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CHROMOSOME NUMBERS AND SEX-DETERMINING MECHANISM IN AUSTRALIAN CARABIDAE (COLEOPTERA)

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ABSTRACT

The chromosome number and sex-chromosome mechanism are listed for 70 species of the family Carabidae of the Australian fauna. Male diploid numbers vary between 2n = 16 and 2n = 55 and the male sex-chromosome mechanisms are XO or XY. The chromosome number 2n = 37, corresponding to a meioformula n = 18 + X (which possibly represents the ancestral condition in the family) is present in 13 species including primitive and characteristically Australian groups such as the Pseudomorphinae. The data obtained in this work represent the first approach to the cytogenetics of Australian carabid beetles.

Recent papers have increased the number of carabid beetles cytogenetically studied to more than 800 species (Nettmann 1986; Serrano *et al.* 1986; Yadav *et al.* 1986; Yadav and Burra 1987; Rozek 1988, 1989, 1992; Rozek and Warchalowska-Sliwa 1987; Rozek and Maryanska-Nadachowska 1991; Rozek and Rudek 1992; Collares-Pereira and Serrano 1990; Galián *et al.* 1990*a,* 1991*a, b,* 1992*a, b*; and additional references in Galián *et al.* 1990*b*). These studies have dealt with the Palearctic, Nearctic and Oriental faunas. Nothing has been published on the chromosomes of the Australian fauna, which has about 1,800 described and valid species (Moore *et al.* 1987). In the present paper, the chromosome numbers of 70 of these species are reported and their cytotaxonomical significance is discussed.

MATERIALS AND METHODS

The number of individuals studied per species and the collecting localities are listed in Table 1. Identifications were made by one of the authors (B.P.M.) and the nomenclature is as given by Moore *et al.* (1987). The beetles have been deposited in the Australian National Insect Collection (ANIC), Canberra, Australia. Karyological analyses were carried out on gonads using a routine orcein-squashing method (Galián *et al.* 1990*a*). In some specimens a 0.04 M sodium acetate plus 0.05% colchicine solution was injected a few minutes prior to dissection of the gonads. Chromosome counts were made mainly from males, some from females and in some species from both. Data in Table 1 are referred to males unless otherwise indicated.

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Results and Discussion

The results obtained are discussed at supertribal or subfamily level.

The two species of Paussinae studied have high chromosome numbers, 2n = 43 and 2n = 46. The chromosomes of these species are characterized by their small size, less than 2 μm, a feature that has already been observed in the only Palearctic species of the group, *Edaphopaussus favieri* (Fairmaire) (chromosome size ranging from 2 μm to 1 μm), with 2n = 50 (Galián *et al.* 1992*b*).

Sphallomorpha albopicta Newman is the first species in the Pseudomorphinae karyotypically studied. The haploid chromosome number is n = 18 + X. Fig. 1 shows a metaphase I plate with 18 bivalents of gradually decreasing sizes plus a univalent at the periphery. This karyotype is also the most widespread within the Carabidae and it is considered to be the ancestral condition for the family (Serrano 1981). The presence of this number in Pseudomorphinae agrees with the observation of high chromosome numbers in other groups of the Loxomeriformes (as defined by Erwin 1985) as discussed by Galián *et al.* (1992*b*).

The three species of *Pamborus* Latreille studied have identical chromosome numbers: 2n = 22. This suggests that *Pamborus* is characterized by a karyotypic stability similar to that already observed in *Carabus* Linnaeus and *Calosoma* Weber (2n = 28) (list in Serrano and Yadav 1984), although with fewer and larger chromosomes. The presence of an XY sex-chromosome mechanism in these three genera suggests that this system was present in the ancestors of the supertribe Carabitae, according to the phylogeny suggested by Moore (1966). The XO system of Cychrini observed in *Cychrus* Fabricius (Bouix 1965) and *Scaphinotus* Latreille (Galián *et al.* 1992*b*) may be of later origin, as members of this tribe are related to Australian *Pamborus* on the basis of larval and adult morphological and ecological characters (Moore 1966).

The three studied species of Scarititae, *Clivina dilutipes* Putzeys, *C. australasiae* Boheman and *Carenus interruptum* Macleay, belong to two different subgroups, but they have the same chromosome number, 2n = 24 and n = 11 + XY. Two other species of *Clivina* Latreille from the Palearctic region have very different numbers, 2n = 30 (Serrano 1982) and 2n = 46 (Nettmann 1986; Rozek 1989), but they share the XY sex-chromosome mechanism. In the genus *Dyschirius* Bonelli, related to *Clivina,* low numbers such as n = 10 + XY (Serrano 1981), n = 12 + XY (Serrano 1982) and n = 14 + XY (Galián 1989) have been recorded.

The four species of Australian Broscitae have different chromosome numbers. Two of them have high numbers, namely 2n = 45, 2n = 47, whereas the other two have lower numbers, 2n = 34 and 2n = 35. These results confirm the presence of high numbers in the lineage of Melaeniformes, as defined in the phylogeny proposed by Erwin (1985).

The supertribe Psydritae is characterized by the presence of relatively low numbers from 2n = 30 to 2n = 16 showing a tendency towards compaction of the karyogram. Numbers also lower than 37 have been observed in *Gehringia olympica* Darlington, 2n = 18–20? (Maddison 1985) and in *Penetretus rufipennis* (Dejean), 2n = 33 (Serrano 1986). These two species are also included in the supertribe Psydritae in Erwin's (1985) phylogeny. Incidentally, *Mecyclothorax punctipennis* (Macleay), n = 7 + XY, has the lowest chromosome number yet found in any Australian carabid species.

The supertribe Pterostichitae was the most intensively studied (36 species)

Table 1. Chromosome numbers and sex-chromosome mechanism in 70 species of Carabidae (Coleoptera) of the Australian fauna.

Species	Diploid number	Meioformula	Localities (*) and number of individuals studied
PAUSSINAE			
Mystropomus subcostatus Chaudoir	43	—	Barrington House, NSW (2)
Arthropterus sp.	46/46 ♀	—	Black Mountain, ACT (2)
PSEUDOMORPHINAE			
Sphallomorpha albopicta Newman	—	18+X	Gundaroo, NSW (1)
CARABINAE			
CARABITAE			
Pamborus alternans Latreille	22	10+XY	Dorrigo N.P., NSW (2)
P. opacus Géhin	22	10+XY	Mt. Lewis, N.Qld (2)
P. tropicus Darlington	22 ♀	—	Wongabel S.F., N. Qld (1)
SCARITITAE			
Clivina dilutipes Putzeys	24 ♀	—	ANU Campus, ACT (2)
C. australasiae Boheman	24	11+XY	ANU Campus, ACT (1)
Carenum interruptum Macleay	24	11+XY	Ooyella, Via Collector, NSW (1)
BROSCITAE			
Promecoderus mastersii Macleay	47	23+X	Gundaroo, NSW (2)
Promecoderus sp.	—	22+X	Monga S.F., NSW (1)
Eurylychnus blagravei Castelnau	35	17+X	Blundells Creek, ACT (3)
Percosoma substriatum Moore	34	16+XY	Mt. Donna Buang, Vic (1)
PSYDRITAE			
Amblytelus curtus Fabricius	30/30 ♀	14+XY	Blundells Creek, ACT (2)
Teraphis sp.	—	14+XY	Monga S.F., NSW (1)
Mecyclothorax lewisensis Moore	—	11+X	Mt. Lewis, N.Qld (1)
M. punctipennis Macleay	16	7+XY	Blundells Creek, ACT (1)

Table 1. Continued.

Species	Diploid number	Meioformula	Localities (*) and number of individuals studied
PTEROSTICHITAE			
Lesticus chloronotus Chaudoir	37	18+X	Julatten, N.Qld (1)
Trichosternus vigorsi Gory	45	—	Barrington House, NSW (1)
T. relictus Darlington	—	27+X	Margaret River, WA (1)
Castelnaudia wilsoni Castelnau	51	25+X	Mt.Glorious, S.Qld (1)
Notonomus mediosulcatus Chaudoir	56 ♀	—	Margaret River, WA (1)
N. phillipsii Castelnau	45+Bs	22+X+Bs	Bonang, Vic (1)
N. triplogenioides Chaudoir	42 ♀	—	Kangaroo Valley, NSW (1)
N. bodeae Sloane	37	18+X	Murramarang N.P., NSW (1)
	37+Bs	18+X+Bs	Murramarang N.P., NSW (1)
N. opulentus Castelnau	35+Bs	17+X+Bs	Blundells Creek, ACT (4)
N. masculinus Darlington	35/36 ♀	17+X	Wongabel S.F., N.Qld (3)
N. flos Darlington	35	17+X	Mt. Lewis, N.Qld (1)
N. hopsoni Sloane	35	—	Barringon House, NSW (3)
N. marginatus Castelnau	35/36 ♀	17+X	Windsor, NSW (2)
N. variicollis Chaudoir	35	17+X	Monga S.F., NSW (3)
	35	17+X	Mt. Cambewarra, NSW (1)
N. rainbowi Sloane	35	17+X	Monga S.F., NSW (1)
N. taylori Sloane	35	—	Wombeyan Caves, NSW (1)
N. satrapa Cast.	35	17+X	Errinundra S.F., Vic (2)
N. philippi Newman	35	17+X	Healesville, Vic (1)
N. pluripunctatus Sloane	35	17+X	Bonang, Vic (1)
N. macoyi Sloane	35	17+X	Yarra Glen, Vic (1)
N. muelleri Sloane	33+Bs	16+X+Bs	Blundells Creek, ACT (3)
N. peronii Castelnau	30	14+XY	Lakes Entrance, Vic (1)
	30	14+XY	Bonang, Vic (1)
N. obscurus Moore	29	14+X	Mt. Donna Buang Vic (1)
Sarticus monarensis Sloane	—	22+X	Gundaroo, NSW (1)
S. habitans Sloane	35/36 ♀	17+X	Black Mountain, ACT (3)

Table 1. Continued.

Species	Diploid number	Meioformula	Localities (*) and number of individuals studied
Prosopogmus oodiformis Macleay	38 ♀	–	ANU Campus, ACT (1)
P. chalybeipennis Chaudoir	35	17+X	Barrington House, NSW (1)
P. impressifrons Chaudoir	35	17+X	Mt. Cambewarra, NSW (1)
Simodontus australis Dejean	33/34 ♀	16+X	Cape Jervis, SA (4)
Setalis rubripes Sloane	37	–	Wongabel, N.Qld (1)
Phaenaulax sp.	37	18+X	Monga S.F., NSW (1)
Loxandrus sp. 1	35	17+X	Gundaroo, NSW (1)
Loxandrus sp. 2	35	17+X	Gundaroo, NSW (1)
Loxandrus sp. 3	33/34 ♀	–	Julatten, N.Qld (2)
Notagonum submetalicum White	26 ♀	–	ANU Campus, ACT (1)
Notagonum sp.	28	13+XY	Thredbo, NSW (1)
HARPALITAE			
Stenolophus piceus Guérin-Méneville	38 ♀	–	ANU Campus, ACT (2)
Lecanomerus sp.	34 ♀	–	Monga S.F., NSW (1)
Euthenarus promptus Erichson	26	12+XY	Morton N.P., NSW (1)
Notiobia melanaria Dejean	37	18+X	Julatten, N.Qld (2)
N. germari Castelnau	–	20+X	Ginninderra, ACT (1)
Amblystomus quadriguttatus Motschulsky	28 ♀	–	Julatten, N.Qld (1)
CALLISTITAE			
Chlaenius greyanus White	37	–	Margaret River, WA (1)
C. darlingensis Castelnau	37	18+X	Lake George, NSW (2)
C. hamifer Chaudoir	–	18+X	Julatten, N.Qld (1)
Oodes modestus Castelnau	38 ♀	–	Gundaroo, NSW (1)
Dicrochile brevicollis Chaudoir	55	27+X	Gundaroo, NSW (1)
Siagonyx blackburni Sloane	48/48 ♀	–	Mt. Donna Buang, Vic (2)

Table 1. Continued.

Species	Diploid number	Meioformula	Localities (*) and number of individuals studied
ODACANTHITAE			
Eudalia macleayi Bates	33	–	Gundaroo, NSW (1)
MASOREITAE			
Sarothrocrepis corticalis Fabricius	33	16+X	Blundells Creek, ACT (1)
LEBIITAE			
Drypta australis Dejean	34+Bs	16+XY+Bs	Black Mountain, ACT (1) Julatten, N.Qld (4)
Philophloeus sp.	29/30 ♀	14+X	Gundaroo, NSW (2)
BRACHININAE			
Pheropsophus verticalis Dejean	29	14+X	Murramurrang N.P. NSW (1)

* ANU: Australian National University; ACT: Australian Capital Territory; N.Qld: North Queensland; NSW: New South Wales; N.P.: National Park; SA South Australia; S.F.: State Forest; S.Qld: South Queensland; Vic: Victoria; WA: Western Australia.

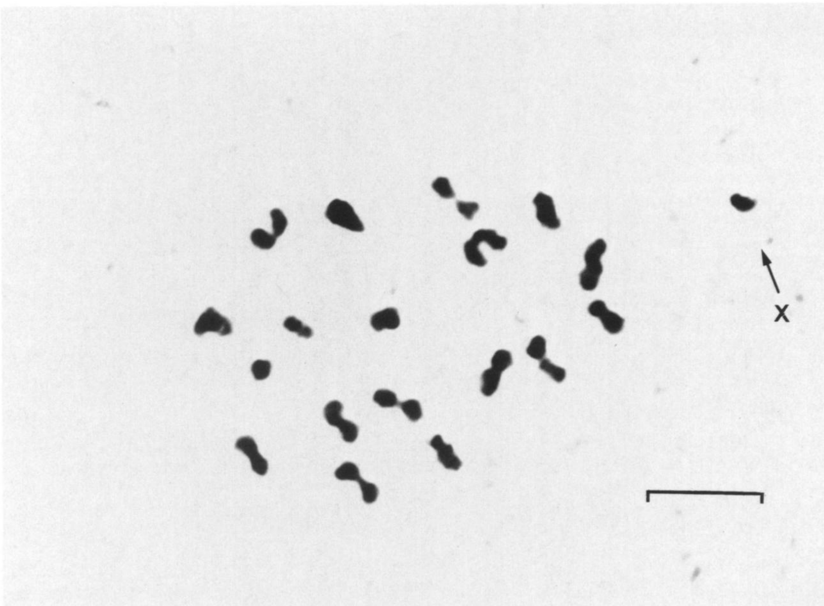

Fig. 1. Metaphase I of *Sphallomorpha albopicta*; n = 18 + X. The bar equals 5 μm.

in the present work. Six of the species, belonging to five genera, have the basic chromosome number of Pterostichitae, 2n = 36 + X (males) and 2n = 36 + XX (females), and eighteen have 2n = 35. Numbers higher than 2n = 37 have been observed in the species of *Trichosternus* Chaudoir and *Castelnaudia* Tschitschérine, and lower numbers are present in *Prosopogmus* Chaudoir, *Simodontus* Chaudoir, *Loxandrus* LeConte and *Notagonum* Darlington. More species of these genera must be studied before determining the evolutionary pattern of the chromosome number. This pattern can be established in *Notonomus* Chaudoir, the genus most studied (19 species), in which thirteen species have 2n = 35, and the others have numbers ranging from 2n = 29 to 2n = 56. These data suggest that the diploid number 2n = 35 is the basic number of *Notonomus* with tendencies towards lower and higher numbers. These two tendencies to increase or decrease the basic number are also observed in other genera of Pterostichitae, such as *Poecilus* Bonelli and *Pterostichus* Bonelli (Serrano and Yadav 1984; Galián 1989; Galián *et al.* 1992*a*). The XO sex-chromosome mechanism predominates in *Notonomus,* with only one species, *N. peronii* (Castelnau), so far showing an XY mechanism. This species is also aberrant within its genus in several of its morphological features, such as female elytral sculpture and unmodified male fore tarsi.

In the supertribe Harpalitae, the two species of Stenolophina have chromosome numbers that corroborate the previously observed heterogeneity of the subtribe (2n = 24–39). Whereas *Stenolophus* (*Egadroma*) *piceus* (Guérin) (2n = 38, female) is close to other *Egadroma* (Motschulsky) or *Loxoncus* (Schmidt-Goebel) (2n = 37–39) (Serrano and Yadav 1984), *Euthenarus promptus* (Erichson) (2n = 26) is closer to other species of *Stenolophus* Dejean (2n = 24; Serrano and Yadav 1984). *Lecanomerus* sp. (2n = 34) is the first species studied of Pelmatellina (*sensu* Noonan 1976), and its chromosome number is near the basic 2n = 37 of the tribe. The two species of *Notiobia* Perty (subtribe Anisodactylina) differ clearly in number. The 2n = 37 karyotype has been reported in the American *Notiobia schnusei* van Emden and is present in other Anisodactylines (Serrano and Yadav 1984) so that the number of the Australian *N. germari* (Castelnau) must be considered as derived. The chromosome number of *Amblystomus quadriguttatus* (Motschulsky) (2n = 28) is much lower than 37, as is the case for *A. binottatus* Andrewes (2n = 24) (Serrano and Yadav 1984). More data are needed to verify the existence of a definite trend to low numbers in this subtribe (Amblystomina) of Harpalini.

The result of *Chlaenius hamifer* Chaudoir, 2n = 37, agrees with the report of Yadav and Karamjeet (1983) for individuals from India. The other two species of *Chlaenius* Bonelli have also the same chromosome number. This number predominates within the different subgenera of the genus (*Chlaenius* s. str., *Chlaenites* Motschulsky, *Chlaeniellus* Reitter, *Callistoides* Motschulsky, *Epomis* Bonelli and *Ocybatus* Laferté) and it is also present in akin genera (*Dinodes* Bonelli and *Anomoglosus* Chaudoir) (Serrano and Yadav 1984). These data suggest a high degree of karyotypic stability in *Chlaenius* s. lat., with few species showing increases (2n = 39) or decreases (2n = 34) (Serrano and Yadav 1984). The chromosome number observed in the female of *Oodes modestus*, 2n = 38, is higher than the number of two congeneric species from India, with 2n = 22 and 2n = 24 (Yadav *et al.* 1989). This tendency towards numbers lower than 2n = 37 in *Oodes* Bonelli is in contrast to the karyotypic stability of *Chlaenius*. *Dicrochile brevicollis* Chaudoir and *Saigonix blackburni* Sloane (Tribe Licinini) have high numbers, 2n = 55, 2n = 48. These results corroborate the pattern of high variability of chromosome numbers within this tribe in which the diploid number ranges between 2n = 26 and 2n = 55 (Serrano and Yadav 1984; Serrano 1986).

Of the groups considered to be morphologically advanced, such as Odacanthinae, Masoreitae, and Lebiitae, we only had results from 4 species. All of these have numbers lower than 2n = 37. This circumstance is in agreement with the tendency towards low numbered karyotypes observed in Iberian Lebiinae (Galián *et al.* 1991*b*). A species of Masoreini previously studied (2n = 35) (Galián *et al.* 1991*b*), has a number close to that of *Sarothrocrepis corticalis* (Fabricius), 2n = 33. The two species of Lebiitae, *Drypta australis* Dejean and *Philophloeus* sp., also have numbers similar to those previously reported for this tribe (Serrano and Yadav 1984).

The number of *Pheropsophus verticalis* (Dejean), n = 14 + X, is within the limits of the species of the genus already studied (listed in Serrano and Yadav 1984), n = 17 + X (or n = 17 + XY) and n = 7 + X. This genus shows the tendency towards low numbers also observed in *Brachinus* Weber (Galián *et al.* 1990*a*).

General Remarks

The chromosome number of the species studied in this work represents the first cytogenetic data of Australian Carabidae. These data are in accordance with the pattern of high variability observed on supraspecific taxa of other faunas, with their diploid number here ranging from 2n = 16 to 2n = 55 (Table 1). The predominance of mediocentric morphology and a size between 2 and 3.5 μm are in agreement with previous findings in carabid species of other regions. Accessory chromosomes (Bs) were found in individuals of 5 species and may serve as a source of centromeres for numerical rearrangements. The male sex-determining mechanism in Australian Carabidae is of two types, XO and XY, a feature which characterizes the family. No multiple systems have been observed in the species analyzed. The hypothetic ancestral chromosome number in the family Carabidae, 2n = 37, n = 18 + X (males) and 2n = 38 (females), is present in 13 species of 4 supertribes. One of this species is *Sphallomorpha albopicta,* which belongs to the primitive group Pseudomorphinae, fulfilling the predictions of the hypothesis of Serrano (1981) and Galián *et al.* (1992*b*) of primitive carabids with high chromosome numbers.

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