Three sibling chromosomal subspecies of *Dundocoris nodulicarinus* nov.sp. (Heteroptera, Aradidae, Carventinae) with notes on the applicability of some species concepts on sibling taxa with different chromosome numbers[1]

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Abstract: *Dundocoris nodulicarinus* nov.sp. with three sibling chromosomal subspecies are described and figured. The three subspecies *D. nodulicarinus nodulicarinus* with 2n = 14XY, *D. nodulicarinus novenus* with 2n = $9XY_1Y_2$ and *D. nodulicarinus septeni* with 2n = $7XY_1Y_2$ occur allopatrically in isolated patches of indigenous evergreen forest in the eastern parts of South Africa. The nature of chromosome differences between sibling taxa, the effect of chromosome fusions on hybrid meiosis and fertility, and the genetic relationship between chromosome races are briefly discussed with special reference to *Mus musculus domesticus* and *D. nodulicarinus*. The taxonomic treatment of sibling taxa with different chromosome numbers is evaluated in terms of the biological species concept, the cohesion species concept, the phylogenetic species concept, the evolutionary species concept and the morphological species concept. It is concluded that none of the existing species concepts can treat sibling populations with different chromosome numbers satisfactorily and in the case of *D. nodulicarinus*, it was decided to describe them as subspecies.

Key words: Aradidae, Carventinae, chromosome fusion, chromosome race, *Dundocoris*, Heteroptera, hybrid fertility, hybrid meiosis, multiple sex chromosome system, sibling species, species concepts.

Introduction

The subfamily Carventinae of the Aradidae contains about 270 described species worldwide belonging to about 70 genera. They are well represented in all the major geographic regions except the Palaearctic, where they are absent, and the Nearctic, where only three species occur. The Carventinae are small (3-8 mm) bugs, restricted to evergreen forests where they are usually found on fallen twigs and branches where they reportedly feed on the wood-rotting fungi. About 90 % of all species are apterous and have extremely limited vagility. Consequently most genera and species are restricted to relatively small geographic areas.

In the Afrotropical Region 16 genera, of which 12 are apterous, occur. Of the apterous genera, eight (*Adamanotus* JACOBS, *Dundocoris* HOBERLANDT, *Miteronotus* JACOBS, *Pondocoris* HEISS & JACOBS, *Rwandaptera* HEISS, *Silvacoris* JACOBS, *Trichocarventus* HEISS & JACOBS and *Veroncaptera* VÁSÁRHELYI) are endemic to Africa, three (*Andobocoris* HOBERLANDT, *Malgasyaptera* HEISS and *Stysaptera* HEISS) to Madagascar and one (*Comorocoris* HEISS) to the Comores Islands. JACOBS (2002) provided a key to the genera of the Afrotropical Region. *Dundocoris* is by far the most species rich of the apterous genera and it is also the only genus that is widely distributed in central and southern Africa. *Dundocoris* was origi-

[1]This paper is dedicated to Ernst Heiss. Besides his inexhaustible, proficient and invaluable work on the Aradidae and other Heteroptera, he is also an unwavering and compassionate friend. Ernst, thank you for your true friendship.

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nally described from Angola (HOBERLANDT 1952) but was subsequently reported from Rwanda (HOBERLANDT 1956) and South Africa (HOBERLANDT 1959; KORMILEV 1961; HEISS & JACOBS 1989). I have also seen specimens from Mozambique. It has not yet been recorded from countries like Zimbabwe, Malawi, Zambia, Tanzania and Kenya, where areas of evergreen forest also occur, but that is nearly certainly because of a lack of collecting and undoubtedly many new species await discovery there.

In South Africa the evergreen forests (especially the montane forests) have a patchy distribution. Many of these patches are isolated and often separated by long distances from other similar forests. While a few species have a relatively wide distribution, most of these forest patches have their own unique complement of carventine species. Given the very limited dispersal potential of the species, the isolation of their habitats and the holocentric nature of their chromosomes, it was altogether not surprising when I discovered morphologically inseparably populations with different chromosome numbers of 14XY, $9XY_1Y_2$, and $7XY_1Y_2$ respectively.

There is no consensus on how to taxonomically treat sibling taxa with different chromosome numbers. They have been described as chromosomal races, chromosomal subspecies, semispecies or good biological species. Very often taxonomists describe one or two species on strength of morphological differences and then cytogeneticists or geneticists split them into more species on account of chromosome and/or genetic differences. These species are usually not formally described and are often only indicated by one or the other code. The rigorous application of any of the existing species concepts to these cases also seems to be impossible as, for example, some of these 'chromosomal' races may be fully interfertile while others may be completely isolated reproductively while they are often genetically almost identical. In the process of deciding how to deal taxonomically with these sibling taxa it was necessary to evaluate the most popular species concepts and their capacity and suitability to accommodate and facilitate the classification of such chromosomal sibling taxa.

In this paper I describe the three sibling taxa with chromosome numbers of 14XY, $9XY_1Y_2$, and $7XY_1Y_2$ respectively as subspecies of *Dundocoris nodulicarinus* nov.sp. I also briefly discuss the nature and consequences of chromosome number differences between sibling taxa with special reference to Robertsonian races of *Mus musculus domesticus*, and I evaluate five popular species concepts namely the biological species concept (BSC), cohesion species concept (CSC), phylogenetic species concept (PSC), evolutionary species concept (ECS) and morphological species concept (MSC), for applicability to such cases.

Material and Methods

As described by JACOBS (1990, 1996, 2004) with the following addition. Colour photographs were taken with the aid of a Nikon SMZ800 stereo-microscope using a Zeiss Axiocam MRc5 digital camera. Several photographs of a subject were taken at different focus levels before they were stacked with the Helicon Focus or Combine-Z software program.

The morphological terminology follows JACOBS (1986), and abbreviations are as follows: DELTg – dorsal external laterotergite (= connexivum); MTg – mediotergite; VLTg – ventral laterotergite.

The material examined is in the following collections: Albany Museum, Grahamstown (AMGS); American Museum of Natural History, New York (AMNH); The Natural History Museum, London (BMNH); National Museum, Bloemfontein (BMSA); California Academy of Sciences. San Francisco, California (CASC); D.H. Jacobs collection, Pretoria (DHJS); E. Heiss collection, Innsbruck (EHIA); Institut Royal des Sciences Naturelles de Belgique, Bruxelles (ISNB); Museum National d'Histoire Naturelle, Paris (MNHN); Museé Royal de l'Afrique Centrale, Tervuren (MRAC); Zoological Institute, Lund University, Lund (MZLU); Naturhistoriska Riksmuseet, Stockholm (NHRS); Natal Museum, Pietermaritzburg (NMSA); Queensland Museum, Brisbane (QMBA); South African Museum,

Cape Town (SAMC); National Collection of Insects, Pretoria (SANC); State Museum of Namibia, Windhoek (SMWH); Transvaal Museum, Pretoria (TMSA); Smithsonian Institution, National Museum of Natural History, Washington D.C. (USNM).

Dundocoris nodulicarinus nov.sp. (Figs 1-25)

Size: Length male 3.4-4.4 mm, female 3.7-5.1 mm; width male 1.7-2.2 mm, female 1.9-2.6 mm; measurements are given in Tables 1-3.

Habitus: 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 encrustation removed.

Head: About 1.05x as wide (across eyes) as long (excluding 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).

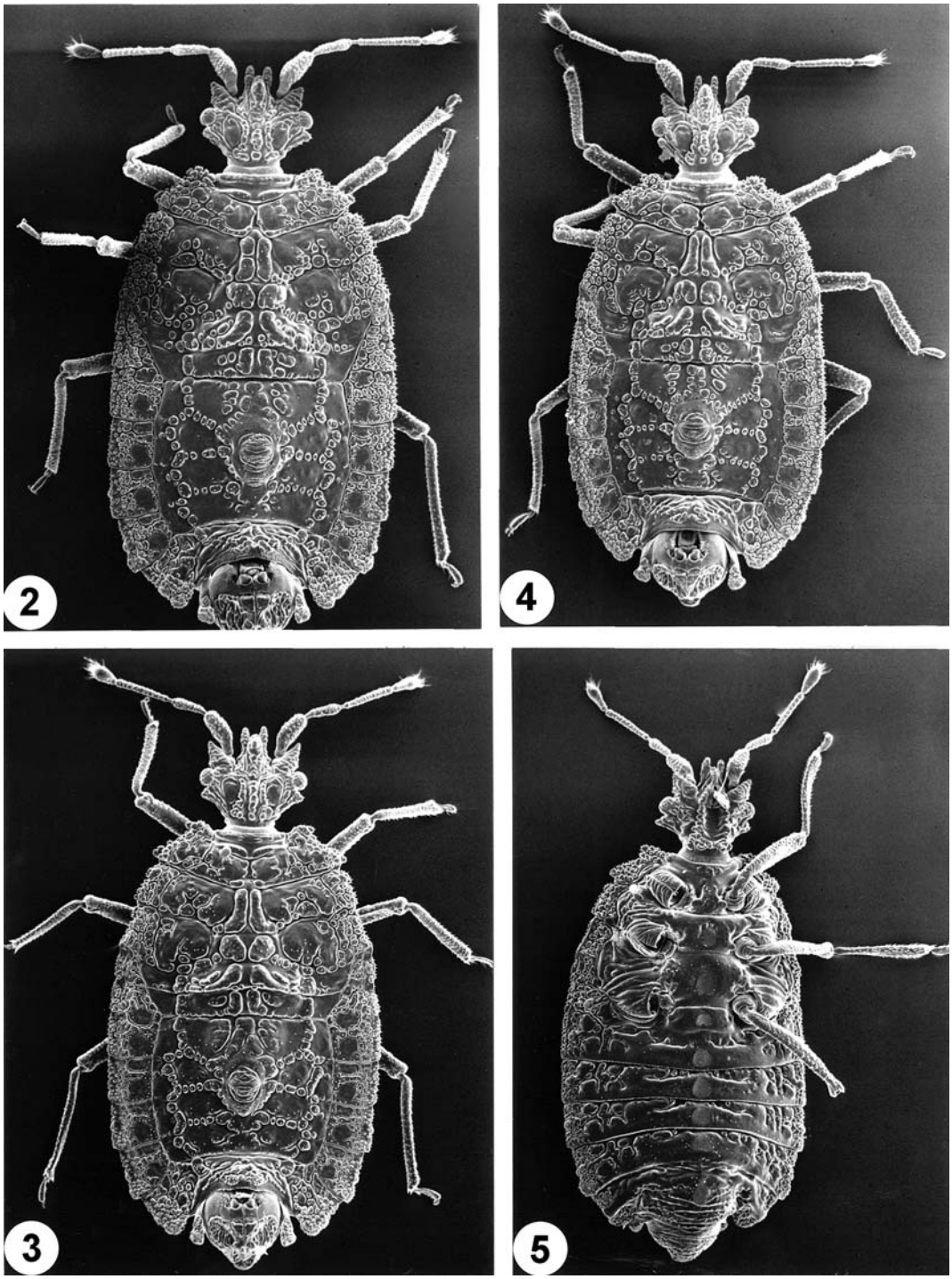
Thorax: Dorsum. Pronotum about 3x as wide as long; lateral lobes not well delimited from disk, coarsely granulate, forming a small anterolateral projecting lobe anteriorly; disk irregularly excavated; transverse ridge behind collar with a median depression.

Mesonotal median ridge consisting of 2(1+1) parallel ridges, split over total length by a longitudinal suture, usually slightly curving laterad posteriorly and continuing 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.

Fig. 1: Photomicrograph of *Dundocoris nodulicarinus novenus* nov.sp. et nov.subsp., dorsal aspect of female paratype.

Suture separating meso- and metanotum very shallow sublaterally, deeper submedially. Metanotal disk smooth anteriorly and laterally; completely fused with MTg 1 but demarcated by a transverse row of tubercles on its posterior margin. 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 with no indication of a suture; slightly and evenly raised rela-



Figs 2-5: Scanning electron photomicrographs of the subspecies of *Dundocoris nodulicarinus* nov.sp. (**2**) *D. nodulicarinus nodulicarinus* nov.sp., dorsal aspect of male paratype (**3**) *D. noclulicarinus septeni* nov.sp. et nov.subsp., dorsal aspect of male paratype (**4-5**) *D. nodu!icarinus novenus* nov.sp. et nov.subsp. (**4**) Dorsal aspect of male paratype (**5**) Ventral aspect of male paratype.

tive to metanotum except laterally where level slightly lower. 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 with irregular elevations 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; with 2(1+1) submedian and 2(1+1) sublateral longitudinal ridges, the remainder fairly smooth except for some irregular elevations just lateral of submedian ridges.

Venter: Collar fairly well developed ventral of lateral tubercles.

Abdomen: Dorsum. Tergal disk about 1.3x as wide as long in males and 1.13x in females; moderately elevated along median

Table 1: Measurements (in mm) of *Dundocoris nodulicarinus nodulicarinus* nov. sp. 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
Total 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
Head 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
Pronotum 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
Tergal disk width	1.24	3	1.27	0.043	1.23-1.33	1.62	2	1.65	0.042	1.61-1.68
Antennal segment I	0.38	3	0.37	0.011	0.35-0.39	0.40	2	0.39	0.001	0.39-0.40
Antennal segment II	0.26	3	0.26	0.004	0.25-0.27	0.28	2	0.28	0.009	0.27-0.29
Antennal segment III	0.43	3	0.46	0.032	0.43-0.50	0.49	2	0.49	0.006	0.48-0.50
Antennal segment 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.										

Table 2: Measurements (in mm) of *Dundocoris nodulicarinus novenus* nov.subsp. from Isidenge forest.

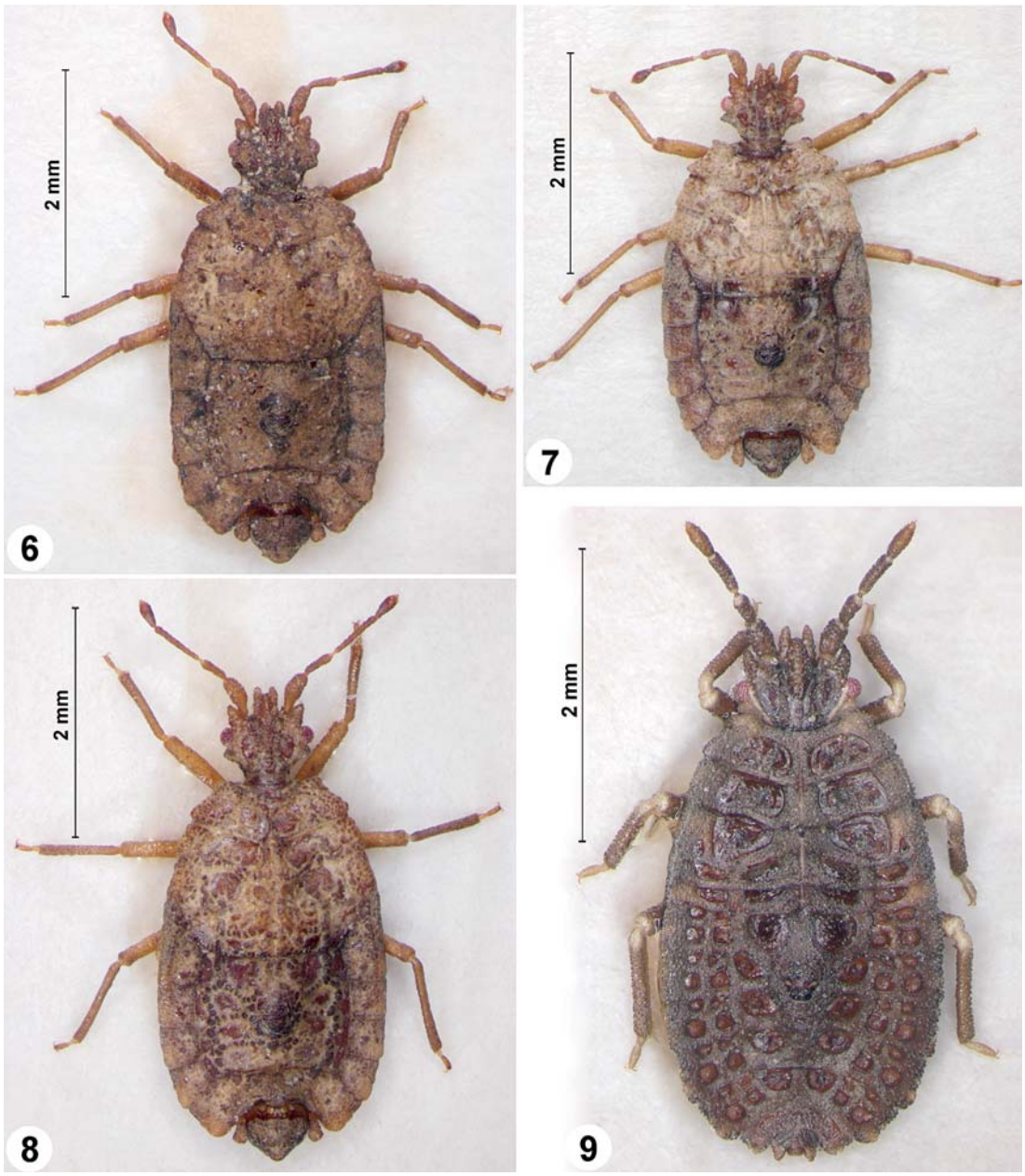
STRUCTURE	MALES					FEMALES				
	HT*	N	Mean	SD	Range***	AT**	N	Mean	SD	Range***
Total length	4.09	10	3.94	0.165	3.69-4.32	4.78	10	4.61	0.193	4.24-4.93
Total width	1.94	10	1.91	0.092	1.74-2.15	2.48	10	2.38	0.105	2.19-2.57
Head length	0.78	10	0.76	0.038	0.69-0.84	0.86	10	0.82	0.043	0.76-0.89
Head width	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
Pronotum 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
Tergal disk width	1.32	10	1.29	0.068	1.15-1.44	1.59	10	1.58	0.044	1.45-1.65
Antennal segment I	0.37	10	0.37	0.011	0.34-0.39	0.42	10	0.40	0.016	0.37-0.43
Antennal segment II	0.27	10	0.26	0.014	0.23-0.29	0.28	10	0.28	0.013	0.25-0.30
Antennal segment III	0.48	10	0.46	0.027	0.41-0.53	0.53	10	0.50	0.034	0.43-0.56
Antennal segment 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.										

Table 3: Measurements (in mm) of *Dundocoris nodulicarinus septeni* nov.subsp. 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
Total 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	0.04	0.65-0.79	0.80	10	0.79	0.053	0.68-0.90
Head width	0.77	10	0.76	0.03	0.71-0.83	0.82	10	0.83	0.047	0.73-0.92
Pronotum length	0.41	10	0.43	0.03	0.38-0.49	0.47	10	0.47	0.038	0.37-0.52
Pronotum 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
Tergal disk width	1.23	10	1.29	0.047	1.19-1.36	1.55	10	1.54	0.071	1.37-1.63
Antennal segment I	0.37	10	0.36	0.022	0.33-0.39	0.39	10	0.39	0.025	0.33-0.43
Antennal segment II	0.26	10	0.25	0.016	0.22-0.2	0.28	10	0.27	0.019	0.23-0.30
Antennal segment III	0.45	9	0.44	0.032	0.39-0.50	0.46	10	0.46	0.040	0.39-0.52
Antennal segment 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.										

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 colour pattern (anterior half dark brown, posterior half yellowish). 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 sublater-



Figs 6-9: Photomicrographs of the subspecies of *Dundocoris nodulicarinus* nov.sp. Note that the levels of incrustation of the individuals differ (**6**) *D. nodulicarinus nodulicarinus* nov.sp., dorsal aspect of male holotype (**7**) *D. noclulicarinus septeni* nov.sp. et nov.subsp., dorsal aspect of male holotype (**8-9**) *D. nodu!icarinus novenus* nov.sp. et nov.subsp. (**8**) Dorsal aspect of male holotype (**9**) Dorsal aspect of nymph (probably 4th instar).

al, 3 more than two spiracle widths from lateral margin in females and about one and a half in males, 4 just less than 2 spiracle widths from lateral margin in females and just more than 1 in males; 5-7 lateral and visible from above, 8 subterminal on paratergites.

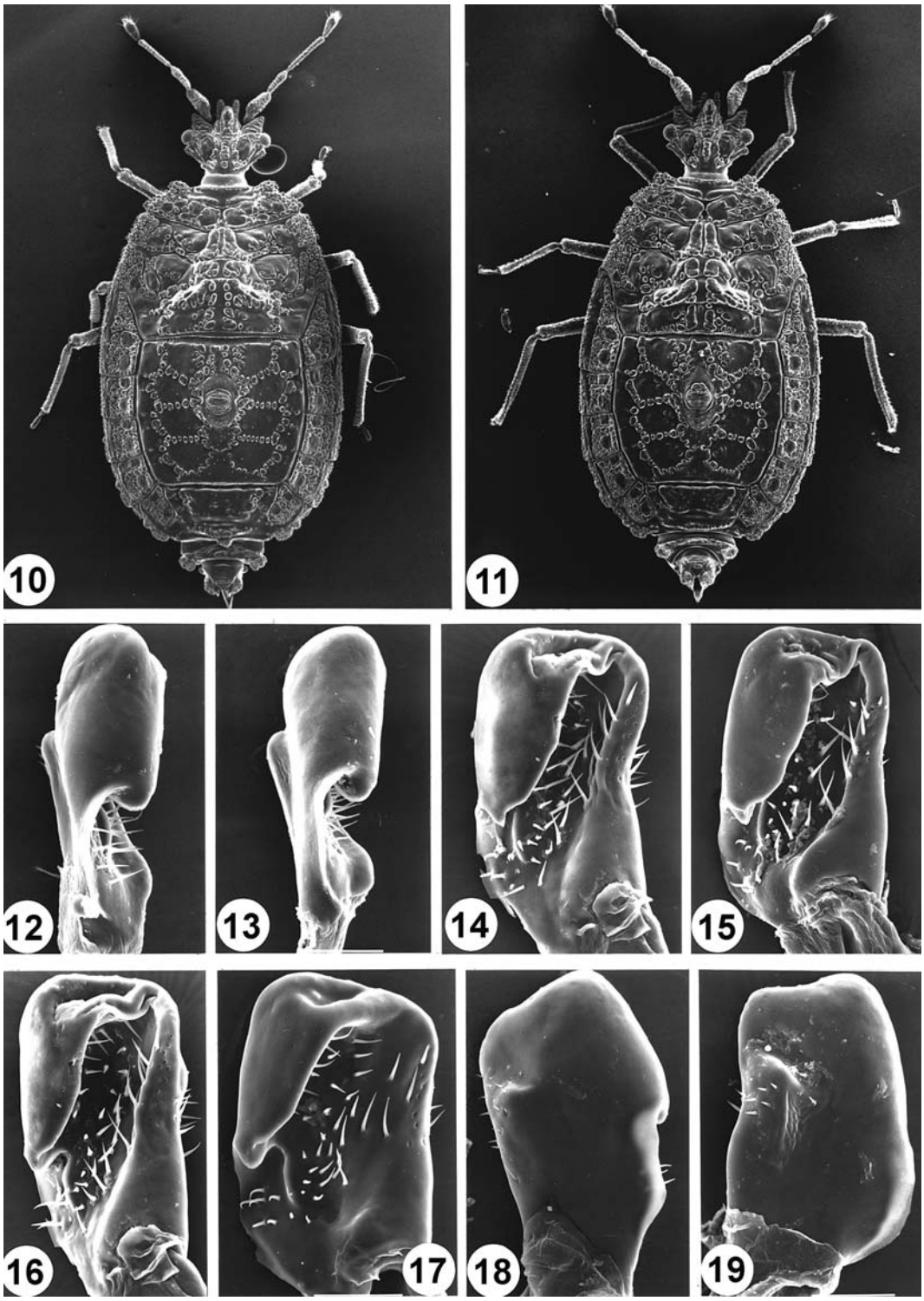
Genitalia: Pygophore as in Figs 20-25. Removed parameres as in Figs 12-19.

Chromosome number: 2n(♂) = 14XY (12 autosomes + XY), $9XY_1Y_2$ (6 autosomes + XY_1Y_2) or $7XY_1Y_2$ (4 autosomes + XY_1Y_2).

Habitat and distribution: Coastal and montane evergreen forests in southern KwaZulu-Natal and the Eastern Cape (Fig. 26).

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

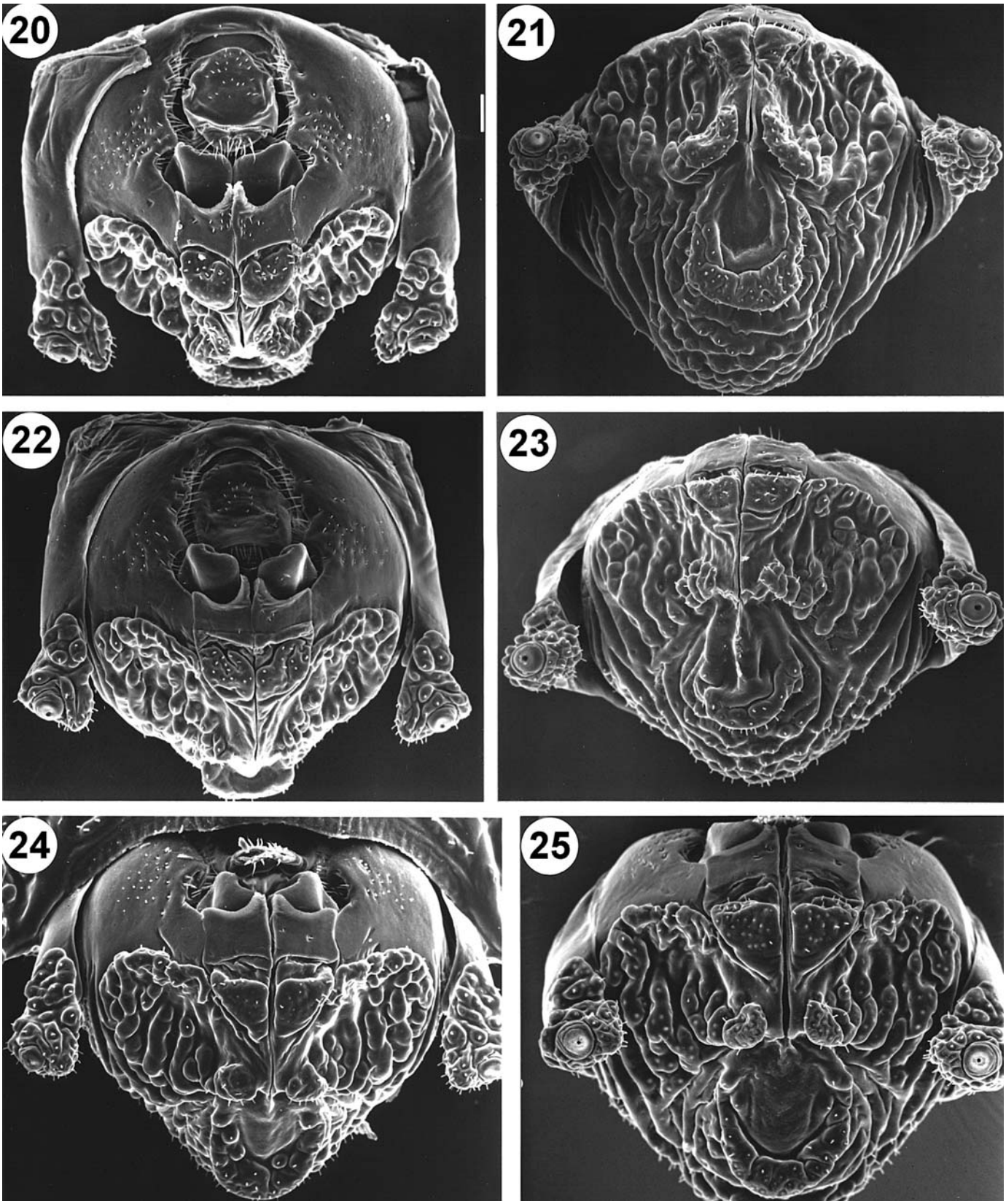
Discussion. *Dundocoris nodulicarinus* nov.sp. is closely related to *Dundocoris marieps* JACOBS and *Dundocoris transvaalensis* JACOBS with which it shares the nodulate carinae on the tergal disk, but can be distinguished from both by having no indication of a suture between the metanotum and MTg 1, by having the antennae more than 1.6x as long as width across eyes (less than 1.55x in other two species), by having spiracle 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



Figs 10-19: Scanning electron photomicrographs of the subspecies of *Dundocoris nodulicarinus* nov.sp. (**10**) *D. nodulicarinus nodulicarinus* nov.sp., dorsal aspect of female paratype (**11**) *D. nodulicarinus novenus* nov.sp. et nov.subsp., dorsal aspect of female paratype (**12-19**) Different aspects of the left parameres of males (scale bar = 50 µm). (**14, 16**) *D. nodulicarinus nodulicarinus* nov.sp. (**13, 15, 19**) *D. nodulicarinus novenus* nov.sp. et nov.subsp. (**12, 17-18**) *D. nodulicarinus septeni* nov.sp. et nov.subsp.

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.



Figs 20-25: Scanning electron photomicrographs of the pygophores of the subspecies of *Dundocoris nodulicarinus* nov.sp. (**20-21**) *D. nodulicarinus nodulicarinus* nov.sp. (**20**) Dorsal aspect (scale bar = 50 µm) (**21**) Caudal aspect (**22-23**) *D. nodulicarinus novenus* nov.sp. et nov.subsp. (**22**) Dorsal aspect (**23**) Caudal aspect (**24-25**) *D. nodulicarinus septeni* nov.sp. et nov.subsp. (**24**) Dorsal aspect (**25**) Caudal aspect.

Dundocoris nodulicarinus nodulicarinus nov.sp. et nov.subsp. (Figs 2, 6, 10, 14, 16, 20-21)

Measurements are given in Table 1.

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 also seems to be slightly 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. 26).

Discussion: I have specifically chosen the 14XY cytotype as the nominate subspecies as the other two chromosome numbers are in all likelihood derived from it.

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 (4♂♂ 4 ♀♀ DHJS, 1♂ 1 ♀ TMSA). I have also collected a single male at Lesser Stinkwood forest (30°33'S 29°43'E) that I used for cytogenetic studies.

Dundocoris nodulicarinus novenus nov.sp. et nov.subsp. (Figs 1, 4-5, 8-9, 11, 13, 15, 19, 22-23)

Measurements are given in Table 2.

Dundocoris nodulicarinus novenus seems to be slightly 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. 26).

Etymology: Novenus (Lat.) = 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); 457 paratypes as follows: 17♂♂ 10 ♀♀: Qacu Forest Reserve, nr. Stutterheim, 32°25'S 27°18'E, 17.xii.1981, D.H. Jacobs (8♂♂ 6 ♀♀ DHJS, 3♂♂ 1 ♀ SAMC, 3♂♂ 1 ♀ SANC, 3♂♂ 2 ♀♀ TMSA); 1♂ 1 ♀ Schwarzwald forest, nr. Hogsback, 32°39'S 27°00'E, 16.xii.1981, D.H. Jacobs (DHJS); 216♂♂ 133 ♀♀: Same data as holotype (7♂♂ 5 ♀♀ each: AMGS, AMNH, BMNH, BMSA, CASC, EHIA, ISNB, MNHN, MRAC, MZLU, NHRS, NMSA, QMBA, SAMC, SANC, SMWH, USNM, 67♂♂ 33 ♀♀ DHJS, 30♂♂ 15 ♀♀ TMSA); 20♂♂ 20 ♀♀: ditto, 26-31.i.1984 (15♂♂ 15 ♀♀ DHJS, 5♂♂ 5 ♀♀ 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).

Dundocoris nodulicarinus septeni nov.sp. et nov.subsp. (Figs 3, 7, 12, 17-18, 24-25)

Measurements are given in Table 3.

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

Habitat and distribution: So far it has only been collected in the Alexandria forest nr. Alexandria (Fig. 26).

Etymology: Septeni (Lat.) = 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 (9♂♂ 9 ♀♀ DHJS, 2♂♂ 2 ♀♀ each: BMNH, MRAC, SAMC, 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).

The cytogenetics of *Dundocoris nodulicarinus*

The cytogenetics and karyotype evolution of the genus *Dundocoris* were discussed by JACOBS (2003a, 2003b, 2004). The evolution of the karyotypes of the subspecies of *D. nodulicarinus* in particular has been dis-

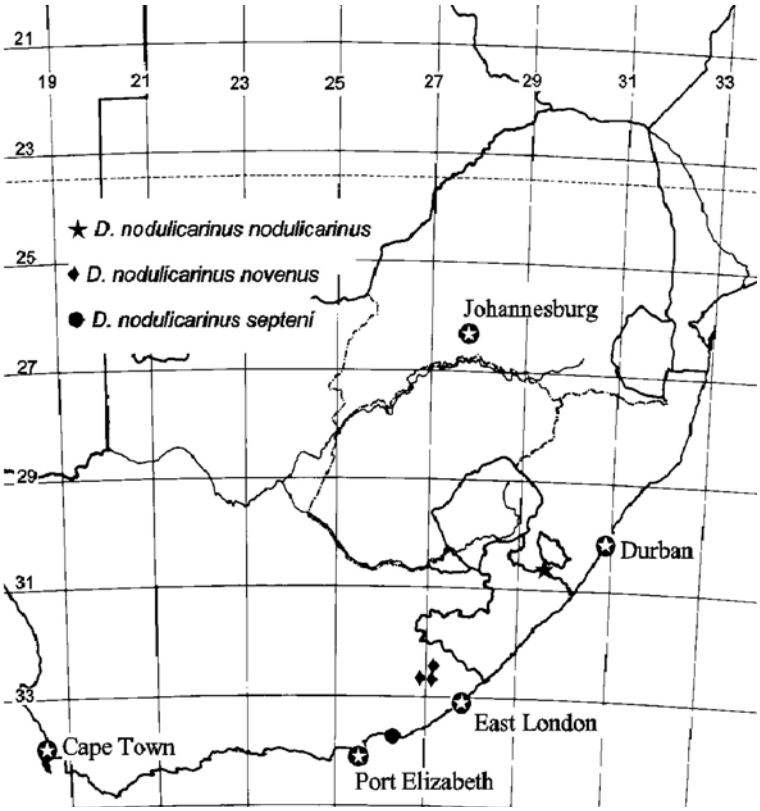


Fig. 26: Recorded distribution of *D. nodulicarinus*.

cussed in detail by JACOBS (2004). The ancestral chromosome number of *Dundocoris* is 2n(♂) = 28XY (26 autosomes + XY) where the autosomes form a more or less gradual size series while the sex chromosomes are the largest chromosomes in the complement (Fig. 27). Chromosome fusions resulted in various other chromosome numbers in the genus.

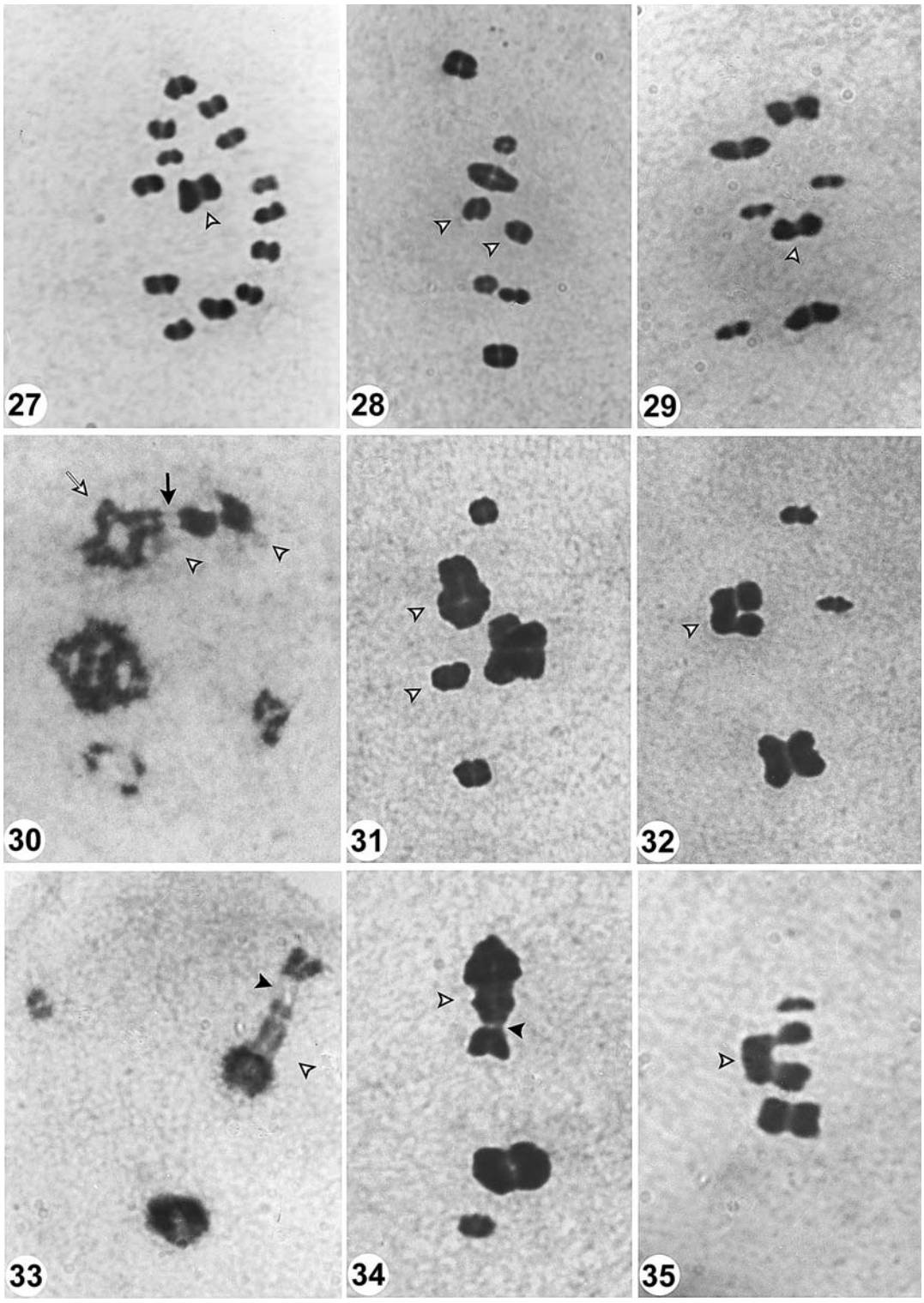
The chromosome number of *D. nodulicarinus nodulicarinus* is 2n(♂) = 14XY (12 autosomes + XY). In its karyotype three of the autosomes are distinctly larger than the other three and the sex chromosomes are similar in size to the large autosomes. At metaphase I (MI) (Fig. 28) eight structures are visible – the six autosomal bivalents and the X and Y univalents. The sex chromosome univalents resemble autosomal bivalents and undergo chromatid segregation at anaphase I (AI). At metaphase II (MII) (Fig. 29) the X and Y chromosomes (chromatids) form a 'pseudobivalent' in the centre of the autosomes which orientate to form a ring. The karyotype of *D. nodulicarinus nodulicarinus* probably originated from a 28XY ancestor by means of 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 from the fusion of two of the smallest original chromosomes.

The chromosome number of *Dundocoris nodulicarinus novenus* 2n(♂) = 9 XY_1Y_2 (6 autosomes + XY_1Y_2). 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). During diplotene/diakinesis (Fig. 30) the neo-Y and and 'autosomal' part of the neo-X are euchromatic and regularly form one chiasma (Fig. 30: open arrow). The original X-chromosome part of the neo-X is heterochromatic and often some distance apart from its autosomal part and only connected by two thin strands (Fig 30: solid arrow). The original Y-chromosome (Y_2) is also heterochromatic and usually associated with the heterochromatic original X until pre-metaphase I. At MI (Fig. 31) five structures are present, namely the neo-X-neo-Y (which has condensed into a heteromorphic structure), the original Y-chromosome (Y_2) which resembles a bivalent and the three autosomes (one very large and two small bivalents). During AI the neo-X-neo-Y and original Y chromosomes undergo chromatid segregation resulting in the presence of four structures at MII (Fig. 32) – the three autosomes and a tripartite structure consisting of the three sex chromosomes (the large neo-X on the one side and the two Y-chromosomes on the other side).

The karyotype of *D. nodulicarinus novenus* presumably originated from that of *D. nodulicarinus nodulicarinus* by means of three fusions namely:

1. Fusion between one of the small and one of the large autosomes.
2. Fusion between two of the large autosomes to form a very large autosome.
3. Fusion between the remaining large autosomes and the X-chromosome.

The chromosome number of *Dundocoris nodulicarinus septeni* is 2n(♂♂) = 7 XY_1Y_2 (4



Figs 27-35: Meiotic stages in *Dundocoris callani* and *D. nodulicarinus* (**27**) Metaphase II in *D. callani callani*, 2n(♂) = 28XY (26 autosomes + XY) as example of the proposed ancestral karyotype of the genus (**28-29**) *D. nodulicarinus nodulicarinus*, 2n(♂) = 14 XY (12 autosomes + XY). (**28**) Metaphase I (**29**) Metaphase II (**30-32**) *D. nodulicarinus novenus*, 2n(♂) = 9 XY_1Y_2 (6 autosomes + XY_1Y_2) (**30**) Diplotene/diakinesis illustrating the neo-X-neo-Y sex chromosome system where the neo-Y (= Y_1) and 'autosomal' part of the neo-X (open arrow) are euchromatic and regularly exhibit a chiasma while the original X-chromosome part is heterochromatic and attached to the 'autosomal' part thin strands (solid arrow) (**31**) Metaphase I showing three autosomal bivalents and two sex chromosome structures (open arrowheads) – the large heteromorphic one being the neo-X-neo-Y and the smaller one the original Y-chromosome (**32**) Metaphase II showing three autosomes and the tripartite sex chromosome structure. (**33-35**) *D. nodulicarinus septeni*, 2n(♂) = 7 XY_1Y_2 (4 autosomes + XY_1Y_2) (**33**) Diplotene/diakinesis illustrating the fusion of a small autosomal pair of chromosomes to the original X- and Y-chromosomes respectively – solid arrowhead indicates the terminal chiasma between the neo-Y_2-chromosome and neo-neo-X-chromosome (**34**) Metaphase I showing two autosomal bivalents and the 'fish-like' sex chromosome system that contains all three sex chromosomes. The terminal chiasma between the neo-Y_2-chromosome and neo-neo-X-chromosome (solid arrowhead) is regularly visible (**35**) Metaphase II showing two autosomes and the tripartite sex chromosome structure. In all figures open arrowheads indicate the sex chromosomes.

autosomes + XY_1Y_2) where Y_1 represents the neo-Y like in *D. nodulicarinus novenus*; Y_2 represents a neo-Y that originated by the fusion of an autosome to the original Y-chromosome; and X represents 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 the homologue of the autosome that fused with the Y-chromosome, on the other side. The two homologues of one small autosome have thus been involved in fusions with the original X and Y chromosomes respectively. The karyotype consists of one large autosome, one small autosome and the three neo sex chromosomes as described above.

During diplotene/diakinesis (Fig. 33) three chromosomal structures are present: the two autosomal bivalents and a structure containing the three sex chromosomes (Fig. 33: open arrowhead). The latter structure has the neo-Y_1 forming one or two chiasmata with the large 'autosomal' part of the neo-neo-X on the one side while the neo-Y_2 is connected to it by a terminal chiasma (Figs 33-34: solid arrowheads) on the other side. During MI (Fig. 34) the three structures are more compact with the sex chromosome structure regularly forming a 'fish-like' structure that orientates equatorially and undergoes chromatid segregation at AI. Three structures are also present at MII (Fig. 35): the two autosomes and a tripartite sex chromosome structure with the neo-Y_1 and neo-Y_2 on the one side and the neo-neo-X on the other side.

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*.

Discussion

The nature of chromosome number differences between sibling populations

A very common cause for chromosome number differences between sibling populations is Robertsonian fusions where two acrocentric chromosomes translocate in their centromeric regions to form a single metacentric chromosome with presumably the loss of a centromere and a small piece of heterochromatin. As the breakpoints are in constitutive heterochromatin near the centromere the resultant individual and population (if it becomes fixed) are genetically identical to the parental stock except perhaps for a position effect on gene control. Robertsonian fusions are widespread in the animal and plant kingdoms, but are especially prevalent in many rodents where they have been very well studied. In the house mouse *Mus musculus domesticus* more than 40 natural occurring chromosomal races have been reported (NACHMAN & SEARLE 1995) and new ones are still discovered. Some of the Robertsonian races seem to have originated in a very short time in the evolutionary sense: the six races on Madeira have appeared in less than 500 years (BRITTON-DAVIDIAN et al. 2000) and the Seveso race in Italy seems to originated in less than 20 years (GARAGNA et al. 1997).

The ancestral karyotype of *Mus musculus domesticus* is 2n = 40XY with all the chromosomes acrocentric. The chromosome numbers of the Robertsonian races varies from 2n = 22XY to 2n = 38XY. All of the autosomes, except for the smallest one (chromosome 19), have been reported taking part in Robertsonian fusions in wild populations of mice. Chromosome 19 has, however, been involved in Robertsonian fusions in laboratory stocks of mice. The sex chromosomes, however, do not seem to be readily involved in Robertsonian fusions although fusions involving the X chromosome have been reported in laboratory strains (NACHMAN & SEARLE 1995).

The Heteroptera have holocentric chromosomes (i.e. chromosomes without a localised centromere where the spindle usually attaches along the entire length of the

chromosome during mitosis, or to the chromosome ends during meiosis) and chromosome fusion as well as chromosome fission can be a source of new chromosome numbers. The former, of course, decreases the chromosome number while the latter would result in an increase of the number of chromosomes. Chromosome fusions in the Heteroptera are in effect comparable to Robertsonian fusions, with a few differences. Firstly, supposedly the chromosomes join at their telomeres and there is no loss of heterochromatin. Secondly, and very importantly, more than two chromosomes can fuse to form a single chromosome and having a profound effect on the meiosis and fertility of hybrids (refer to discussion below). Thirdly, in the case of *Dundocoris nodulicarinus*, the sex chromosomes are also involved in the fusions, resulting in a multiple sex chromosome system (a neo-XY_1Y_2 system in two of the populations) as discussed above.

Effect of Robertsonian fusions and chromosome fusions in the Heteroptera on hybrid meiosis and fertility

The detrimental effect of a single Robertsonian fusion on the fertility of hybrids in mice is very small (GROPP et al. 1972; CAPANNA et al. 1976; REDI & CAPANNA 1988), depending on the particular chromosomes that are involved in the fusion as well as on the specific population in which they occur. During metaphase I in hybrids a regular trivalent forms and during anaphase I some malsegregation (usually 3-20 % in males, and somewhat higher in females, depending on the particular chromosomes involved) occur, giving rise to unbalanced (aneuploid) gametes. In hybrids heterozygous for more Robertsonian fusions, nondisjunction is expected to result in a greater percentage of aneuploid gametes, but even in hybrid males heterozygous for three fusions it was less than 25 % (BAKER & BICKHAM 1986) or less than 10 % in some wild populations (NACHMAN & SEARLE 1995).

The situation is more complicated when mice belonging to populations with different Robertsonian fusions are crossed, especially if the same chromosome is involved in different fusions in the respective populations. GROPP et al. (1972) demonstrated 58 % aneuploidy in a male heterozygous for a single monobrachial fusion. Depending on the number of such fusions long chains and rings of chromosomes form during meiosis, often resulting in the complete sterility of the carrier (REDI & CAPANNA 1988; HAUFFE & SEARLE 1993). In the house mouse several populations that are intersterile have been reported (CAPANNA & CORTI 1982; BRITTON-DAVIDIAN et al. 2000).

In the $9XY_1Y_2$ race of *D. nodulicarinus* three of the autosomes of the 14XY race have fused to form one large autosome while another autosome has fused with the X chromosome to give rise to the neo-XY_1Y_2 sex chromosome system (JACOBS 2004). The $7XY_1Y_2$ population presumably originated from the $9XY_1Y_2$ race when one homologue of an autosomal pair fused with the X chromosome (at the opposite end of the first fusion) while the other one fused with the Y chromosome (JACOBS 2004). Where more than two chromosomes have fused to a single chromosome a heterozygous hybrid would undoubtedly be sterile as malsegregation as well as the products of crossovers would result in unbalanced gametes. Both the $9XY_1Y_2$ and the $7XY_1Y_2$ populations are thus expected to be reproductively isolated from the 14XY population. It would not be wise to speculate on the fertility of hybrids between the $9XY_1Y_2$ and $7XY_1Y_2$ populations due to their unique composition and the involvement of both the X and Y chromosomes in fusions, but one would expect at least some reduction in fertility.

The genetic relationship between chromosomal races

Genetic and morphological differences between mice with different karyotypes are small or non-existent and both allozyme and mitochondrial data show that Robertsonian and non-Robertsonian populations have similar levels of genetic variability (NACHMAN & SEARLE 1995). It has long been known that karyotypic and genetic evolution often proceed at vastly different rates. At 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. At the other extreme we find populations which are virtu-

ally identical morphologically and genetically but have vastly different karyotypes or chromosome numbers as in the case of the house mouse. At the very extreme it is conceivable that different populations of the same species could have evolved different chromosome numbers and are reproductively isolated (as a result of abnormal meiosis), but have remained genetically identical.

The different chromosomal races of *D. nodulicarinus* probably approximate such a case: they are morphologically identical and inseparable and to all indications occupy the same niche in different evergreen forests, but they are reproductively isolated as argued above.

Taxonomic treatment of sibling taxa with different chromosome numbers

The first reported Robertsonian population of the house mouse with a chromosome number of 2n = 26XY was described in the tobacco mouse *Mus poschiavinus* (GROPP et al. 1969). Since then many new Robertsonian races have been found with chromosome numbers ranging between 2n = 22 and 2n = 38, and it was realised that *M. poschiavinus* is just a chromosomal race of *M. musculus domesticus* and that its phenotype falls within the variation spectrum of the latter. None of the Robertsonian races reported subsequently have been assigned any formal taxonomic status although some of them are reproductively isolated and are good biological species (BAKER et al. 1985).

The general procedure for taxonomists is to describe species and subspecies on account of morphology, variation and geographic distribution of the group under consideration, often making use of museum specimens alone. In many groups, cytogenetic studies subsequently reveal karyotypic variation and good biological species are postulated on the grounds of observed or expected reproductive isolation between populations as a result of meiotic abnormalities that would render the F1 hybrids sterile. Very few of these species are, however, formally described as they are genetically very similar, can only be identified by cytogenetic investigation and fall outside the resolution of the morphological or phenetic species concepts that are usually applied by taxonomists. There is also a reluctancy to describe such species as it can complicate already complex situations further. For example the Pocket Gopher, *Thomomys talpoides* complex, has about 60 described subspecies (THAELER 1968, 1974). Some of these have the same or nearly the same chromosome number and are fully interfertile, others have different chromosome numbers and are to various degrees reproductively isolated. Different chromosome numbers sometimes also occur in different populations of the same subspecies and these are also variously reproductively isolated from each other. Only when sibling populations with different chromosome numbers occur sympatrically and do not hybridise, are they sometimes formally described as species e.g. *Rhogeessa genowaysi* (Chiroptera: Vespertilionidae) (BAKER 1984).

The application of different species concepts to these cases could lead to different answers concerning the specific status of these populations. I therefore deem it appropriate to examine a few of the most popular and contemporary species concepts to find how they would treat such taxa. There are more than 20 species concepts that are in use today (MAYDEN 1997), but I shall only discuss the five which, to my mind, are the most popular or applied concepts. They are the biological species concept (BSC), cohesion species concept (CSC), phylogenetic species concept (PSC), evolutionary species concept (ECS) and the morphological or phenetic species concept (MSC).

The Biological Species Concept (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 1963). Although many weaknesses of the BSC have repeatedly been exposed in the past (e.g. TEMPLETON 1989; CRACRAFT 1989), it is still the most widely adopted species concept. The BSC is appealing because of its simplicity and usefulness in thinking about evolution and it is also easy to apply population genetics to 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 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 (1981) refers to them as 'semispecies'. Syngameons, or superspecies as MAYR (1963) 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; TEMPLETON 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 and that without gene flow, given enough time, speciation is an inevitable consequence (TURELLI et al. 2001). 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 aneurine (Aradidae) which is a weak flyer, was originally described from Madagascar but was subsequently found to occur widespread in south-

ern 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. Under the BSC two populations that can not interbreed successfully would in theory belong to two separate species but in practice it is more complicated. In *Mus musculus domesticus* CAPANNA & CORTI (1982) could not find any hybrids between a 24 chromosome race and a 26 chromosome race although they occurred in the same buildings. They concluded that postmating barriers (because of meiotic abnormalities) as well as premating barriers existed between these races and that they are good biological species as they comply with the BSC in all respects. However they specifically did not propose a taxonomic division for these Robertsonian races.

Under the BSC at least the 14XY population of *D. nodulicarinus* would be a separate species from the $9XY_1Y_2$ and $7XY_1Y_2$ populations. The status of the latter two populations would be uncertain as it is uncertain whether they are reproductively isolated.

The Cohesion Species Concept (CSC)

This concept defines a species as "the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (TEMPLETON 1989). Where the BSC defines a species in terms of isolating mechanisms, the CSC defines a species in terms of mechanisms yielding cohesion. These mechanisms include genetically based (genetic exchangeability) as well as environmentally based (demographic exchangeability) mechanisms. Genetic exchangeability is defined as the factors that define the limits of spread of new genetic variants through gene flow and include mechanisms promoting genetic relatedness through gene flow as well as isolating mechanisms. Demographic exchangeability is defined as the factors that define the fundamental niche of the species and determine the populational boundaries for the action of microevolutionary forces like gene flow, genetic drift and natural selection.

Not all species will be maintained by the same cohesion mechanism or mixture of cohesion mechanisms. Each species will probably have it own unique combination of mechanisms as each of the mechanisms can vary from weak to strong in its contribution to a specific species. For sexually reproducing species genetic exchangeability will usually be more important than demographic exchangeability while the species status of asexual taxa is determined exclusively by demographic exchangeability because genetic exchangeability has no relevance.

The main advantage of the CSC is that it is applicable to the total spectrum of biological taxa, from asexual taxa to syngameons. Furthermore it can provide guidance in understanding speciation as an evolutionary process. Speciation is now regarded as the evolution of cohesion mechanisms and not of isolating mechanisms alone as under the BSC.

The main problem with the CSC is that it is poor when we try to make it operational (ENDLER 1989). It is impossible to determine the role and importance of the various cohesion mechanisms for every species and it is not clear how to interpret varying degrees of cohesion between groups. When there is a conflict between genetic and demographic exchangeability, TEMPLETON (1989) ascribed it to the process of speciation and named them 'bad' species. However, he offers no suggestions on how to handle such cases in formal taxonomy - should they be described as species, subspecies or only mentioned as varieties? This problem is probably more widespread than it seems at first glance. Because all the cohesion mechanisms can occur in varying degrees, we would expect to find a wide range of variation of the cohesion mechanisms, not only between species but also between populations of the same species, especially where isolated populations exist. Many, if not the majority of species would be expected to have some 'bad' populations that vary in the strength and perhaps also the nature of the cohesion mechanisms. How different must

such populations be to be regarded as separate species (or subspecies)? The original definition of the CSC states "the most inclusive population of individuals having the potential for phenotypic cohesion" suggesting that the phenotype will be important in evaluating populations and ENDLER (1989) remarked that the CSC can degenerate into the phenetic species concept. Several subsequent definitions of the CSC, however, abandoned the reference to phenotypic cohesion (TEMPLETON 1989: 20, 25; TEMPLETON et al. 2000; TEMPLETON 2001).

It is unclear how cases like the reproductively isolated populations of *Mus musculus domesticus* and *Dundocoris nodulicarinus* would be handled in terms of the CSC, except that they probably represent 'bad' species.

The Phylogenetic Species Concept (PSC)

With the advent and use of the cladistic methods of HENNIG (1966) by systematists the stage was set for species concepts based on the patterns revealed by these methods. The PSC is the most successful that was subsequently formulated on cladistic principles (but see below). The PSC can be regarded as an operational lineage definition that is process free in the sense that it makes no assumptions on the process of speciation. There are several different definitions of the PSC that may be classified into two main categories, namely: 1. where monophyly is a strict prerequisite, also called the monophyletic (or autapomorphic) version, and 2. where it is based on descent and diagnosability, also known as the diagnosable version (HULL 1997). The latter is in effect not a concept based on cladistics anymore as the most important principle of cladistics, namely monophyly based on autapomorphic character states, has been discarded.

1. The monophyletic version

According to this version "a geographically constrained group of individuals with some unique apomorphous character, is the unit of evolutionary significance" (ROSEN 1978) or a species is "the smallest diagnosable cluster of individual organisms forming a monophyletic group within which there is a parental pattern of ancestry and descent" (MAYDEN 1997) or "the least inclusive monophyletic group definable by at least one autapomorphy" (HULL 1997). This version of the PSC stays true to cladistic principles in requiring monophyly for a species, but at the same time it is also one of its major weaknesses as monophyly is not reconcilable with biological reality. Consider a widespread species with many somewhat isolated populations. If one of these populations speciates it would become a descendant 'species'. Within the remaining populations those that are geographically close to the descendant species may be more closely related (in a genealogical sense) to members of the descendant species than they are to more distant populations of the 'ancestral' species (BAUM 1992). Furthermore the ancestral species will cease to be monophyletic, leaving, according to BAUM (1992), only three ways to accommodate such a pattern: i) treat the descendant as a distinct species only when the ancestor becomes monophyletic through interbreeding and extinction; ii) recognise the ancestor as some entity other than a species e.g. a 'metaspecies' or iii) recognise both species, thereby discarding the monophyly criterion. The latter seems to be the logical and biologically sensible option, but then this version becomes synonymous with the diagnosable version.

2. The diagnosable version

The following definitions are often used for this version. A species is "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (CRACRAFT 1983) or "an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent" (CRACRAFT 1989) or "the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states" (WHEELER & PLATNICK 2000).

The objective of the PSC is to identify the terminal twigs on the evolutionary tree. This is done on the basis of differentiation between populations. Some differentiation results in reproductive isolation and some does not (CRACRAFT 1989) and the PSC

does not require reproductive isolation as a prerequisite for species status. Any population that is diagnosably distinct i.e. having at least one diagnostic character that is discrete, fixed within the population and absent from close relatives (BAUM 1992) or having a unique combination of character states (WHEELER & PLATNICK 2000), should be regarded as a species (CRACRAFT 1997). Although phylogenetic species can be diagnosed on morphology alone (CRACRAFT 1997), diagnostic characters need not be morphological but can be chemical or behavioural, provided that they can be inferred to have a genetic basis (BAUM 1992) or they can be represented by any intrinsic attribute of organisms, from the genome level on up (CRACRAFT 1989). Diagnosably distinct allopatric populations will be regarded as separate species, presumably, however slight the difference (CLARIDGE et al. 1997). For this reason the subspecies category is irrelevant to the PSC.

The most ardent proponents of the PSC are ornithologists. They reckon that the number of bird species will only increase about two-fold if the PSC is applied. As most of the potential new species have already been described as subspecies, there would also not be a escalation in the number of scientific names. This may be true for groups like the birds that generally have high vagilities but in many groups with low vagilities the situation is quite different. Many species consist of several to many allopatric or parapatric populations that can be identified diagnostically. The situation may reach absurdity if characters like allozymes and molecular data are used since almost every population would theoretically then constitute a separate species. This flaw in the PSC is also pertinently exposed by the Robertsonian races of *Mus musculus domesticus* and many other rodent and mammalian species. Chromosome number is a valid diagnostic character and therefore all Robertsonian races, whether they are reproductively isolated or not, should be regarded as valid separate species. The present *Mus musculus domesticus* would thus be fragmented into more than 40 species if the PSC is applied. In *Thomomys talpoides* some of the chromosomal races literally occur a few metres apart (THAELER 1974) and one would not be able to identify a specimen before performing a cytogenetic investigation on it. One wonders what would happen to *Homo sapiens* under the PSC.

HULL (1997) pointed out that a further problem with the PSC is that it can divide organisms into overlapping and incompatible species, depending on which characters are picked to be diagnostic. As diagnostic characters need not to be autapomorphic, they need not to nest.

In the case of *D. nodulicarinus* the three chromosomal populations would undoubtedly qualify as separate species under the PSC.

The Evolutionary Species Concept (ESC)

The ESC defines a species as "a lineage (an ancestor-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies" (SIMPSON 1961) or "a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (WILEY 1978).

MAYDEN (1997) considers the ESC as the only existing species concept suitable as a primary species concept. The ESC is a lineage concept where species are lineages extended in time, and it process free as no assumptions on the origin of the lineages are implied. It is applicable to all life forms, sexual or asexual, past or present – all organisms belong to some evolutionary species. The main drawback of the ESC is that it is not operational – species status can be determined only in retrospect (HULL 1997).

WILEY (1978) argued that a hypothesis on whether two populations maintain separate identifiable lineages can be drawn and tested. Evidence to test such hypotheses can come from a wide variety of sources which may include genetic, phenetic, spatial, temporal, ecological, biochemical and behavioural evidence (WILEY 1978). However, what exactly a separate evolutionary tendency is and what is necessary to maintain it, is very vague and in practice it is impossible (or at least very subjective) to decide

(except in retrospect) if a certain population has an evolutionary tendency of its own. For example, does a population that is slightly morphologically or otherwise differentiated and is reproductively isolated by distance (and perhaps not genetically) from other presumably conspecific populations, have an evolutionary tendency of its own? If so, then most insular populations and many peripheral populations should be regarded as good species.

It is clear that the ESC is not operational and to make decisions on the evolutionary distinctness of two populations, it relies on some of the secondary species concepts. Depending which of these concepts is invoked in the particular case, the ESC in essence becomes synonymous with that concept and subject to all the deficiencies and limitations of the particular concept.

How the ESC would handle the chromosomal populations of *Mus musculus domesticus* and *Dundocoris nodulicarinus* will depend on which of the secondary species concepts will be used to assess the situation. It is evident from the discussion of WILEY (1978) that he assigns high importance to reproductive isolation (although not necessarily complete reproductive isolation) as a prerequisite for the ESC as he states: "Separate evolutionary lineages (species) must be reproductively isolated from one another to the extent that this is required for maintaining their separate identities, tendencies, and historical fates" while HULL (1997) states that the ESC extends the BSC through time. If the BSC is invoked to assess the chromosomal populations, one would end up with the same problems and failure as discussed under the BSC above.

The Morphological Species Concept (MSC)

Many definitions, that differ somewhat from each other, exist for the MSC e.g. "species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (CRONQUIST 1978) or species are "the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes" (DU RIETZ 1930) or "a species is a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name" (REGAN 1926).

It is debatable if the MSC can really be regarded as a species concept – CLARIDGE et al. (1997) regarded it only as a method of description. I include the MSC in the discussion for the only reason that it is the most commonly used method of species definition by taxonomists. By far the majority of species (especially invertebrates) are described from museum specimens with very little or no data on their biology, ecology, behaviour, etc. Taxonomists are thus forced to apply the MSC although they themselves usually regard morphological distinctness as an indication of something else (e.g. reproductive isolation if they are proponents of the BSC), depending on which species concept they favour.

The advantage of the MSC is that it is very operational and easily applicable to most life forms, sexual or asexual. It has several disadvantages: it is not based on modern genetic principles; it can not recognize sibling species; it over-accentuates the importance of different phenotypes in an interbreeding population and it is very subjective in deciding how much difference is needed to assign species status.

In the case of *M. musculus domesticus* and *D. nodulicarinus* the sibling chromosomal populations would not be recognized and in the latter only one species without any subspecies would be described.

Conclusion

It is evident that sibling populations with different chromosome numbers pose a serious problem for all the species concepts and that none of the existing species concepts can handle such cases satisfactorily. The ESC and CSC do not provide conclusive answers on the species status of such populations while the conclusions of the BSC, PSC and MSC do not make biological sense and/or are impractical to apply. According to the BSC some of the chromosomal populations should be regarded as species (if they are reproductively isolated)

while the rest should not, notwithstanding the fact that there are no or very few genetical or morphological differences between any of them. The PSC regards all chromosomal races as different species. This will, apart from being biologically unsound, lead to the chaotic situation that cytogenetic investigations would have to be carried out before many specimens could be identified. The MSC does not recognise chromosome races, and subdivisions on account of morphology are often not congruent with cytogenetic or genetic data.

In the case of *D. nodulicarinus* I have decided to describe the chromosome populations as subspecies for the following reasons:

It is convenient to have names when discussing the origin and evolution of the different chromosome races.

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.

To my mind a classification system must adhere to established scientific principles but it must also be as convenient and practical as possible at the same time. An ecologist doing a species survey would be able to attach a specific name to a specimen although he might not be able to determine 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.

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Zusammenfassung

Dundocoris nodulicarinus nov.sp. wird mit drei chromosomalen Unterarten beschrieben und abgebildet. Die drei Unterarten *D. nodulicarinus nodulicarinus* (2n=14XY), *D. nodulicarinus novenus* (2n=9XY$_1$Y$_2$) und *D. nodulicarinus septeni* (2n=7XY$_1$Y$_2$) kommen allopatrisch, in isolierten, immergrünen Waldstandorten im östlichen Südafrika vor. Chromosomale Unterschiede zwischen nahe verwandten Taxa, die Effekte chromosomaler Fusion auf Hybridisierung und Fertilität, und die genetische Beziehung zwischen chromosomalen Rassen werden anhand von *Mus musculus domesticus* und *D. nodulicarinus* diskutiert. Die taxonomische Bewertung nahe verwandter Arten mit unterschiedlicher Chromosomenzahl wird anhand verschiedener Artkonzepte (das Kohäsions-Artkonzept, das phylogenetische A., das evolutionäre A., das morphologische A.) diskutiert. Keines dieser Konzepte bietet eine zufriedenstellende Lösung für das taxonomische Problem verwandter Arten mit unterschiedlichen Chromosomenzahlen und im Fall von *D. nodulicarinus* werden diese als Unterarten beschrieben.

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