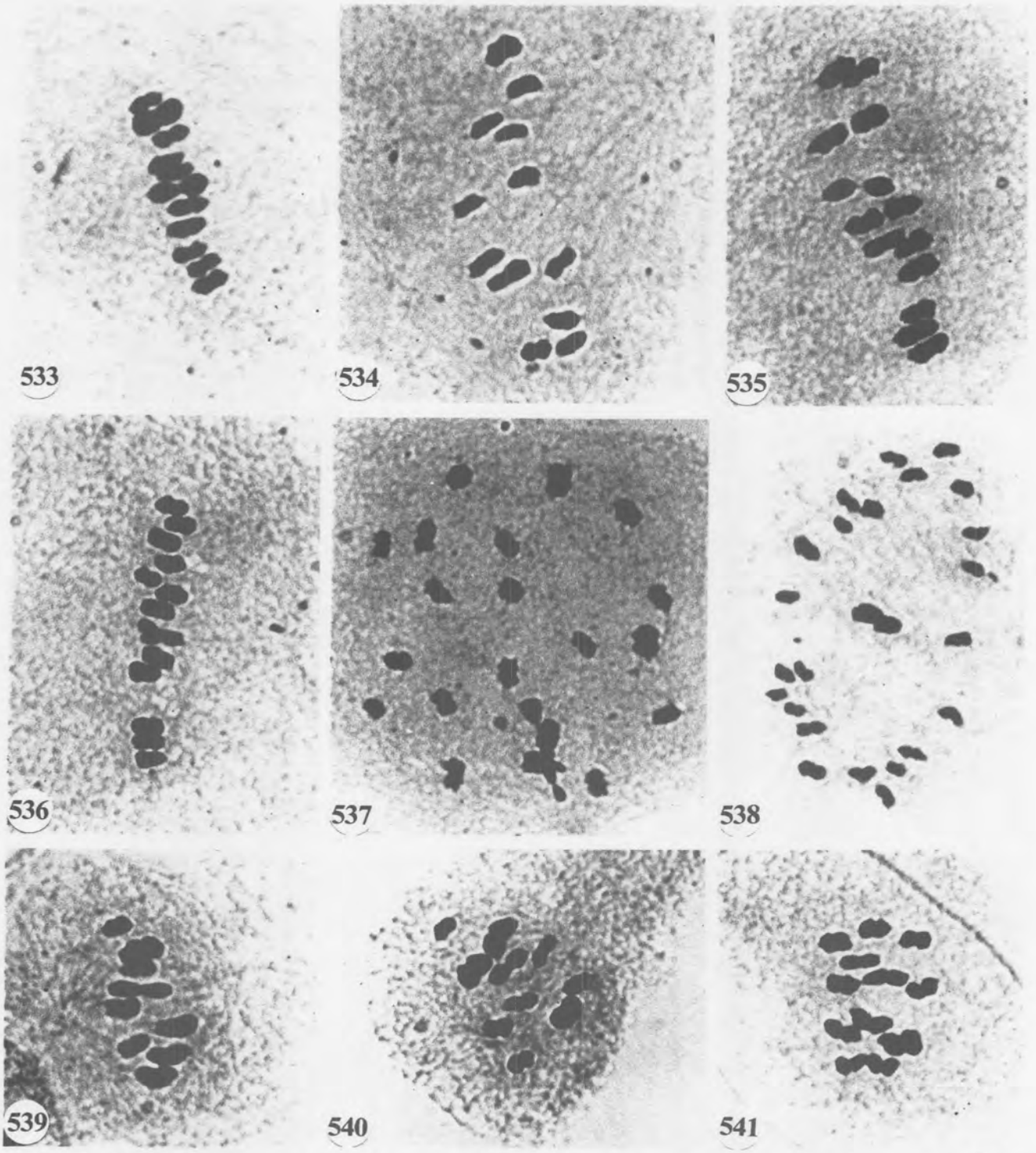
From the above it is obvious that the chromosome numbers in the other subfamilies are just as varied, if not more so, than in the Carventinae. The extremely low vagility of members of the latter subfamily alone can thus not be accountable for its karyotype evolution. Most winged Aradidae, except perhaps the Calisiinae, live subcortically on dead branches of trees. Here they lay their eggs and go through their life cycle rapidly, building up large colonies to exploit their temporary habitat (Monteith 1997). Inbreeding must be quite extensive in such 'family groups' and may assist chromosome mutations to become fixed and later it may perhaps spread over an area and eventually become fixed in a whole population. The population structure and dynamics of the Aradidae may thus be the key to the extensive karyotype evolution in the group.

The following patterns also emerge from the data:

1. Multiple sex chromosome systems are associated with high chromosome numbers - the higher the number the more X-chromosomes may be present as evident from *Paraneurus congolensis* ($40X_1X_2X_3Y$) and the *Brachyrhynchus* species ($45X_1X_2X_3X_4Y$).
2. The higher the chromosome number the larger the sex chromosomes (both the X- and Y-chromosomes in XY sex determining systems and the Y-chromosome in multiple sex chromosome system) are relative to the size of the autosomes. For example: the Y-chromosome of *Paraneurus congolensis* is about three times the size of the largest autosome. Both the sex chromosomes of the 48XY *Brachyrhynchus* species are also extremely large. It is evident that the autosomes often fragmented in the course of evolution, but not the sex chromosomes or only the X-chromosome in the multiple sex chromosome systems.



Figs 523-532. Meiotic stages in Aneurinae taxa. 523-526. Metaphase II. 523. *Breviscutaneurus breviscutatus*. 524. *B. helenae*. 525. *B. medioscutatus*. 526. *Aneurillus foliaceus*. 527-528. *Paraneurus congolensis*. 527. Metaphase II. 528. Anaphase I. 529-532. Metaphase II. 529. *Paraneurus ruandae multifarius*. 530. *P. nodosus*. 531. *P. brincki marieps*. 532. *P. brincki brincki*.



Figs 533-541. Meiotic stages in Mezirinae taxa. 533-536. Metaphase II in *Brachyrhynchus* species. 533. 22XY species. 534. 24XY species from South Africa. 535. *B. germari* (26XY). 536. $27X_1X_2Y$ species. 537. Late Diakinesis in $45X_1X_2\ X_3X_4Y$ species. 538. Metaphase II in 48XY species. 539-541. Metaphase II in *Neuroctenus* species. 539. *N. caffer* (18XY). 540. 20XY species. 541. 24XY species. Arrows indicate the sex chromosomes.

Chapter 12

DISCUSSION, CONCLUSION AND RECOMMENDATIONS

12.1 Discussion.

12.1.1 The ancestral chromosome number of the Aradidae.

The Aradidae together with the Termitapididae form the Aradoidea, which together with the Pentatomoidea, Lygaeoidea, Pyrrhocoroidea and Coreoidea make up the infraorder Pentatomorpha. Within the Pentatomorpha the Aradoidea is considered to have branched off very early from the other four superfamilies, that make up the Trichophora on account of the presence of trichobothria on their abdomen.

Manna (1958, 1984) and Banerjee (1958) considered 2n = 14XY to be the ancestral number of the Heteroptera. They based their decision mainly on the presumed (but very doubtful) affinities of the fossil *Paraknightia magnifica* from the upper Permian deposits of Australia with the Halyini of the Pentatomidae. Banerjee (1958) concluded that "according to his" (that is Manna's) "assumption, the family Pentatomidae is the most primitive of all the living families of Heteroptera".

In addition Manna (1984) gave the following reasons to support his view:

1. "The same chromosomal constitution is present in 325 species belonging to 11 families among 1200 species studied so far."

Most of these species belong to the Pentatomorpha - the only family outside the Pentatomorpha with a substantial number of species with 2n = 14XY is the Tingidae (Cimicomorpha), where it seems to be the modal number of the family.

2. "Since sex chromosomes differentiated from a pair of autosomes, the XY:XX mechanism would be primitive. Out of 1145 species, 846 had an XY:XX mechanism."

This is basically true but the sex chromosomes probably developed long before the origin of the Heteroptera and some of the primitive insect orders like Collembola have a X0:XX mechanism. Grozeva & Nokkala (1996) found both XY:XX and X0:XX systems in the primitive heteropteran infraorder Dipsocoromorpha. Ueshima (1979) believed that the XY:XX system evolved from a X0:XX system in the Heteroptera, while Nokkala & Nokkala (1983, 1984b) argue for the opposite.

3. "As fragmentation has been favoured in the evolution of chromosome number in Heteroptera, it would involve increase in chromosome number."

As has been argued by Thomas (1987), fragmentation has been overemphasized in heteropteran karyotype evolution. Fusion is as important, if not more so, than fragmentation, as has been shown in this thesis.

4. "Some primitive families with a high diploid number had some species with a low diploid number and XY:XX sex mechanism."

These species could also have evolved by fusions from species with a high diploid number, as has been shown in the case of *Dundocoris* where *D. nodulicarinus septeni* with 2n = $7XY_1Y_2$ evolved from a 28XY ancestor. Every case should be individually studied to determine the direction of chromosomal number changes.

5. "The *m* pair, which seemed to have originated later by the degradation of a pair of autosomes is absent in Pentatomoidea and in many other families, while it is present in some primitive taxa."

The nature, origin and evolution of the m-chromosomes are still unsettled. They seem to be present in all species of the Dipsocoromorpha thus far studied and thus may be a primitive characteristic. They also occur in some taxa of the infraorders Nepomorpha, Leptopodomorpha and Pentatomorpha, while they are absent in the Gerromorpha and Cimicomorpha.

Most of the recent studies, however, conclude that the Pentatomorpha is probably one of the most advanced of the heteropteran infraorders. Schuh (1979) uses the data assembled by Cobben (1978) in a cladistic analysis and came to the conclusion that the Enicocephalomorpha is the most primitive Heteroptera, followed by the Dipsocoromorpha, Gerromorpha, Nepomorpha, Leptopodomorpha, and the Cimicomorpha and Pentatomorpha, which are sister groups, are the most advanced. Wheeler et al. (1993), using morphological data as well as the sequence of 669 bases of the 18S nuclear rDNA, came to virtually the same conclusion (they only differ on the placement of the Nepomorpha).

The chromosome numbers in the majority of the families of the infraorders other than the Pentatomorpha are generally high. It is thus unlikely that the ancestral number of the Heteroptera is 2n = 14XY.

Leston (1958) argued that the early Pentatomorpha originated with a reduction of the diploid chromosome number to 2n =14XY and that two branches emerged very early: Pentatomoidea (2n = 12XY) and Lygaeoidea-Coreoidea (2n = 14XY). At that time the chromosome number of only one Aradidae (*Dysodius lunatus*, 2n = 31XXY) was known and Leston wisely did not make any deductions from this single record. Recently Thomas (1996) suggested that the ancestral number for all the heteropteran infraorders including the Pentatomorpha is '20 autosomes' (thus 2n = 20 + sex chromosomes). For the Pentatomorpha he based his assumption mainly on his statement that the "aradids have the ancestral number of 20 autosomes". This assumption seems to be unsubstantiated - of the 63 aradid taxa (Fig. 542) thus far studied only five have 20 autosomes and in the four of them which I have studied, there are strong indications that they are derived from a 26XY or 28XY ancestor.

The chromosome numbers in the Aradidae range from 7XYY to 48XY. When one considers their distribution (Fig. 542) there is a peak from 26XY to 28XY and the modal number for the Aradidae is probably 26XY or 27XXY, which are both found in the three subfamilies of which at least ten taxa have been cytologically studied. The number of species with chromosome numbers of 24XY, 22XY, 20XY, etc. then gradually decline but a second smaller peak occurs at 14XY, also represented by three subfamilies.

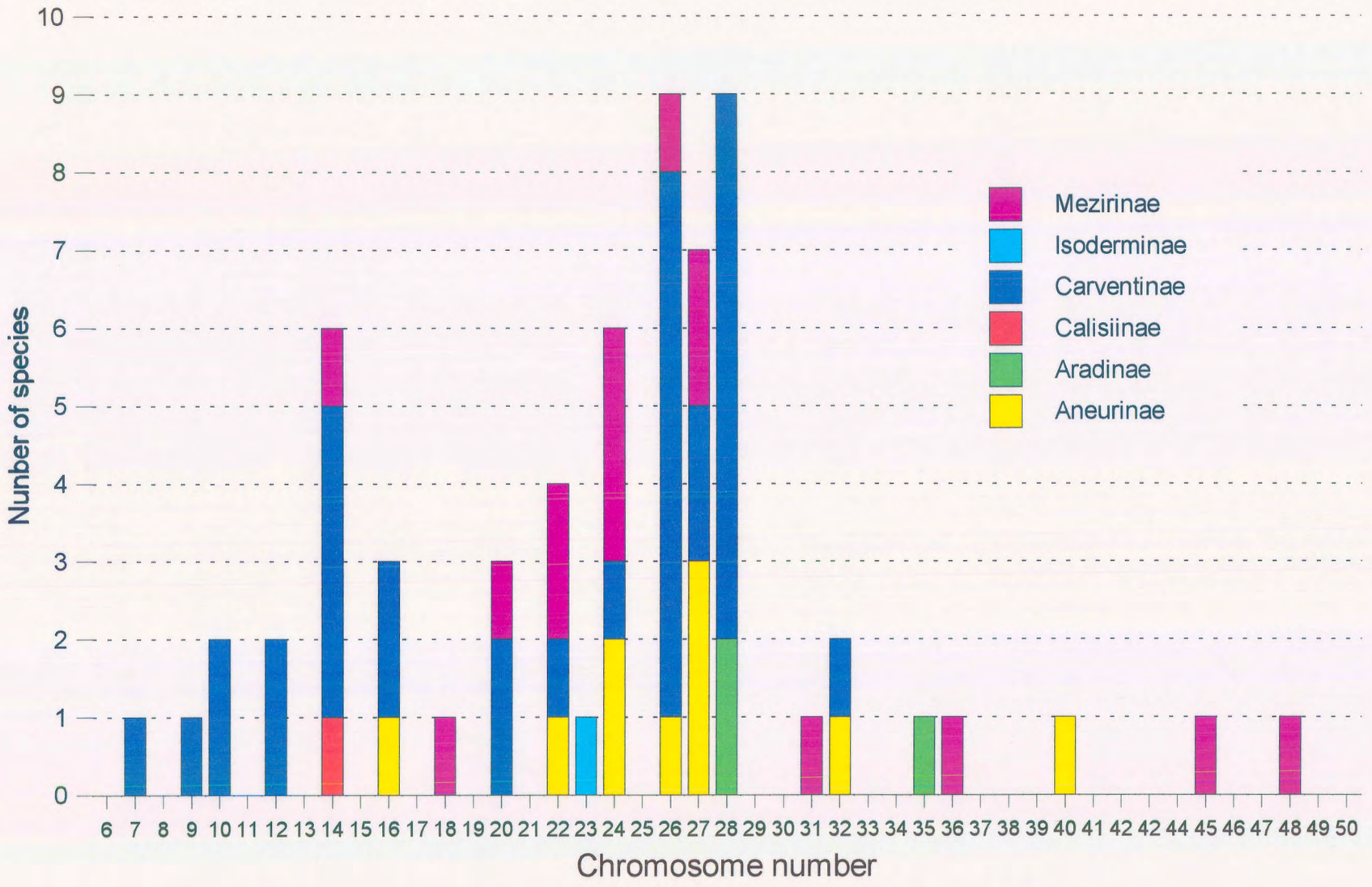


Figure 542. The chromosome numbers of the Aradidae.

This pattern is consistent with my hypothesis that:

a. 2n =14XY is the ancestral chromosome number of the Aradidae.

b. the autosomes (and sometimes also the X-chromosome) have doubled independently several times (by a mechanism that is still disputed - see 12.1.2) to give rise to 26XY or 27XXY karyotypes.

c. mainly fusions gave rise to the intermediate chromosome numbers like 24XY, 22XY, etc.

It can be argued that the intermediate chromosome numbers originated by fragmentation from a 14XY ancestor and is part of an agmatoploid series. In the case of *Dundocoris* it is, however, almost certain that they originated by means of fusions (refer to discussion at 9.2.12) and that more than 20 fusions and not a single fragmentation took place in the evolution of this genus. In the case of the 22XY *Brachyrhynchus* species, the one very large autosome could only have arisen by the fusion of three autosomes. There is no reason to believe that fragmentation played any part in the origin of any of the 20XY, 22XY or 24XY taxa.

It can also be argued that the ancestral chromosome number of the Aradidae is 2n = 26XY and that the 14XY karyotypes originated by means of fusions from the 26XY or other ancestor. This has undoubtedly happened in the case of *Dundocoris nodulicarinus nodulicarinus*, which has evolved from a 28XY ancestor by seven autosomal fusions (refer to 9.2.1.1) and probably also in the case of *Pondocoris latebrosus quattuordecimus*. Both these species have some autosomes distinctly larger than others, as can be expected by the random fusion of autosomes. The remaining four species, representing three subfamilies, have very similar karyotypes where the autosomes form a gradual size series and the sex chromosomes are smaller than the largest autosome. It is very unlikely that their karyotypes would be so similar if they had developed independently from a 26XY ancestor. Furthermore the karyotypes of the genera *Adamanotus* and *Spiculanotus* have probably originated from a 14XY karyotype by means of the fragmentation of a single autosome.

It is thus very likely that the ancestral chromosome number of the Aradidae and also of the Pentatomorpha as Leston (1958) envisaged is 2n = 14XY. The ancestral karyotype contains six autosomes that form a more or less gradual size series and the X and Y sex chromosomes that are smaller than the largest autosome.

12.1.2 Saltational increases in chromosome number and DNA content.

In various living organisms with holocentric chromosomes, including both plants and animals, closely related species often have vastly different chromosome numbers. The chromosome numbers often form a geometrical (doubled and redoubled) series with few or no intermediates. In the *campestris-multiflora* complex of the plant genus *Luzula*, the basic chromosome number is 2n = 12 with all the chromosomes the same size. True polyploids (2n = 24, 36 or 48) where the chromosomes are the same size as in the diploid, as well as species with 2n = 24 and 48 where the chromosomes are respectively half and quarter

the size of that of the diploid, occur (Nordenskiöld 1949, 1951, 1956, 1961). These latter species, which she termed endonuclear polyploids, easily cross with the diploid species, but they do not cross with the true tetraploids or octaploids of the same chromosome numbers. Battaglia (1955) has termed the phenomenon pseudoploidy and Malheiros-Gardé & Gardé (1950) (with the assumption that it originated by means of fragmentation and that intermediates exist or had existed) have called it agmatoploidy. A similar type of pseudoploidy has also been found in several genera of the Lepidoptera (Lorković 1941, 1949). In the genus *Lycaena* he found chromosome numbers of 2n = 23, 45 and 90, in *Lepidea* the numbers 28, 54 and 104 and in *Erebia* 2n = 20 and 40. Pseudoploidy has also been observed in the Dermaptera (Ortiz 1969) and the Heteroptera (Schrader & Hughes-Schrader 1956, 1958).

In the Heteroptera the phenomenon was well investigated in the genera *Thyanta* (Schrader & Hughes-Schrader 1956) and *Banasa* (Schrader & Hughes-Schrader 1958). Both these genera belong to the family Pentatomidae which is renowned for its stable chromosome number of 2n = 14XY (nearly 90% of about 250 species thus far studied have this number). Three of the *Thyanta* species they studied have 2n = 14XY, two have 2n = 16XY and *T. calceata* has 2n = $27X_1X_2Y$. The DNA contents of all the species are similar, which makes polyploidy an unlikely explanation. In the related species *Arvelius albopunctatus* (belonging to the same tribe) which has a typical pentatomid karyotype of 2n = 14XY, they found the DNA content to be double that of *Thyanta*. Subsequently they (Hughes-Schrader & Schrader 1956) found the DNA content of *Acrosternum marginatum*, also of the tribe Pentatomini and with 2n = 14XY, to be three times that of *Thyanta*. They explained it in terms of polyteny of the chromosomes. In *Banasa* they found one species with 2n = 14XY, three with 2n = 16XY and six with 2n =26XY. In the 14XY and 16XY species the X-chromosome is of intermediate size while the Y-chromosome is smaller than the smallest autosome. In the 26XY species, however, the X-chromosome is larger than the largest autosome, while the Y-chromosome is about equal in size to the smallest autosome. Here also they found the DNA content of all the species to be roughly the same. In both genera they found the autosomes of the 26 or 27 chromosome species to be distinctly smaller than those of the 14 or 16 chromosome species. Thomas and Yonke (1985) found in *Banasa* that the most rapid speciation has occurred following the expansion of the 'polyploid' karyotypes (they perceive the pseudoploids as true polyploids) into higher-altitude habitats and that the 'polyploid' condition has adaptational advantages.

The phenomenon that the DNA contents of closely related species vary considerably has been observed in many taxa of living organisms of both the plant and animal kingdoms. In their review Sparrow & Nauman (1976) termed this cryptopolyploidy which implies an increase (normally doublings) of genome size (DNA content per genome) by increase in chromosome size (DNA per chromosome). These doublings are independent of both chromosome number and ploidy level. In the 56 species of the genus *Vicia* (Leguminosae) that were studied, the 2C DNA amounts range from 3.85pg in *V. monantha* (2n = 14) to 27.07pg in *V. faba* (2n = 12) (Raina & Bisht 1988). Furthermore this seven-fold variation is discontinuous and the species cluster together in nine groups of which the first eight are separated by intervals of 2.23pg on the average. A greater interval, however, exists between *V. faba* (27.07pg) and

V. michauxii (20.68pg) which has the second largest DNA content. They also found that the DNA increases affect all the chromosomes and that both euchromatin and heterochromatin increase, although there is a tendency for species with high DNA content to have a larger percentage of heterochromatin (e.g. 11.11% in *V. eriocarpa* with 4.5pg DNA, 21.92% in *V. johannis* with 14.14pg DNA and 24.12% in *V. melanops* with 20.02pg DNA). In the genus *Lathyrus*, which is closely related to *Vicia,* Narayan (1982) found a four-fold discontinuous variation in the 2C DNA content in the 21 species he studied. The DNA amounts range from 6.86pg in *L. miniatus* to 29.22pg in *L. vistitis*. They could divide the species into seven groups which differ with 3.71pg intervals from each other. They also found that the DNA content differences affect all chromosomes of the genome to more or less the same extent. In the copepod genera *Calanus* and *Pseudocalanus* McLaren *et al.*(1988, 1989) found a six-fold quantum series in DNA content, ranging from 4.32pg to 25.3pg, and increasing with 4.19pg quanta. In the interstitial polychaete species of the genus *Ophryotrocha*, Sella *et al.* (1993) reported a three-fold 2C DNA content series, ranging from 0.81pg to 2.25pg. They suggest that the saltational differences in genome size could be due to the amplification of the whole basic genome size rather than to the duplication of distinct quantities of selected genomic fractions. Among the insects significant 2C DNA variation have been reported in the Acrididae (three-fold) (John & Hewitt 1966, Rees *et al.* 1978), *Dermestes* (Dermestidae) (three-fold) (Fox 1969), Chrysomelidae (twenty-fold) (Juan et al. 1989) and Aphididae (five-fold) (Finston et al. 1995). The latter case is of importance because the Aphididae belong to the Homoptera, the sister group of the Heteroptera, and they also have holocentric chromosomes. The chromosome numbers in the 34 species studied, range from 2n = 6 to 2n = 22 and their 2C DNA content show a five-fold range (0.36-1.77pg) which is unassociated with chromosome number. Genome sizes appear to vary in a discontinuous fashion, with quanta corresponding to the basal genome size detected in the study.

It is not certain what cryptopolyploidy actually entails and few explanations are offered for the process by which it comes about. Some researchers speculate that it is the duplication of only certain DNA sequences or certain parts of the chromosomes, while others think it is the duplication of the whole nuclear genome. Some investigators suspect it comes about by a stepwise continuous process while others believe it is a sudden, *de novo*, process. It seems that the genome can exist only in certain sizes called 'stable states' (Narayan 1982) and if it is a continuous process, intermediates must have a disadvantage and progress to the 'stable states' must be fairly rapid. The obvious explanation for the phenomenon of cryptopolyploidy would be that the chromosomes (and chromatids) are multi-stranded and that the addition of an extra strand would be responsible for the next quantum in the series. The multineme chromosome theory gained wide support in the fifties and sixties, especially as there was strong cytogenetic evidence for it. Half-chromatids and even quarter-chromatids were observed in the Coccoidea (Homoptera) where, in some species, the half-chromatids are sometimes separate from each other (Hughes-Schrader 1948), and also in many other organisms (refer to Wolff 1969 for a review). The results of many autoradiography experiments and occurrence of subchromatid rearrangements at mitosis and meiosis (refer to White 1973 for an overview) strongly support the multineme model. After some convincing evidence that the chromosomes are unineme (Laird 1971, Kavenoff & Zimm 1973,

Schwartz 1975), support for the multineme model dwindled and in the eighties and nineties it was rarely mentioned as an option. Recently Finston *et al.* (1995) and also Hales *et al.* (1997) again revived multineme chromosomes as an explanation and Finston *et al.* (1995) pointed out that the experiments of Laird (1971) and Kavenoff & Zimm were done on *Drosophila* which has very small DNA contents and of which the chromosomes may be unineme. They recommended that taxa where the DNA content is known to be elevated above the content which is basal for the group, should also be investigated. Other objections to the multineme chromosome model include:

1. The chromatid is the unit of crossing over during meiosis. A special mechanism would thus be required that ensures that all the strands in a chromatid break at the same point and reconnect with the strands of the opposite chromatid where all the strands have also broken. Such a mechanism is not known and seems unnecessarily complex and thus unlikely.
2. If new strands originate through the duplication of the total nuclear genome they would be identical to the existing strands and at least two copies of each gene would be present. This would result in a modified polysomic pattern of inheritance and that recessive point mutations would not show in the F2 but in later generations. However, with some exceptions, the inheritance is usually disomic and recessive mutations usually become visible in the F2 generation.

If tandem duplications of the genome exist, as some authors have suggested, the first objection would be nullified but the second one would still be valid and in addition one would expect some problems with synapsis that was not observed. At present no described process or model can explain cryptopolyploidy satisfactorily. The reinvestigation of chromosome structure and nature of the phenomenon in cryptopolyploid species by modern molecular methods is overdue.

A connection between cryptopolyploidy and pseudoploidy probably exists. However, in most cases thus far, the chromosome numbers in the latter usually seem to vary in a geometrical series (doubled and redoubled) while the DNA content in cryptopolyploidy varies in an arithmetical series. In the Dermaptera chromosome numbers of 12XY, 14XY, 24XY, $25X_1X_2Y$ and $38X_1X_2X_3Y$ have been recorded (Goldschmidt 1953) and it may be indicative of an arithmetical pseudoploid series. The case of *Paraneurus congolensis* with $2n = 40X_1X_2X_3Y$ is also in agreement with the hypothesis that the autosomes and X-chromosome of a 14XY ancestor have tripled to give rise to this species.

Cryptopolyploidy seems to occur widely in the animal and plant kingdoms and it is possible that it will be found in most families of living organisms. Much has been speculated about its evolutionary role and it is logical that a genome with double the number of genes and DNA would unlock much potential for mutations, evolutionary adaptation and subsequently for speciation. Pseudoploidy seems to occur only in organisms with holocentric chromosomes. It is possible that the fragmentation process of pseudoploidy is blocked by the localized centromere of most organisms and is therefore only successful in organisms with holocentric chromosomes. The adaptive value of pseudoploidy is probably the doubling of the linkage groups that will result in more recombination and variation.

The process responsible for pseudoploidy is still unknown but three explanations namely fragmentation (Agmatoploidy), chromatid autonomy and polyploidy have been offered. They will subsequently be discussed.

12.1.2.1. Agmatoploidy or fragmentation

The term agmatoploidy was coined by Malheiros-Gardé & Gardé (1950) as explanation for the situation in the genus *Luzula* (see above). In its simplest form it can be defined as the sequential transverse fragmentation of the chromosomes of a karyotype to form pseudoaneuploids and pseudopolyploids (= pseudoploids). The main objections to this model are as follows:

1. If it is a sequential fragmentation, then all intermediates must exist or have existed. Intermediate genotypes are usually not found or very rarely so and for example in the Lepidopteran genera *Lycaena* (2n = 23, 45 and 90) and *Lepidea* (2n = 28, 54 and 104) it is hard to believe that all intermediates existed at some point in time. It is also not clear why the process would stop exactly at the point where all the chromosomes have fragmented.
2. With random fragmentation one would expect a range in the sizes of the resultant chromosomes. This is not the case and it seems that every chromosome is always fragmented into two equal sized daughter chromosomes. If the cases of the Dermaptera and *Paraneurus congolensis* prove to be pseudoploidy, it would demonstrate that each chromosome could also fragment into three equal sized daughter chromosomes in some cases.

The above objections could easily be addressed if one assumes that there is a structural basis for the fragmentations. It is then easy to assume that an aberration in a biochemical process during replication or meiosis may lead to the breakage of all chromosomes at a certain place on them in one step. Tandem repeats of the basic chromosomal DNA would be the simplest explanation, but as I have pointed out previously, there exist no indications of such subdivisions in the chromosome structure and their existence is unlikely. Agmatoploidy thus seems as unlikely an explanation for pseudoploidy as any of the other hypotheses.

12.1.2.2. Chromatid autonomy

Chromatid autonomy was coined and described by Schrader & Hughes-Schrader (1956, 1958) and Hughes-Schrader & Schrader (1956) to explain the situation in *Thyanta* and *Banasa*. It is where the two chromatids of a chromosome split and each forms a new chromosome - thus the longitudinal fragmentation of a chromosome. As the DNA amount of the species stays the same, a prerequisite for chromatid autonomy is that the chromosome is multineme. Although the Schraders defined it as above, the following would probably be a better description of the process:

1. The DNA content of a species is doubled by means of the doubling of the number of strands in each chromatid (cryptopolyploidy).
2. At first the new strand is identical to the existing one but with time each strand builds up its own set of mutations.
3. With pseudoploidization the strands of the chromatid separate and not the chromatids of the chromosome.

With the demise of the multineme chromosome model in the seventies, chromatid autonomy as explanation for pseudoploidy also fell into disuse. White (1978) mentioned the concept only briefly and described it as "an ancient and now discredited concept".

A further possible objection to the concept of chromatid autonomy may be that after pseudoploidization, four copies of each chromosome (which are essentially identical) exist (much like in the case of true polyploids) and one could expect mispairing and abnormalities during meiosis. Wilson (1932) has, however, shown that in a tetraploid cyst he found in *Archimerus alternatus* (Coreidae), only bivalents were present at metaphase I.

Chromatid autonomy is as likely (or unlikely) an explanation for pseudoploidy as the other two hypotheses. If the multineme chromosome model is ever revived, it would be the preferred explanation.

12.1.2.3. Polyploidy

True polyploidy has often been invoked as an explanation for the chromosome number series in many organisms, often only because of a lack of other acceptable explanations. Thomas (1987, 1996) is, however, a serious proponent of true polyploidy in the Heteroptera. There is, however, strong evidence against it.

1. In *Luzula* true polyploids as well as pseudoploids exist (Nordenskiöld 1961). Pseudoploids cross easily with their diploid ancestors but they do not cross with polyploids, even if they possess the same chromosome number. In the crosses between a 'tetrapseudoploid' and a diploid the hybrids have regular trivalents at metaphase I, while in 'octapseudoploid'/diploid hybrids, four of the small 'octapseudoploid chromosomes' are associated with each large 'diploid chromosome' confirming the origin of the pseudoploid chromosomes. The occurrence of both polyploids and pseudoploids in the same genus prove that pseudoploidy is a real phenomenon which can be distinguished from polyploidy by the smaller size of their chromosomes and their similar DNA contents to the diploids.
2. The chromosomes of 'tetrapseudoploids' are about half the size of those of the diploids and those of 'octapseudoploids' about a quarter the size. In true polyploids one would expect them to be more or less the same size (as was also observed in *Luzula*). Thomas (1996) tried to explain the smaller size of the chromosomes in the organisms he reckoned to be true polyploids in terms of greater condensation of the chromatin and chromatin loss by the process of rediploidization. The first of his reasons is

unconvincing and rediploidization is a slow and long evolutionary process which seldom results in substantial chromatin loss. Equal or intermediate chromosome sizes would rather be expected than half sized chromosomes which are regularly found.

3. The DNA content of true polyploids is expected to be much more (double in the case of tetraploids) than that of their diploid ancestors, but in all the studied cases of pseudoploidy it is similar. It is extremely unlikely that rediploidization would have this result in any one case, not to mention all the studied cases.
4. In the Heteroptera large sex chromosomes (both the X- and Y-chromosomes in a XY sex chromosome system or only the Y-chromosome in a X_nY sex chromosome system) are regularly associated with the doubled chromosome numbers. It would be very difficult to explain it in terms of polyploidy while it is a logical consequence in the other two explanations.

True polyploidy seems to be the most unlikely of the explanations for the observed chromosome number series.

Notwithstanding the process by which pseudoploidization takes place it has undoubtedly played a major role in the evolution of the Aradidae and probably of other Heteropteran families as well. If we accept 2n =14XY as the ancestral chromosome number for the Aradidae, then it has at least occurred in four of the subfamilies namely the Aneurinae, Aradinae, Carventinae and the Mezirinae. In the Carventinae, *Dundocoris*, *Miteronotus* and *Trichocarventus* have probably evolved after pseudoploidization of their 14XY ancestor. *Dundocoris* is by far the most successful genus, with at least 12 species in South Africa and *Miteronotus* the second most successful with six species (including two undescribed species that I am aware of). Pseudoploidization most probably contributed to the evolutionary success of these genera as in the case of the pentatomid genus *Banasa* as found by Thomas & Yonke (1985).

12.1.3. Karyotype evolution in the Carventinae and Heteroptera.

It is evident that two processes played the major role in the karyotype evolution of the Carventinae namely pseudoploidy and chromosome fusion. Although the frequency of pseudoploidization events may be relatively low, its effect (doubling of the chromosome number) is so large that it must be viewed as a major process. Pseudoploidy is responsible for the saltational increases in chromosome number while chromosome fusion tends to lower the chromosome number subsequently. Although it has been indisputably shown in the Carventinae (especially *Dundocoris*) that fusion and not fragmentation is the main process of karyotype change, the latter has also played a role. The genera *Adamanotus* and *Spiculanotus* originated (probably independently) from the 14XY ancestor by the fragmentation of one autosome and *Miteronotus knysnaensis* probably evolved from a 26XY ancestor by three fragmentations.

These findings are at variance with the general perception that fragmentation played the most important role in the karyotype evolution of the Heteroptera. It may, however, well be that fragmentation played

a more dominant role in families with a low modal chromosome number, like the Pentatomidae where the modal number is 2n = 14XY. Table 12.1 was compiled from the chromosome numbers of the Pentatomidae listed in Ueshima (1979). Where several species of the same genus exhibit a deviant chromosome number it was scored as a single event of chromosome number change.

Chromosome number	Number of unrelated occurrences	Origin
6XY	1 (involving 5 fusions)	Fusions
12XY	3	Fusion
15XXY	1	Fragmentation
16XY	9	Fragmentation
26XY	1	Pseudoploidy
27XXY	1	Pseudoploidy

Table 12.1. Number of occurrences and origin of aberrant chromosome numbers in the Pentatomidae.

From Table 12.1 it is clear that ten independent cases of fragmentation took place but that each only involved one fragmentation. Although there are only four independent fusion cases, one of them involved 5 fusions so that in total eight fusions took place. Nevertheless, fragmentations seem to have played a slightly more important role in the karyotype evolution of Pentatomidae than fusions.

Other processes like chromosome deletions and duplications and perhaps even inversions might have played a role in the karyotype evolution of the Carventinae and Aradidae. They are, however, very difficult to detect and no special efforts were made or methods were used in this study to detect them. In the Reduviidae (Panzera et al. 1992, 1995, 1997; Tavares & De Azeredo-Oliveira 1997) and Belostomatidae (Papeschi 1991) substantial differences in the C-positive heterochromatin was observed between closely related species. In *Spiculanotus montanus* it is possible that C-heterochromatin also occurs, and that C-heterochromatin variation plays a role in the karyotype evolution of the Aradidae.

12.1.4. The species concept as used in the Carventinae

A long discussion of the species concept and the process of speciation falls outside the scope of this thesis. However, a few comments and a short discussion is necessary to explain and defend decisions regarding species made within this thesis.

Several species concepts exist e.g. the classical phenetic species concept, the biological species concept (BSC), the evolutionary species concept and the recognition species concept. Each of the species concepts has its own advantages, strong points and limitations but none of them seem to be universally

applicable. In practice most taxonomists use the phenetic species concept (as the material they use is often only pinned museum specimens) or a combination of the phenetic and biological species concepts. I shall limit my discussion to the latter two concepts and the species concept as I see it.

In terms of the phenetic species concept the species is a group of organisms with no phenotypic gaps within the group but which is separated by phenotypic gaps from other such groups (Michener 1970). It is based on morphological differences and is therefore easy to use. Its main weaknesses are:

1. It is not based on modern genetic principles.
2. It exaggerates the significance of different phenotypes in the same interbreeding population and every local race may be named a species.
3. It cannot deal with the existence of sibling species that are reproductively isolated but exhibit minimal or no morphological differences and would lump together whole complexes of sibling species.

Phenetics in the narrow sense, i.e. without accompanying data from population genetics, experimental hybridization, karyotype studies and biochemical investigations, is thus a very inadequate tool for understanding either species or speciation (White 1978). If, however, the phenetic species concept is conceived and defined to include all these types of information it becomes almost synonymous with the BSC.

In terms of the BSC a species is defined as groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups (Mayr 1942). Although the BSC presents many practical difficulties in determining whether a set of populations belongs to one or more biological species, it is appealing because of its simplicity and usefulness in thinking about evolution. It is also easy to apply population genetics to the BSC. Most biologists today foster the BSC. The BSC is also known as the isolation species concept, as genetic isolation is central to it. The BSC, however, has a few major flaws as will be pointed out subsequently.

Firstly, apomictic species are excluded. Most parthenogenetic species, however, display the same patterns of phenotypic cohesion within and discontinuity between as do sexual species (Templeton 1989). In the rotifers the species in the asexual taxa are actually more consistently recognized than those from the sexual taxa (Holman 1987). This failure of the BSC is actually more extensive than many people realize. The evolutionary genetics of self-mating populations is simply a special case of automictic parthenogenetic populations and therefore self-mating sexual species are also outside the logical domain of the BSC (Templeton 1989).

Secondly, non-gene flow (= isolation) between species is an essential property of the BSC. As soon as two populations cannot interbreed successfully (in the sense that there is no gene flow between them and not in the sense that they cannot interbreed and produce hybrids) they are different species. However, Grant (1957) found that less than 50% of the outcrossing species in 11 genera of Californian plants were well delimited by isolation from other species. In plants, taxonomists have repeatedly defined sympatric

species that exist in larger units known as syngameons that are characterized by natural hybridization and limited gene exchange. The members of a syngameon are often real units in terms of morphology, ecology, genetics and evolution. For example, the fossil record indicates that balsam poplars and cottonwoods (both from the genus *Populus*) have been distinct for at least 12 million years and have produced hybrids throughout this period (Eckenwalder 1984). Even though the hybrids are widespread and fertile these tree species have and are maintaining their genetic, phenotypic, and ecological cohesion within and distinction between them (Templeton 1989). To comply with the BSC one solution would be to deny the species status of members of a syngameon and indeed Grant (1981a) refers to them as 'semispecies'. Syngameons, or superspecies as Mayr (1942) calls them in the case of allopatric taxa, are also not uncommon in the animal kingdom. Templeton (1989) and Cracraft (1989) cited several examples in their critique of the BSC. The case of the Hawaiian *Drosophila* species *D. heteroneura* and *D. silvestris* has been particularly well studied (Val 1977, Kaneshiro & Val 1977, Tenpleton 1977, DeSalle *et al.* 1986, DeSalle & Templeton 1987, Ahearn & Templeton 1989, Hunt & Carson 1983, Hunt *et al.* 1984). These species are broadly sympatric on the Island of Hawaii, they are morphologically extremely distinct but phylogenetically very close. When they are hybridized in the laboratory, the hybrids and subsequent F2 and backcrosses are completely fertile and viable. Interspecific hybrids were also found in nature and these hybrids can and do backcross to such an extent that a *heteroneura* mitochondrial haplotype can occasionally be overlaid on a normal-looking *silvestris* morphology. In spite of this hybridization the species maintain their very distinct, genetically based morphologies and they have distinct nuclear DNA phylogenies.

Thirdly, although the assumption that there is a constant gene flow between the populations of a species is not an essential property of the BSC, many proponents of the BSC view gene flow as the most important mechanism to maintain the integrity of the species. This view stems from and is implied by the general, but simplistic, perception of allopatric speciation that a species becomes divided into two populations by a geographic barrier that prevents gene flow between them. Because of the lack of gene flow and different environmental pressures the two populations evolve differently genetically until (after a considerable time) they become genetically distinct so that they could not interbreed should they come in contact again. Many species with wide distributions or of which the habitat has a patchy occurrence are, however, divided into populations which have had no gene flow between them for considerable lengths of times. Notwithstanding this they have maintained their species identity and genetic integrity. For example *Breviscutaneurus breviscutatus* (Bergroth), a small aneurid (Aradidae) which is a weak flyer, was originally described from Madagascar but was subsequently found to occur widespread in southern Africa. The specimens from Madagascar are morphologically virtually identical to those from Africa, yet they must have been separate with no gene flow between them for many millions of years.

From the above it is evident that gene flow is not necessary to maintain the integrity of a species nor will limited gene flow between different species undermine their identities. One question that has not been asked in literature yet is that if two populations can not interbreed successfully can they belong to the same species? Under the BSC two such populations would belong to two separate species but also here

the BSC runs into serious difficulties. It has often been found in plants and animals that two populations (say A and B) cannot interbreed but that both of them can interbreed with population C; or that A can only interbreed with C, B only with D, but that C and D can interbreed. The situation can become much more complex with certain crossings that are only viable or fertile in one direction while the reciprocal crossings are not.

It is known that karyotypic and genetic evolution often proceed at vastly different rates. On one extreme we find groups where speciation has been profound but the karyotypes of all or most of the species are virtually identical, for example in some orthopteran taxa like the Acrididae. On the other extreme we find taxa which are virtually identical morphologically but have vastly different karyotypes and chromosome numbers, for example in the taxa of *Pondocoris latebrosus* and *Dundocoris nodulicarinus* described in this thesis. At the very extreme it is conceivable that different populations of the same species could have evolved different chromosome numbers but have remained genetically identical. They might not be able to interbreed successfully because meiotic abnormalities may render their offspring infertile or not viable but they may be morphologically and genetically identical and may occupy exactly the same niche. Should we place them in different species just because they cannot interbreed successfully? The three taxa of *Dundocoris nodulicarinus* probably approximates this situation - they are morphologically identical and inseparable and occupy the same niche in different evergreen forests, but they have different chromosome numbers and sex chromosome systems namely 14XY, $9XY_1Y_2$ and $7XY_1Y_2$ respectively.

The species concept cannot stand loose from the process of speciation as it is the result of the latter. In most models of the speciation process natural selection on the phenotype plays the all important role. It is generally believed that genetic events like deletions, duplications and particularly mutations have certain phenotypic effects which are subjected to natural selection (and perhaps chance in small populations) and a certain genotype may increase and eventually become fixed in the population if it is advantageous. When eventually enough such genetic differences have built up between the populations, they become separate species. The change of population through natural selection is a very slow process and it cannot explain the origin of new structures or characteristics, and the many differences between species that seem to be selectively neutral. To my mind the role of the phenotype and natural selection have been overemphasized in speciation to the loss of the role of the internal organisation of the genotype. The genotype, with its interaction between genes and epistatic and pleiotropic effects of the different loci, forms a complex, integrated, co-adapted and homeostatic system. Even relatively small changes to this system may have large biochemical and phenotypic effects for example trisomy 21 (= Down's Syndrome) in man, where an extra copy of the second smallest chromosome (or part of it) is present, has profound phenotypic and behavioural effects notwithstanding that all the genes are present. Most of the other trisomics in man are not viable and those that sometimes are (trisomy for chromosome numbers 13, 16, 18 and 22) have serious effects like mental retardation, hypertonicity, low-set, malformed ears, deafness, small mandible, eye defects, etc. The internal balance of genes and

organisation is very important - an organism has to be able to live with itself before its interaction with the environment becomes important.

I consider the integrated, co-adapted, homeostatic genetic composition of the genome as the essence of a species and of the species concept that I shall call the 'homeostatic genetic species concept' (HGSC). The homeostatic gene complex is the main cohesive force that maintains the species identity and integrity. It defines the boundaries with respect to the tolerances for environmental conditions within which the species can operate under normal circumstances and establish a fundamental niche (Hutchinson 1965) within which intraspecific variation is contained. The fundamental niche is defined by the intrinsic (i.e. genetic) tolerances of the individuals to various environmental factors that determine the range of environments in which the individuals are potentially capable of surviving and reproducing. The realized niche (Hutchinson 1965) refers to that subset of the fundamental niche that is actually occupied by a species or population.

Although many workers have discussed the existence and importance of co-adapted gene complexes (e.g. Grant 1963, 1981b; Mayr 1963, 1970; Carson 1985; Carson & Templeton 1984; Templeton 1989) in species and speciation, they all combine it with other species concepts. Grant (1963, 1981b) stated that "the formation of a new species is basically the fixation of a new isolated adapted gene combination". He was, however, a proponent of the BSC and saw the gene combination concept of a species as compatible with it.

I regard the essence of the speciation process as follows: A population (or even a single or few individuals in the case of a founder event) is subjected to environmental circumstances that are outside its fundamental niche. The co-adapted gene complexes break up and new ones form that define a new species. The exact process and mechanism of the disintegration of an existing gene complex and the formation of a new complex is not yet well understood. Carson & Templeton (1984) discussed three possible ways in which it could happen in founder populations. I find it perceivable that stress in a organism could unleash internal genetic mechanisms that disassemble the co-adapted gene complex and increase variation. Factors like increased crossovers, mutator genes and mobile genetic elements like transposons may play a role in this process. The stressed population enters a period of increased variation after which a new adaptive state may be reached. During the period of increased variation the internal organisation of the genome is the main substrate for selection and only the most important environmental factors have an influence on the process through natural selection. After a new adapted gene complex has been formed, natural selection takes over and proceeds with the fine tuning of the genotype to the environment.

It must be stressed that speciation is a rare event and that most times a population in flux would probably not reach a new adapted gene complex but die out. Occasionally the new adaptive state may not be much altered from the original one and then we would probably view such a population as a subspecies of the original one - originated by a failed speciation event.

The HGSC has a few interesting implications that are contrary to the general perception of species and speciation:

1. Gene flow within and isolation between species is not necessary to maintain the identity and integrity of a species - it is maintained by the integrated, co-adapted, homeostatic gene complex. In extreme cases individuals or populations of the same species may not be able to interbreed.
2. Speciation is not a slow process directed by natural selection. It is usually a relatively quick process and although environmentally induced natural selection may trigger the speciation event, it is not the main driving force during speciation.
3. A new adaptive gene complex usually affects the control, interaction and pleiotropic effects of many genes and therefore species usually differ in respect of many characteristics. Most of the differences are not the result of natural selection and are selectively neutral and some may even be slightly deleterious.
4. Chromosome number changes, isolation, or altered specific mate recognition systems are not causes of a speciation event - they are consequences.
5. The main role of natural selection in evolution is the fine tuning of the genotype to an environment in the fundamental niche of an organism. For example: open savanna, rain forest and desert all fall in the fundamental niche of the African elephant and populations living in each these diverse environments have attained certain adaptations through natural selection. The status of the African elephant as a species is, however, not in question at all.
6. Subspecies are not incipient species. They are either the result of the adaptation to a certain environment in the fundamental niche of the species or the result of a 'failed' speciation event.

The practical implementation of the HGSC is no more problematic than that of other species concepts like the BSC. Although no methods exist at present to exactly measure differences in the homeostatic gene complex between species, it may change in future when we understand these differences better and more molecular genetic methods become available. The phenotype is usually a fairly good indication of genotypic differences and most species distinguished in the conventional way will prove to be good species in terms of the HGSC. As with other species concepts, the more information available (like karyotype, molecular genetic data, biochemical data, ecology and anatomy), the more accurately species will be distinguished.

In applying the HGSC to the Carventinae I had to decide how to handle the different chromosome number 'races' (which should be separate species according to the BSC) of some species. In the case of several *Dundocoris* species (e.g. *D. nodulicarinus*) they are morphologically identical and I have little doubt that they are conspecific. In these cases I described them as subspecies for the following reasons:

i) It is convenient to have names when discussing the origin and evolution of the different chromosome races.
ii) If someone who adheres to another species concept wants to refer to them as different species, names already exist and it may thus prevent confusion in the future.

In the case where there are some morphological differences between the chromosome number 'races', I either described them as separate species (if the differences were of the kind and magnitude normally associated with species) as in the case of *Silvacoris heissi* and *S. karkloofensis*, or I described them as subspecies (if the differences were not of the kind or magnitude normally associated with species) as in the case of *Pondocoris latebrosus* and some *Dundocoris* species.

To my mind a classification system must adhere to established scientific principles but it must also be as convenient and practical at the same time. The HGSC lends itself to such an approach in that populations that are identical in morphology and ecology but cannot interbreed can be the same species. An ecologist doing a species survey would be able to attach a name to a specimen although he might not be able to determine for example the chromosome race to which the individual belongs. In the case where every chromosome number race is described as a different species this would not be possible.

12.1.5. The phylogeny of the Carventinae of South Africa

The differences among congeneric taxa in the Carventinae are often of a more quantitative than qualitative nature. They often differ randomly between taxa and produce little information for cladistics. In several of the genera the best indication of the phylogeny of the species and subspecies is provided by the reconstruction of karyotype evolution as indicated by karyotype differences between related taxa. This has been discussed under cytogenetics of the genera.

To determine the phylogeny of the seven genera occurring in southern Africa, Winclada and Hennig86 were used to calculate trees and analyse character state distributions. Initially the seven genera and the outgroup *Calisius africanus* (Calisiinae: Aradidae) were scored for 17 characters. After removing the non-informative characters, the following eight remained with 0 coded for hypothesized pleisiomorphic states and 1 or 2 derived states:

0. **Mesonotal median ridge** 0: consisting of 2(1+1) parallel ridges; 1: fused to form a single ridge.
1. **Meso- and metanotal median ridges** 0: separated by a distinct suture or deep depression; 1: contiguous but separated by a weak suture or shallow depression; 2: fused and usually with no indication of line of fusion.
2. **Mesonotal median ridge** 0: not extended posteriorly; 1: extended posteriorly and wedging in between the elevations of the metanotal median ridge.
3. **MTg 1 and MTg 2** 0: separate; 1: fused medially but separate laterally; 2: fused medially and laterally.
4. **Metanotum and MTg 1** 0: separated by a suture; 1: suture absent (fused).
5. **Median elevated bar on MTg 1 & 2** 0: absent; 1: present.
6. **Carinae on abdominal tergal disk** 0: reaching lateral margins of disk; 1: Y-shaped and usually not reaching lateral margins.
7. **Ancestral chromosome number** 0: 14XY; 1: 16XY; 2: 28XY.

The following data matrix of character states was obtained for the examined taxa:

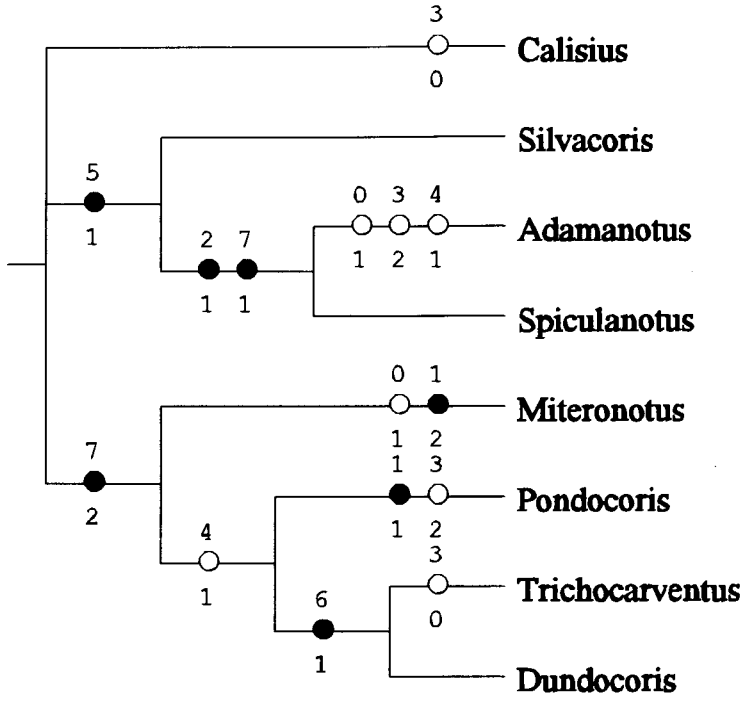


Figure 543. Cladogram of relationships among the Carventinae genera of southern Africa.

Calisius	---000-0
Adamanotus	10121101
Silvacoris	00010100
Pondocoris	0102100?
Trichocarventus	00001012
Miteronotus	12010002
Dundocoris	00011012
Spiculanotus	00110101

Only one parsimonious tree was found (Fig. 543) with a length of 15, consistency index of 0.73, and a retention index of 0.66.

The above phylogeny must be regarded as provisional as only eight characters were used. It is evident that several of the clades are supported by only a single controverted or uncontroverted character state (Fig. 543) and when a more detailed analysis (of e.g. anatomy etc.) reveal more characters, the picture may change significantly. DNA sequencing, in particular, should be invaluable to resolve the phylogenies of the genera as well as the species and subspecies, and it is highly recommended that such research is done in this group.

One interesting result from the proposed phylogeny, is the position of *Pondocoris* in the clade with the 28XY ancestral chromosome number. I have purposely not scored the genus for this character because of the difficulty encountered to envisage the karyotype evolution in it as discussed in section 6.2.3. Pondocoris is characterized by a low chromosome number with two taxa having 2n = 10XY and one taxon each with 2n = 12XY, 14XY and 22XY respectively. If the ancestral chromosome number of *Pondocoris* was indeed 2n = 28XY the existing species and subspecies must have evolved by means of extensive fusion of chromosomes. In retrospect, this hypothesis is as likely or even more so than to try to explain their origins from a 2n =14XY ancestor, as has been attempted in section 6.2.3.

12.2. Conclusions

Various conclusions can be drawn from the study in this thesis. They can be summarized as follows:

1. Cytogenetics have been very helpful in the taxonomic treatment of the Carventinae. Chromosome number differences in morphologically similar taxa have directed me in several cases to find characters useful for distinguishing between the taxa.
2. Measurement and subsequent analysis of chromosome area have proved to be crucial for understanding the karyotype evolution of the group and have also provided sound clues to the phylogenies of the species and genera.
3. The main methods of karyotype evolution in the Carventinae (and probably in all the Aradidae) is pseudoploidy (saltational increases in chromosome number), chromosome fusions and chromosome fragmentation. Chromosome fusions seem to be much more frequent than chromosome fragmentation in the Carventinae.
4. Fusions between autosomes and sex chromosomes to form multiple sex chromosome systems do occur in the Heteroptera and may be more common than anticipated as several have originated in *Dundocoris*.
5. The ancestral chromosome number of the Aradidae as well as the Carventinae is 14XY while the modal number lies between 26XY and 28XY.
6. Pseudoploids seem to be more successful of subsequent speciation than taxa with the ancestral chromosome number.
7. Spindle fibres usually attach to the chromosome ends during meiosis but in the case of long chromosomes they also attach interstitially to parts of the chromosome that lie perpendicular to the spindle axis.

12.3. Recommendations

It is recommended that:

1. Cytogenetic analysis is done in as many Aradidae as possible to elucidate the evolution of the family and its subfamilies. In problem cases it can also be of invaluable help to differentiate between closely related taxa.
2. As there is much controversy regarding the phylogeny of the subfamilies and other taxa of the Aradidae as well as regarding the families of the Pentatomoidea, it is strongly recommended that comparative molecular analyses is done on as many taxa as possible to determine their phylogenetic relationships. Molecular comparisons may also help to determine the true relationship between the 'chromosome races' of certain species. Certain molecular procedures may also help to elucidate the phenomena of cryptopolyploidy and pseudoploidy, both which are not well understood at present.

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