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.

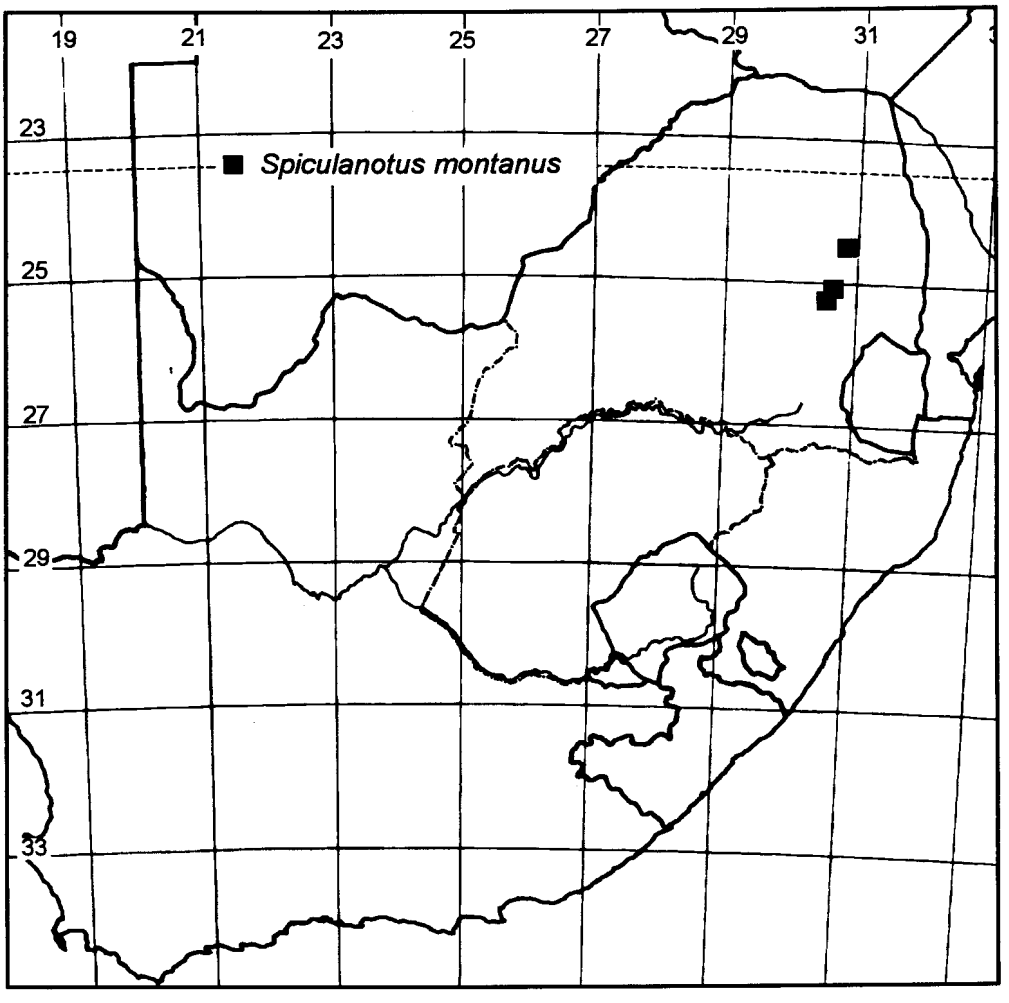



**Figure 506. Distribution of *Spiculanotus montanus* gen. et spec. nov.**

**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)** | |

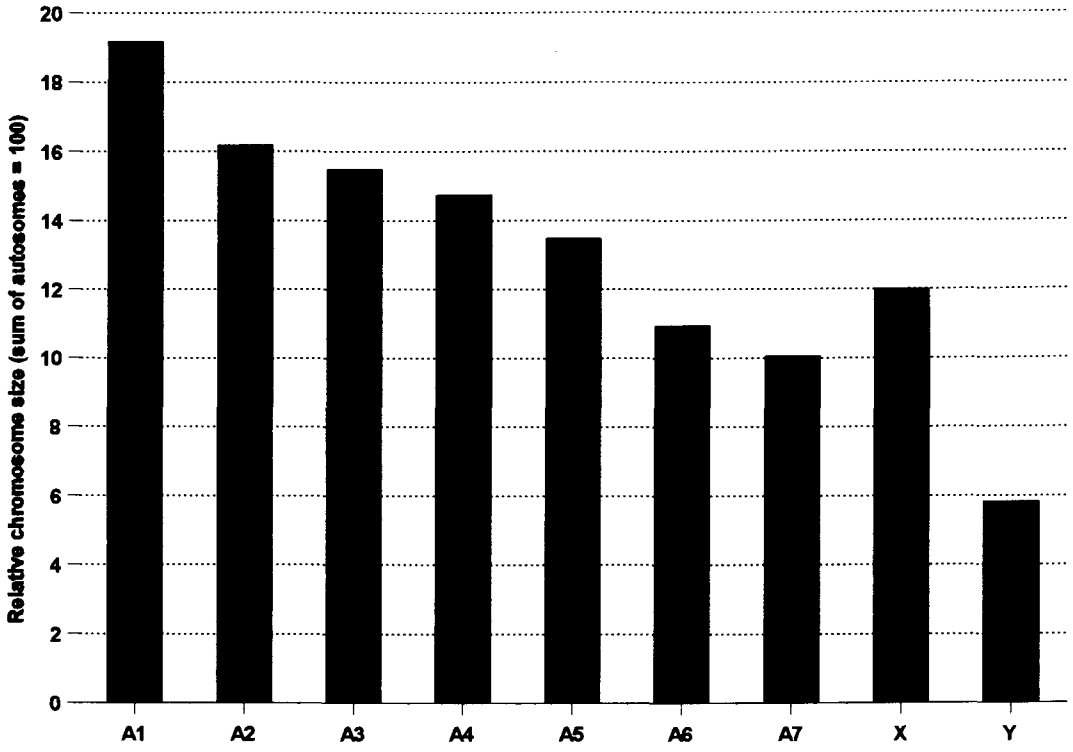



Figure 507. Idiogram of *Spiculanotus montanus*.

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.

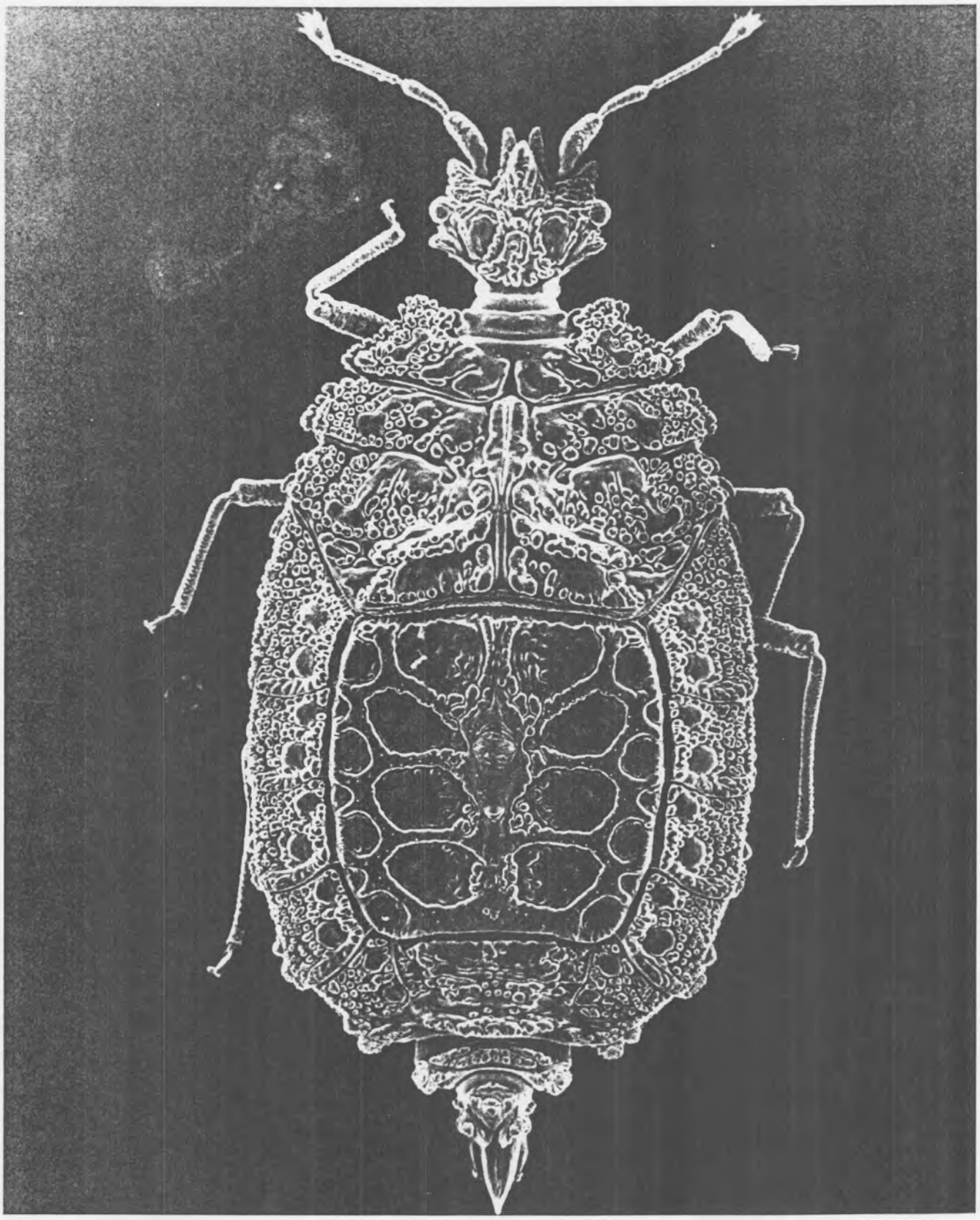
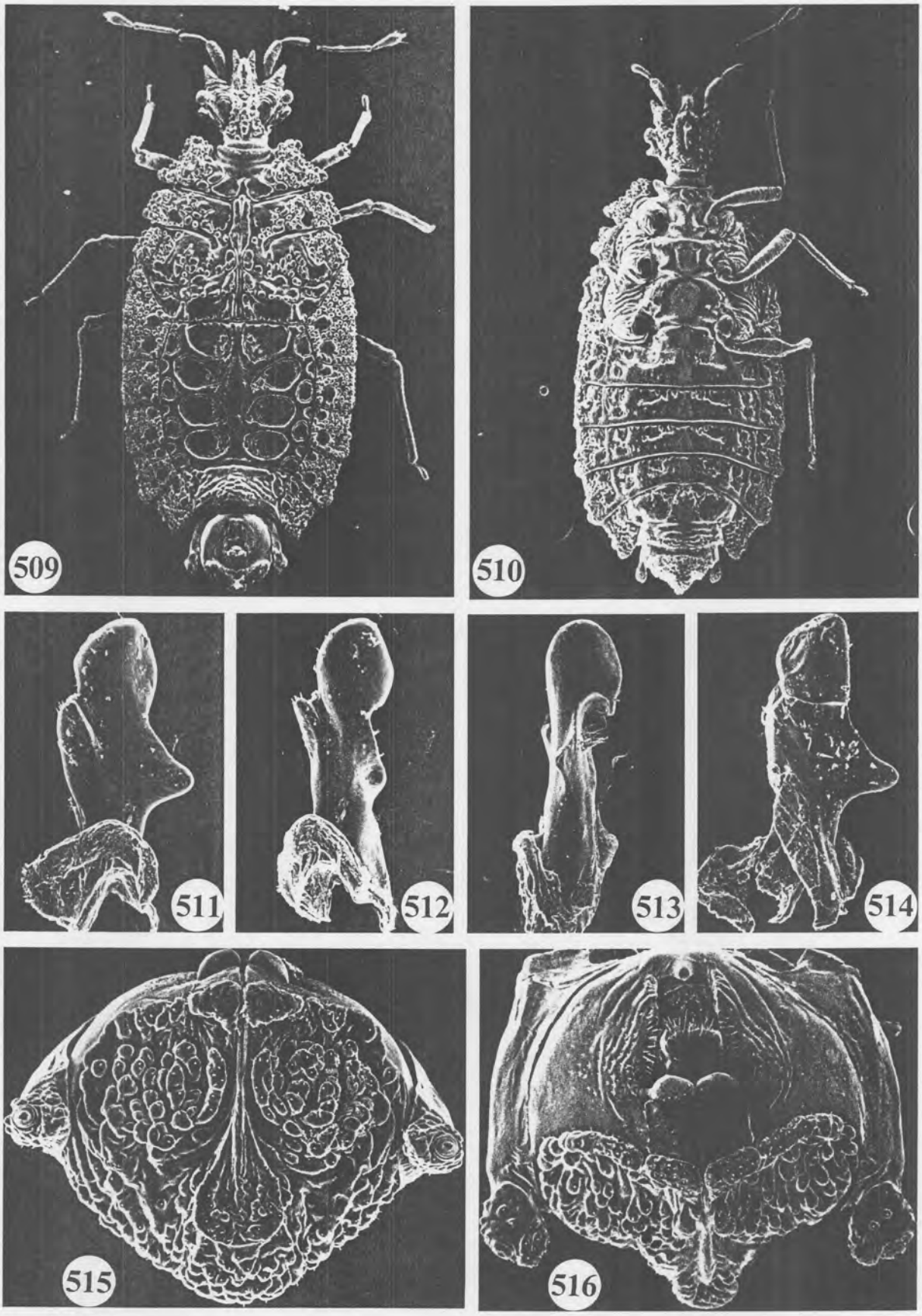
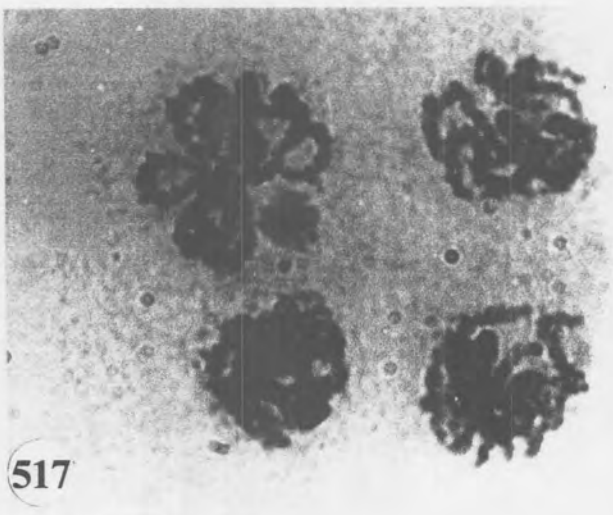


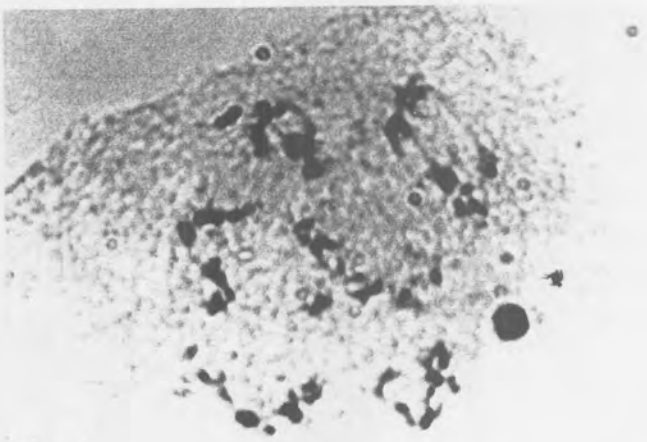
Fig. 508. Scanning electron photomicrograph of *Spiculanotus montanus* **gen. et spec. nov.**, dorsal aspect of female paratype.



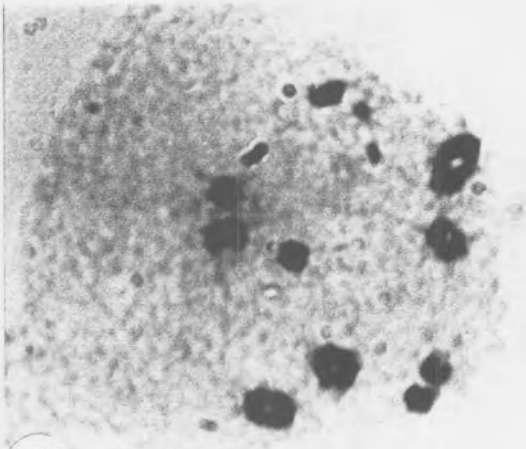

Figs 509-516. Scanning electron photomicrographs of *Spiculanotus montanus* **gen. et spec. nov.** 509. Male paratype, dorsal aspect. 510. Male paratype, ventral aspect. 511-513. Different aspects of the left paramere. 514. Mesal aspect of the right paramere. 515-516. Pygophore. 515. Caudal aspect. 516. Dorsal aspect.



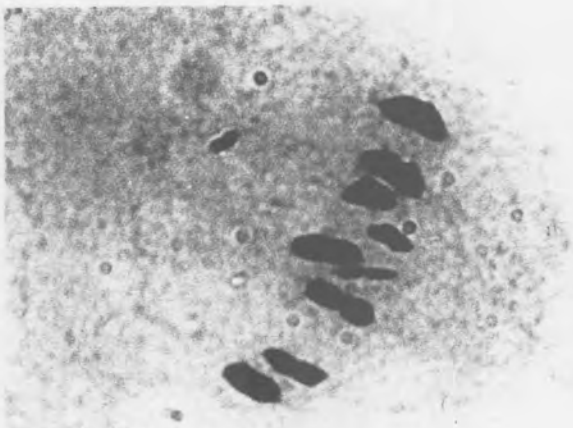
517



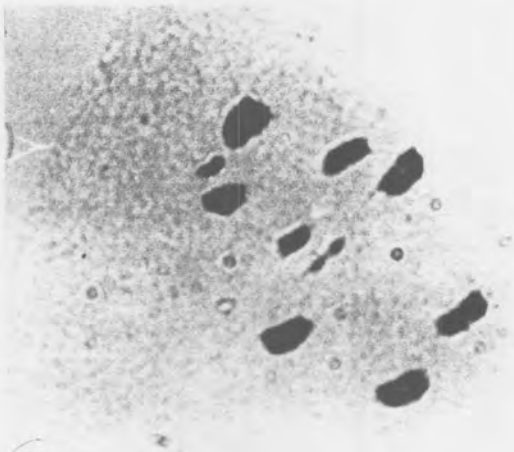
518



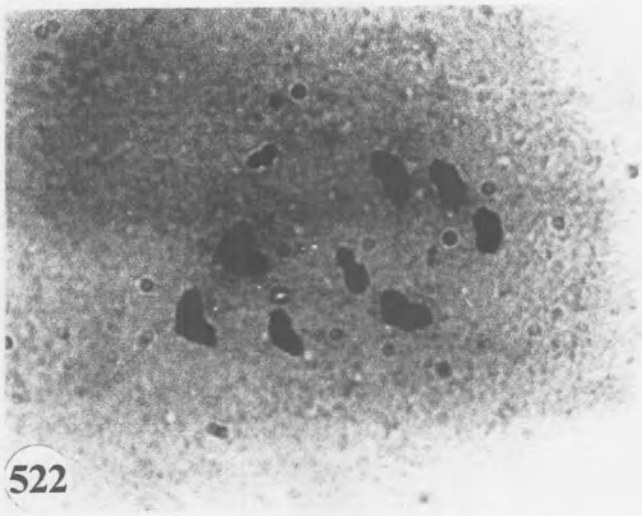
519



520



521



522

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

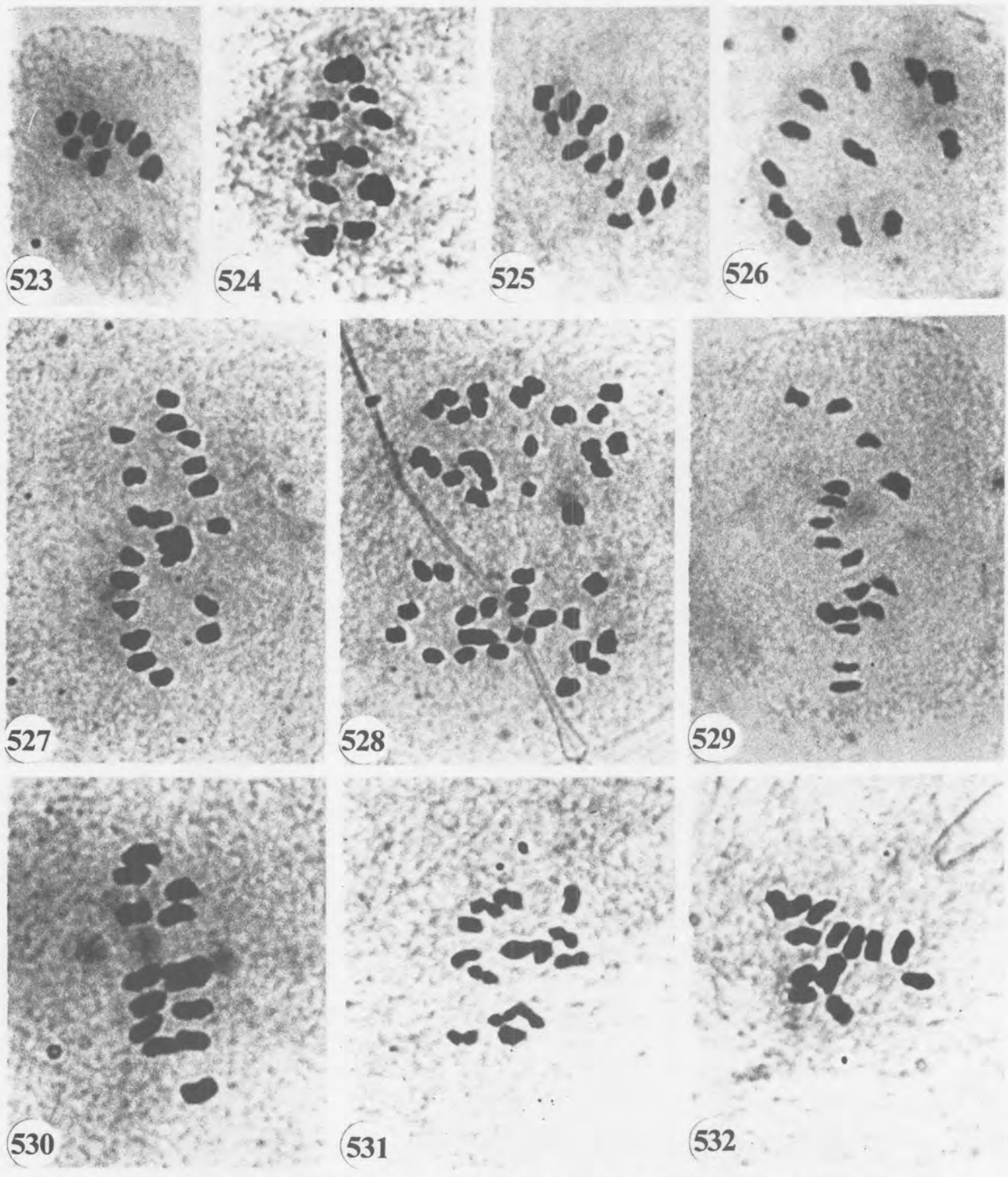
autosomes of a 14XY ancestor or by the repeated fusion of autosomes of a 26XY ancestor. I prefer the latter option because fusions seem to be predominant in the Aradidae and in the case of the 22XY *Brachyrhynchus* species it is clear that it originated by fusion from a 26XY ancestor.

## 11.6 **Discussion**

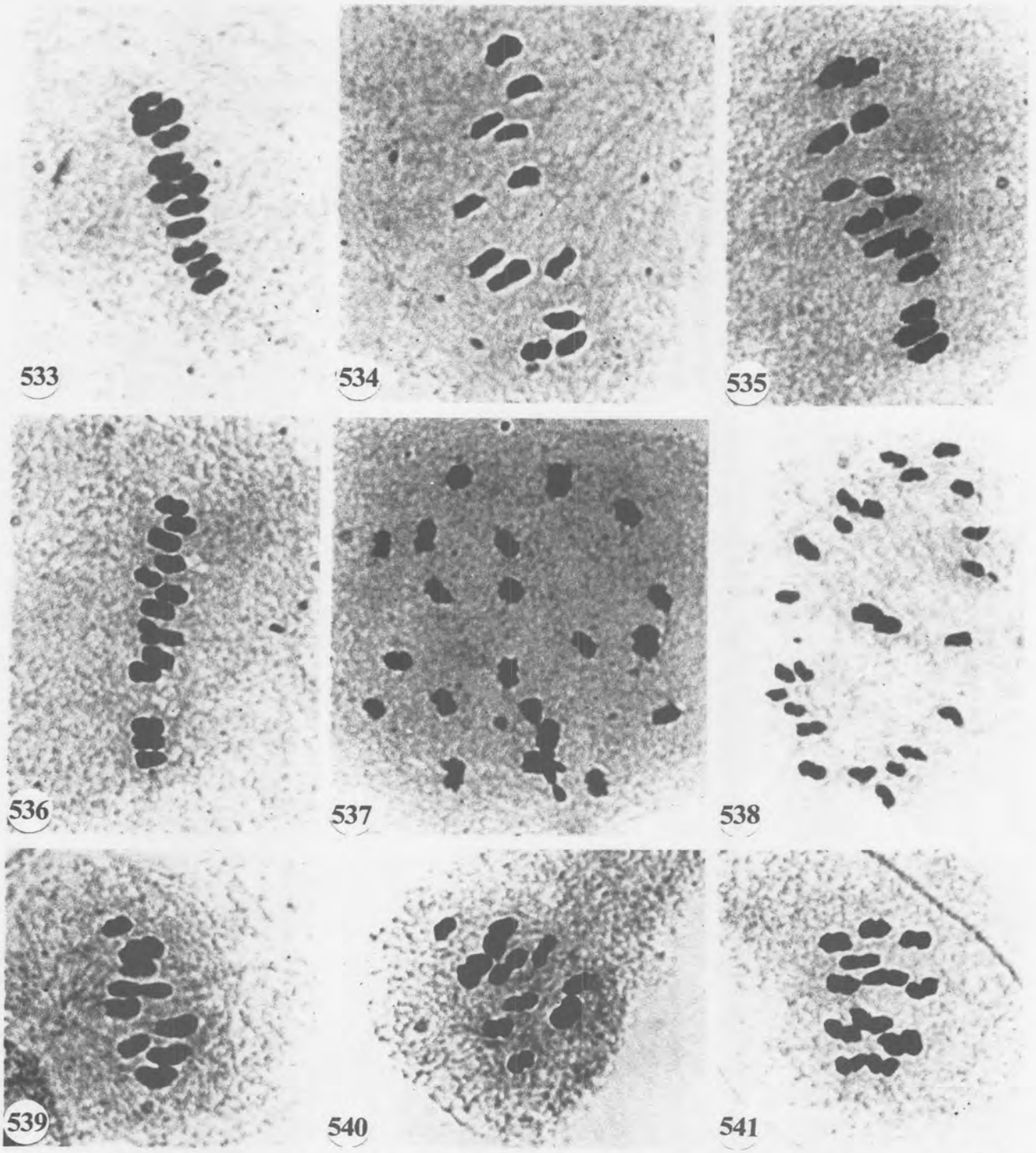
From the above it is obvious that the chromosome numbers in the other subfamilies are just as varied, if not more so, than in the Carventinae. The extremely low vagility of members of the latter subfamily alone can thus not be accountable for its karyotype evolution. Most winged Aradidae, except perhaps 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.

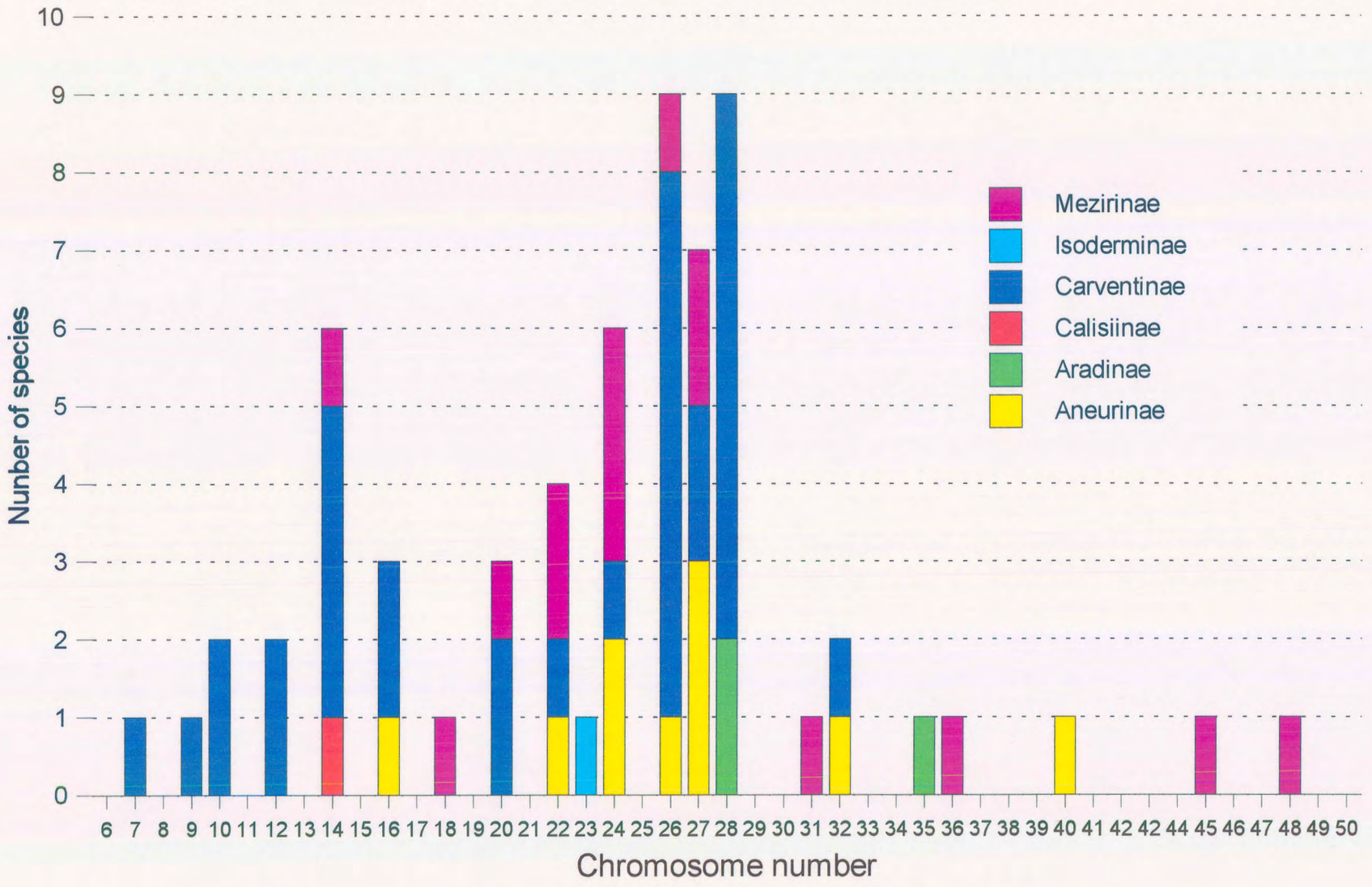



Figure 542. The chromosome numbers of the Aradidae.

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:

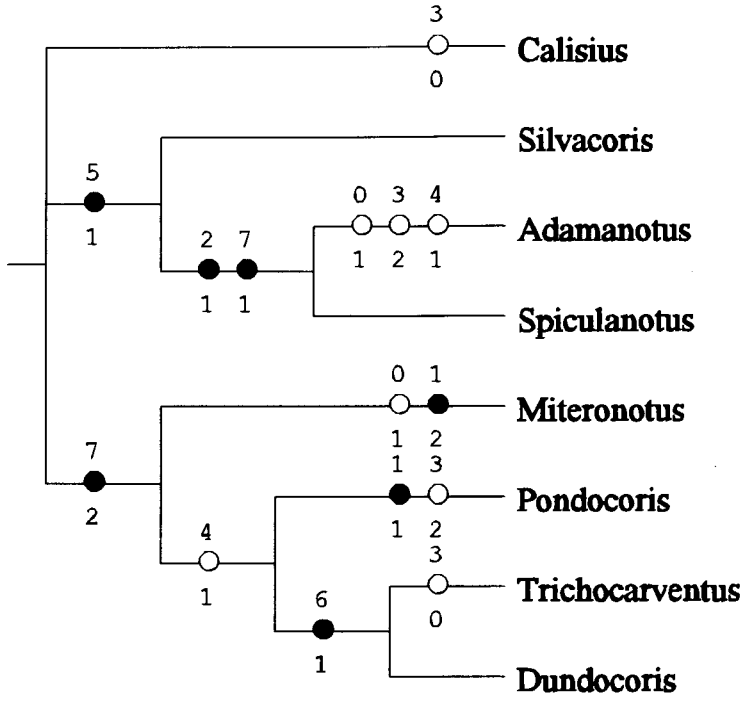



Figure 543. Cladogram of relationships among the Carventinae genera of southern Africa.

| | |
|---|---|
| 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.