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**Records of the
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**CHROMOSOMES AND PHYLOGENY
OF COLEOPTERA**

R. K. KACKER

ZOOLOGICAL SURVEY OF INDIA

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Chromosomes and Phylogeny of Coleoptera

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Zoological Survey of India, Calcutta



सत्यमेव जयते

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INTRODUCTION

The order Coleoptera constitutes an assemblage of species which is numerically largest in the insect world. It is probably the only order whose members have occupied every possible ecological niche. Chromosomally, the insects of this order are, to some extent, heterogeneous. Many cytogenetical peculiarities are seen at different taxonomic levels in respect of initiation of meiotic cycle, chromosome number and form, sex chromosomes and sex determining systems.

More than 2500 species are known cytologically (Barabus and Bezo 1979; Smith and Virkki 1978; Yadav *et al.* 1987, Yadav and Dange 1989a,b, Yadav *et al.* 1985, Yadav and Karamjit 1981, Yadav *et al.* 1990. Yadav, Pillai and Karamjit 1979, Yadav, Lyapunova & Vorontsov 1986). Indian species known chromosomally stand approximately 400 or more.

Data compiled from the above species present a bewildering array of chromosome diversity both in number and behaviour, but it is clear that the typical or modal chromosome complex in males of bisexual species is nine pairs of autosomes plus a pair of heteromorphic sex chromosomes usually associated in a typical parachute-like manner, conveniently denoted as 'Xyp' In the majority of instances the Y chromosome is small and dot-like.

Deviations from the modal karyotype range from a 3 pairs of autosomes in a Puerto Rican flea beetle, *Homoschema nigriventre* (Chrysomelidae : Alticinae) (Virkki and Purcell 1965a,b) and a carabid beetle with eight chromosomes (Wahrman 1966) to a maximum of 28 pairs in a Galerucine (Chrysomelidae) beetle, *Rhaphidopalpa femoralis* (Goto and Yosida 1953; Yosida 1953). Among the Indian species extremes have been observed in an elaterid beetle *Agrypnus* sp. ($2n = 11$; 5 AA + XO) (Kacker 1963) and the chrysomelid *Aulacophora intermedia* ($2n = 57$, 27 AA + XXy) (Dasgupta 1963). Between these extremes of 2 and 28 pairs of autosomes are approximately 1500 species, in 46 families excluding the parthenogenetic and polymorphic species.

The coleoptera is probably unique among insects in having a variety of sex-chromosome systems coupled with an equally wide range of haploid number of autosomes. As a rule the males, in bisexual coleopteran insects, are heterogametic and bear the dissimilar sex chromosomes usually X and y. The most widely occurring, often referred to as 'orthodox' or 'primitive' type of sex-determining mechanism is Xyp : XX type. The sex chromosomes are attached together in an unique fashion typical to polyphagan coleoptera. Notable exceptions are cantharoid families, which have 'XO' system. Since majority of coleopteran are polyphagous Xy system is truly the sex chromosome system in coleoptera first discovered by Stevens (1905).

The XO types of sex-determining mechanism, next in predominance, is seen in the Dytiscidae, Silphidae, Lycidae, Lampyridae, Cantharidae, Melyridae, Latheridiidae, Phalacridae, all of which are mostly XO. The scarabaeids which are predominantly Xy show an XO sex-chromosome system in *Pentodon* sp. and *Copris fricator* (Jones 1960). The Carabidae, Elateridae and Chrysomelidae also include XO species. In the Gyrinidae no sex chromosomes have been identified except in two species, *Gyrinus paykulli* and *G. substriatus*, with XO sex chromosomes (Smith & Virkki 1978). The family Micromalthidae has a rare case of haplo-diploid system of sex-determination (Scott 1936).

Before discussing the multiple sex-chromosomes it will be of some interest to mention the other forms of 'XY' sex-determining mechanism. Smith (1953a) established a category where two sex-chromosomes were indistinguishable or unidentifiable because of their equal size. This may be due to limitation of techniques used. Many known cases reported to have neo-XY studied at metaphase I could in fact be true Xy such as in *Phanaeus maxicanus* and *P. dafinis* (5 II + neo-XY). In fact there are about 30 species which are reliably included in the true XY forms. However, detail analysis of prophase and improved techniques may reveal the exact nature of these sex chromosomes. In *Bembidion transversalis* of carabidae and in seven species of chrysomelidae including *Cryptocephalus sexsignatus* studied in the present report, X and Y are of equal size. Four species of Scarabaeidae (Prowazek 1902 ; Hayden 1925 ; Kacker, 1970) have equal XY. Unequal 'X + Y' are reported in Chrysomelidae (especially Alticinae) (Smith 1953a, 1960a ; Virkki 1961, 1964, 1967a, b) and Coccinellidae (Smith 1960a). These unassociated Xy are always synoriented.

The complex type of sex-determining systems with multiples of X or Y ($X_n Y_n$) are comparatively uncommon. Evolution of such system may arise through some sort of translocation converting Xyp into neo-XY, producing $X_1 Y_1 Y_2$ where the Yp survives. Translocation of Yp on to an autosome probably may establish $X_1 Y_2$ where original X is probably indispensable. Thus the mixed chiasmata nucleolar association produces multiple systems from a simple chiasmata system. The selection of derivatives results in the establishment of more complicated sex-chromosome mechanism. Only Cicindelidae (Guenin 1952; Smith and Edgar 1954), one Coccinellidae (Smith 1960a; Takenouchi 1968a), several Tenebrionidae (Guenin 1949) two Chrysomelidae (Bai & Sugandhi 1968 ; Virkki 1967a, 1968a b; Yosida 1949a) and one Dermestidae (John and Shaw 1967) have multiple sex-chromosome.

Another, though secondary, type of sex-determining mechanism is neo-XY. Classical neo-XY formation takes place by a centric fusion of an acrocentric X-chromosomes with an equally acrocentric autosomes. In fact one would expect the neo-XY sex-chromosome mainly in the forms which have XO system with acrocentric chromosomes such as in grasshoppers.

In coleoptera the autosomes as well as X chromosomes are predominantly metacentric. Neo-Xy formation should be complicated. This situation may however, be eliminated when the euchromatic arm of an autosome fuses with an indispensable arm of the X chromosome. The heterochromatic arm and centromere could be dispensed with. The Y chromosome, might be eliminated or contain genes that may be transposed to the neo-Y or autosomes.

Coleopteran chromosome with both Xy or XO type may be suitable for the formation of neo XY. The neo Xy is reported in Carabidae and Passalidae which have XO type of sex chromosome. Exceptionally, Cantharidae with predominantly XO has no neo XY. We have more than 150 species which have neo XY, mainly in Buprestidae, Coccinellidae, Tenebrionidae, and Chrysomalidae. Present report also enumerates another case of neo XY in *Hyphasoma* sp. belonging to the family Chrysomelidae.

In the present work, chromosome number, form and behaviour during male meiosis are dealt with in 14 species of Coleoptera belonging to 6 families. An attempt has been made to study the phylogenetic relationships between different taxa mainly based on karyotype data available.

MATERIAL AND METHODS

Males of fourteen species were investigated and all were collected in India (Table I). There undescribed species have been cytologically investigated ; one of the genus *Cynolytta* (Meloidae) and one each of the genus *Lema* and *Paridea* of Chrysomelidae.

Colcimid was used in this study with very little success. Spermatogonial divisions were often completed in most of the cases. The gonads were pretreated in 0.85% solution of sodium citrate for 20–25 minutes and subsequently fixed in 1:3 Acetic ethenol for few hours. Stored material in 70% ethanol, in refrigerator, markedly improved the quality. Staining was done, on squashed material by 2% Aceto carmine and geimsa solution. All the photographs were taken on Carl Zeiss photomicroscope and Leitz Ortholux microscope at the initial magnification of ca. X 1000.

TABLE—I

Details of the material employed in the present study

Taxonomic categories	No. of males studied.	Collection Localities
Family : MELOIDAE Subfamily : MELOINAE <i>Cyaneolytta</i> sp.	3	Latifshah, Chakia, Varanasi, U.P.
<i>Psalydolytta</i> sp. nr. <i>rouxi</i>	2	Chandraprabha, Chakia, Varanasi, U.P.
Family : ELATERIDAE Subfamily : PYROPHORINAE <i>Adelocera colonious</i> (Candcz)	4	Latifshah, Chakia, Varanasi, U.P.
Family : COCCINELLIDAE Subfamily : EPILACHNINAE <i>Afissa parvula</i> (Crotch)	3	Gangtok, Sikkim.
Family : TENEBRIONIDAE Subfamily : PEDININAE <i>Platynotus punctalipennis</i> Mulsant	1	Mangror, Chakia, Varanasi, U.P.
Subfamily : TENTYRIINAE <i>Sphenariopsis tristis</i> Kraatz	1	Latifshah, Chakia, Varanasi, U.P.
Family : SCARABAEIDAE Subfamily : COPRINAE <i>Cymnopleurus cyaneus</i> (Fabricius)	7	Latifshah, Chakia, Varanasi, U.P.
Family : CHRYSOMELIDAE Subfamily : CRIOCERINAE <i>Lema</i> sp.	5	Gangtok, Sikkim.
Subfamily : CRYPTOCEPHALINAE <i>Cryptocephalus sexsignatus</i> Fabricius	2	Chandra Prabha, Chakia, Varanasi, U.P.
Subfamily : GALERUCINAE <i>Paridea</i> sp.	7	Gangtok, Sikkim.
<i>Oides bipuncta</i> (Fabricius)	4	Chandra Prabha, Chakia, Varanasi, U.P.
Subfamily : ALTICINAE <i>Ilyphasoma</i> sp.	2	Gangtok, Sikkim.
<i>Lacoptera quadrimaculata</i> Thunberg	3	Gangtok, Sikkim.
Subfamily : HISPINAE <i>Dactylispa atkinsoni</i> Gestro	2	Gangtok, Sikkim.

OBSERVATIONS AND REMARKS

Family : MELOIDAE

1. *Cyaneolytta* sp.

Karyotype formula : ($2n = 20$; 9AA + Xyp.)

Three males of this species, which seems to be hitherto undescribed, were caught in a light trap.

Several spermatogonial metaphases from different individuals revealed a diploid number of 20, in which all the autosomes are metacentric. As is usual in Coleoptera, the X is larger than the Y chromosome, the latter being a small rounded dot (Fig. 1 & 38). On aligning chromosomes cut-outs in decreasing order of length no clear-cut size classes were observed. The longest autosomal pair comprises approximately 12.5% of the length of the haploid set. Second, third and fourth pairs are of almost equal length i.e. 11.5%, 11.4% and 11.0% respectively. The smallest autosomal pairs is 7.3%. The X chromosome, which is also metacentric, measures 8.3%. The smallest member in the spermatogonial complement, the Y, measures 4.5% (Table II).

In the spermatogonial prometaphase stage individual chromosomes show a peculiar phenomenon. The chromosomes appear to have 3 segments, one around the centromere deeply stained and more condensed and two distally placed, feebly stained and less condensed (Fig. 2). Spermatogonial prometaphase stages were available for study in only one male. All males were subjected to 4–6 hours pretreatment of 0.05% colcemid, which according to Smith (1965) can cause differential contraction of heterochromatin and euchromatin. It appears, therefore, that a procentric portion of each chromosome is heterochromatic. Differential contraction was also evident, though not very clearly, in late spermatogonial metaphases.

At the beginning of prophase, a number of conspicuous chromocentres are seen inside the nucleus. One of these heteropycnotic bodies is the sex vesicle. Later prophase stages were not analysable.

First meiotic metaphases invariably show 9 bivalents of nearly equal size. There are no ring bivalents, all of them appear to have a single terminal chiasma. The sex chromosomes form a typical parachute (Fig. 3). There is an achromatic gap in one of the bivalents, the significance of which is not very clear.

At the onset of anaphase I, the sex chromosomes reveal precocious disjunction and anaphase is reductional for the sex chromosomes. As a result dissimilar daughter cells are formed, one with X and the other with Y (Figs. 4 & 5). The second division is equational for the sex chromosome.

2. *Psalydolytta* sp. nr. *rouxi* Laporte

Karyotype formula : ($2n = 20$; 9AA + Xyp.)

This beetle could not be determined to species but is very near *P. rouxi*. It is brown with fine shining pubescence. Out of a total of 7 specimens, 2 males were available for cytological study and their testes showed a few meiotic stages.

A few spermatogonia revealed the diploid number to be 20, with a bigger X and a dot-like Y chromosome (Fig.6). As in the previous species, the chromosomes show a regular size gradation (Fig. 39). Table II shows that pair No. 1 measures approximately 13.0% whereas pair 9 has a mean length of 7.1%. The length of the X chromosome is similar to that of the pair 8, both being approximately 9.0%. The Y is the smallest member of the complement and is 4.9%.

Early stages of meiosis showed features similar to those described in *Cyaneolytta* except that heterochromatic segments are not found. Later stages, up to metaphase I, were not present.

Metaphase I, shows 9 bivalents having a single terminalised chiasma each. The sex chromosomes form a typical parachute like structure (Fig. 7). The behaviour of the chromosomes during subsequent stages of meiosis is similar to that of the preceding species.

Remarks : Twentytwo species are known cytologically in this family, where the diploid number varies from nine to eleven pairs of autosomes and all have an Xyp type of sex chromosomes. The two additional species herein brings the total of Indian species studied to seven.

Several infra-familial classifications, based on morphology and behaviour, have been suggested for the Meloidae (MacSwain 1956; Kaszab 1959; Selander 1964), of which Kaszab's is most generally accepted. He divides Meloidae into three subfamilies; Meloinae, Zonitinae and Horiinae. The first has a more or less uniform chromosomal formula of 9AA + Xyp which is present in six out of seven species of *Epicauta* and a single species of *Psalydolytta*, both in the Epicautini (Stevens 1909; Virkki 1962; present report) and in *Pyrota decorata*, *Paniculolytta sanguineoguttata*, *Tetraonyx frontalis*, *Sybaris paraeustus* (Virkki 1962a; Joneja 1960) and *Cyaneolytta* (present report) all in the Lyttini. The Meloini, where the genus *Meloe* belongs, has also been found to have the typical 9AA + Xyp formula. The Mylabrini shows 10AA + Xyp in the 5 out of six species of *Mylabris* known cytologically (Asana *et al.* 1942; Dasgupta 1974; Dua and Kacker 1976; Joneja 1960; Manna and Lahiri 1972; Yadav 1973). *Epicauta grammica* is exceptional in having a chromosome complex of 11AA + Xyp (Virkki *loc. cit.*), suggesting that *Epicauta* may have its own evolutionary 'Line'

Only one species, *Zonitis tarasca*, is known cytologically from the Zonitinae; it has the formula 9AA + Xyp (Virkki 1962).

Family : ELATERIDAE

3. *Adelocera colonicus* (Candez)
(*Lacon colonicus* Candez)

Karyotype formula : ($2n = 17$; 8AA + XO.)

The current scientific name of this elaterid beetle is *Adelocera colonicus* (Candez). It has a very close resemblance to *A. modesta*, both morphologically and cytologically.

Meiotic stages were quite frequent in this species, even in old males. The diploid number was ascertained from a large number of gonial metaphases obtained from four individuals and found to be 17 (Fig. 8). All the chromosomes are rounded or oval in shape with a distinct longitudinal split. Since no constriction is visible in the chromosomes at this stage, it is concluded that all are acrocentric. The sex determining mechanism is XX : XO type. The X chromosome can be distinguished from autosomes of similar size by its positive heteropycnocity. Measurements were taken from 5 well spread spermatogonial metaphases from 4 individuals, which reveal that the pair 1 is 14.0%. The sex chromosome, pairs 2 and 3 are of almost equal size. The remainder are smaller and range between 8.1% and 10.4% (Fig. 40 and Table II).

The resting spermatocyte nucleus reveals evenly distributed chromatin, and, except for a single positively heteropycnotic X, lacks conspicuous chromocentres. At late diplotene, one bivalent is obviously bichiasmate, and seven unichiasmate. The sex chromosome is still positively heteropycnotic. Figure 9 shows a diakinesis in which the X is more or less isopycnotic with the autosomes.

First metaphases show 8 bivalents and the X chromosome forming an accessory plate (Fig. 10). There were some metaphase plates where the bivalents are comparatively small. Such cells were found in only one individual. The division was reductional for the sex chromosome.

Tetraploid cells : In a single individual, a number of tetraploid spermatocytes were found along with the diploid cells in the same cyst of the testis. At prophase stages, binucleate cells occurred (Fig. 12), and at metaphase I, 16 bivalents and two X univalents were formed (Fig. 11). Since more than one tetraploid cells observed, cytokinesis occurred in an early spermatogonial cyst, chromosomes being acrocentric, one chiasma per chromosome remains the maximum. At metaphase, a single spindle is formed and all the 16 bivalents align on the equator. This doubtlessly leads to the production of diploid sperms.

Remarks : The commonest chromosome formula in this family is 9AA + XO; it is found in 31 of a total of 169 species studied so far.

The Elateridae is sub-divided into 3 subfamilies. The Cardiophorinae shows 10AA + Xy in five of the six *Cardiophorus* species known cytologically. The

Pyrophorinae, in which 41 species have been investigated, shows considerable chromosomal variation at a trival level. In the Lepturoidini 4 species are $8AA + XO$ and 6, $9AA + XO$. Two of 17 *Ctenicera* species viz., *C. inflata* and *C. tarsalis*, retain the model karyotype of $9AA + Xy$, while the remainder consists of 3 species with $8AA + XO$, 6 with $9AA + XO$, 2 with $10AA + XO$ and 4 with $10AA + Xyy$. The probable causes of this variation in chromosome number cannot even be speculated on because no data are available on chromosomal lengths or centromere position. The Pyrophorini likewise shows considerable numerical variation. The genus *Adelocera* (Agrypninae) has an uniform karyotype in all 3 known spp. having $8AA + XO$ (Smith 1953a; Joneja 1960; and present report), but the genus *Agrypnus*, of the same tribe, shows different chromosome numbers in the two species studied. *Agrypnus fuscipes* has $2n = 17$ chromosomes, all of which are acrocentric (Banerjee 1959). An unidentified species has been found to possess $2n = 11$ with 6 metacentric chromosomes conforming with Robertsonian type of translocation (Kacker 1963). Piza (1958b) recorded the lowest chromosome number of the family in *Hemirrhypus lineatus* (Pyrophorini) involving X-A and A-A fusion to get $4AA + neo-XY$. The *Pyrophorus*, viz., *P. nyctophanus* and *P. pellucens* have a complement of $7AA + XO$ (Piza 1958a; Smith 1960a).

The karyotype of the Elaterinae is fairly uniform, having $9AA + XO$ in 18 of the 23 species studied. The exception is found in *Agriotes mancus* which has chromosome formulae; one $9AA + XO$ and another $7AA + Iiv + XO$. It is evident from the latter formula found in a single male, is due to a reciprocal translocation between two non homologous autosomes that consequently form a chain-of-four in the heterozygote (Smith 1954, 1956f). *Agriotes sputator* alone, retains the primitive chromosome formula which is $9AA + Xyp$.

Family : COCCINELLIDAE

4. *Afissa parvula* (Crotch)

Karyotype formula : ($2n = 18$; $8AA + Xyp$.)

The diploid count is 18 in this species with an unusually big X and a normal small Y chromosome. The chromatids of each chromosome, except the Y, are separated even without any colchicine pretreatment. In Fig. 13 is shown a prometaphase nucleus where all the chromosomes except the Y are probably metacentric, but the position of centromeres in the individual chromosomes cannot be detected unequivocally (Fig. 41). A calculation of the mean relative lengths of the chromosomes show that the X is the largest member of the complement, it being 19.4%. The autosomes decrease gradually from 13.7% for the pair 1 to 7.1% for pair 8. The y chromosome measures 2.1% (Table II).

Only a few MI cells were encountered. The bivalents were somewhat bushy in appearance (Fig. 14) and there are 8 bivalents with terminalized chiasmata, the X and

the y forming a typical parachute. It is surprising to find that the X chromosome, at metaphase I, is smaller than some of the autosomes. This is perhaps due to differential condensation of the X chromosome at mitotic and meiotic stages.

Remarks : Cytologically, this is the second most extensively studied family. Cytological data on about 170 species, including 10 polymorphic species, are available. The diploid number ranges from 12 to 26 and the sex-chromosome systems in the males are of eight different types.

The Coccinellidae is divided into the Coccinellinae and Epilachninae. The latter is more or less homogeneous and has the typical coleopteran formula of $9AA + Xyp$ in 8 out of the 14 species known cytologically. We have described the chromosomes of two more species of Epilachninae, *Afissa parvula* and *Epilachna septima*. The former has $2n = 18$; Xyp and the latter $2n = 20$; Xyp . *Afissa parvula* besides having one fewer autosomal pair has a very large X. Reduction in diploid number in Epilachninae has also been noticed in the hybrid between *E. chrysomelina* X *E. capensis* (Strasburger, 1936) and in *E. vigintioctopunctata* (= *Hemosepilachna vigintioctopunctata*) (Bose 1948; Yosida 1944; Agarwal 1961). The reduction in number could, here, be due to A-A fusion and enlargement of the X chromosome in *A. parvula* to X-A fusion.

In the Coccinellinae, which includes mostly entomophagous beetles, the situation is very heterogenous. The diploid number in 12 tribes varies from 12 to 24.

In the tribe Hyperaspini, Smith and Virkki 1978 have studied 17 species of *Hyperaspis*, of which all but two have $6AA + X + y$. Four species of *Brachyacantha* studied have a neo-XY and 7 to 9 pairs of autosomes, which suggest that both X-A and A-A fusion has occurred in these species, cytologically *Hyperaspis* is derivative in relation to *Brachyacantha* (Smith personal communication).

The Synonychini, Coccinellini and a part of the Scymnini show, in most of their species, the typical formula of $9AA + Xyp$ (Li 1940; Smith 1953a, 1960a; Stevens 1906; Yosida 1944). The only aberrant case in the Synonychini is *Aiolocaria mirabilis* in which $2n = 16 + X$ (in Makino 1951). In the Coccinellini too, some deviant karyotypes are reported.

The Scymnini has followed two trends, the first one towards secondary acquisition of neo-XY as evidenced in 4 species of *Scymnus*, which have $7AA + neo-XY$, the second is towards an increase in chromosome number as seen in *Cryptolaemus montrouzieri*, which has $10AA + Xy$. Both fission and fusion mechanisms are presumably have involved in the evolutionary change of chromosome number.

Another trend of cytotaxonomical evolution is seen in the tribe Noviini where loss of the y chromosome has resulted in the formation of XO species.

Chromosomal rearrangements are also witnessed in four more tribes, these are Oeneini, Psylloborini, Azyini and Chilacorini. The last one includes a highly polymorphic species and natural interspecific hybrids (Smith 1956d, 1957a, b,c, 1959, 1960a, b, 1962a, 1965a and 1966a, b).

Family : TENEBRIONIDAE

5. *Platynotus punctatipennis* Mulsant

Karyotype formula : ($2n = 20$; 9AA + Xyp.)

A sufficient number of spermatogonial metaphase were present to enable determination of the diploid number as 20. The sex chromosomes are again typically coleopteran and the X is larger than the Y. All the autosomes and the X chromosome are mediocentric with a distinct bend indicating the approximate position of the centromere (Fig. 15). Morphometric data were calculated from 5 well spread mitotic metaphases. These reveal that the pair 1 is 12.9% of the haploid set. There are no distinct size differences between pairs 3,4 and 5 which is approximately 10.5%. Similarly pairs 7 and 8 are of almost equal length, measuring 8.8% and 8.5% respectively. Pairs 2,6 and 9 are 11.6%, 9.9% and 7.7% respectively. The X chromosome is equal to the pair 7. The Y chromosome is 3.2% (Fig. 42 & Table II).

First spermatocytes reveal 9 bivalents and a sex bivalent formed by the achiasmate association of X and Y (Fig. 16). Six bivalents are larger and 3 comparatively smaller. All the bivalents are similar in shape when viewed equatorially.

The remaining stages are similar to those of other tenebrionid species described by the author (Kacker, 1968) for the sex chromosomes the first division is reductional.

6. *Sphenariopsis tristis* Kraatz

Karyotype formula : ($2n = 20$; 9AA + Xyp.)

This is the first Indian species of the subfamily Tentyriinae to be studied cytologically. This beetle showed the conventional diploid number of 20, with almost all the chromosomes, except the Y, metacentric. The X chromosome is unidentifiable (Fig. 17). Since only a single male was available, the details of meiosis could not be worked out. However, there are clearly 6 pairs of small chromosomes and 3 pairs are larger ones. The X chromosome is probably of medium size but the Y is undoubtedly the smallest in the complement.

Meiotic stages are similar to those in the other species of tenebrionids described by the author.

Metaphase 1 exhibits 9 autosomal bivalents and an Xy parachute (Fig.18). Only one of the 9 auto bivalents is ring shaped, the others monochiasmate.

Remarks : Cytological data are available of about 110 species including the two here studied. The most common formula is 9AA + Xyp, or Xy as seen in 65 species, (Smith and Virkki 1978; Dua and Kacker 1980; Yadav *et. el.* 1980).

The subfamily Erodiinae is represented exclusively by 9AA + Xyp species (Guenin 1951; Yadav and Pillai 1974). The Tentyriinae also has this model number except in *Zopherus haldemani*, which has a constitution of 7AA + Xy (Smith 1952, 1953b). This species, hitherto included in this subfamily has been shifted to a distinct family, the Zopheridae (Crowson 1955). The separation was done purely on its larval dissimilarities from true Tenebrionidae. It is interesting that the species also has other cytological peculiarities such as a pre-metaphase stretch, typical of mantids and blattids, and a precocious anaphase segregation of X and Y as seen, e.g. in Neuroptera.

The Pedininae, Opatrinac, Blaptinae (Eleodini), Scaurinae and Tenebrioninae, generally retain the primitive formula of 9AA + Xyp (Dua and Kacker 1980; Smith 1953a, 1960a; Kacker 1968).

The pimeliinae is characterised by having 8AA + Xyr in all its nine species (Guenin 1950 ; Smith and Virkki 1978). A similar karyotype is reported in *Cossyphus depressus*, the sole example known in Cossyphinae (Kacker 1968). This presumably has arisen by centric fusion of autosomes.

Reduction in chromosome number to 7AA + neo-Xy has been found in *Akis bacarozzo*, of the subfamily Akidinae (Guenin 1950). Further reduction has been recorded in *Diaperis bolati* (6AA + neo-XY) of the Diaperinae, while in two species of Ulominae, *Tribolium confusum* and *T. destructor*, the karyotype is 8AA + neo-XY. These are the extreme of translocation, involving both autosomes and X chromosomes.

The amarygminae, is known cytologically by a single species, *Hoplobrachium asperipinne*, which shows 10AA + Xyp and is presumably an example of centric fission (Kacker 1973).

The case of *Bolitotherus cornutus* of the Bolitophaginae is unique in that due to loss of Y or to its translocation on to some autosome an XO condition has arisen (Smith 1960a).

The Blaptinae other than the tribe Eleodine where the neo-Xy has evolved, exhibits a remarkable degree of chromosomal variation both auto and sex chromosomal (Smith 1953a, 1960a; Smith and Virkki 1978).

Family : SCARABAEIDAE

7. *Gymnopleurus cyaneus* (Fabricius)

Karyotype formula : ($2n = 20$; 9AA + Xyp.)

Seven examples of this common dungrolling beetle were collected for cytological study.

Spermatogonial counts reveal the diploid number to be 20. Except for the Y chromosome, all chromosomes are metacentric (Fig. 19). The relative lengths of the chromosomes are calculated from only 3 spermatogonial plates. Pair 1 measures about 16.4% of the total haploid set; pairs 2 & 3 are 12.0% ; pairs 4 & 5 are almost equal 10.6% and 10.1% respectively, similarly, 7th and 8th pairs are near equal, being 7.8% and 7.7% of the haploid set. The X chromosome is 8.7% and Y is 1.9% (fig. 43 & Table II).

At first metaphase, the bivalents are dumbbell or rounded in shape. In some cells one bivalent forms a ring. Except rarely, for one or two cases in some cells all the chiasmata are terminalised at metaphase I (Fig. 20).

As usual, the first meiotic division is reductional.

Remarks Cytological data from more than 225 species belonging to 72 genera and 16 subfamilies of scarabaeidae are available (Dua and Kacker 1980; Smith and Virkki 1978; Yadav *et al.* 1989).

Cytologically this family shows remarkable uniformity considering the wide range of morphological differences evidenced among its different subfamilies. The basic formula is undoubtedly 9AA + Xyp, as found in majority of the species studied (Dua and Kacker 1980; Smith and Virkki 1978; Yadav, Burra and Dange 1989). The number of autosomal pairs range from 5 in *Phaneus vindex* (Hayden 1925; Virkki 1959) to 14 in *Autoserica assamensis* (Dasgupta 1974) with the intermediate number of 8 and 10 pairs in *Anomala* and *Popillius* (Yosida 1949b) *Adoretus versutus* (Kacker 1970) respectively. The sex chromosomes are of primitive Xyp type, which occurs in 177 species. Only seven species are XO type and three are neo-XY (Dasgupta 1974; Dua and Kacker 1980; Smith and Virkki 1978).

But for *Phaneus vindex* and *P. igneus*, the Coprinae has a uniform karyotype of 9AA + Xyp. The same is true for Aphodinae, Melolonthinae and Cetoniinae.

Although the Troginae has a typical karyotype of 9AA + Xyp, a few species of *Trox* possess morphologically dissimilar chromosome complements differing in the location of centromeres (Virkki and Purcell 1966). Thus the *Scaber* group, *T. foveicollis* and *T. spinulosus dentibius* have metacentric autosomes, whereas in the

Suberosus group, represented by *T. punctatus*, *T. monachus*, *T. scutellaris*, all have **acrocentric** autosomes. They ascribe the change in position to pericentric inversion. Since metacentric chromosomes are typical of scarabs, the acrocentrics must be **secondary**, but it is difficult to visualise from such a change could have materialised unless the Suberosus group is of long evolutionary standing and such a type of chromosomal rearrangement had adaptability. This subfamily is considered to be one of the most primitive.

Allied to the above subfamily is the Geotrupinae which has 22 chromosomes including Xy sex chromosomes in 8 out of 11 chromosomally known species. The geotrupids are also reported to have acrocentric chromosomes (Yadav and Pillai 1979; Yadav *et al.* 1990).

Rutelinae shows two main types of karyotypes. The Indian species have 9AA + Xy (Joneja 1960; Kacker 1970) and the Japanese species *Anomala corpulenta*, *A. rufocuprea*, *Popillia japonica* have 8AA + Xy (Yosida 1949b). The only exception of (10AA + Xyp, without any acrocentric chromosomes) is seen in *Adoretus* (Kacker 1970). It is an open question which way the evolution has proceeded. Either it is from Geotrupids via Rutelinae to proper scarabaeids by way of fusion or it may be in the reverse sequence.

The Chironinae and Hybosorinae have been investigated for the first time (Kacker 1970). Both these subfamilies are primitive Scarabacidae and have typical 9AA + Xyp karyotypes. But *Chiron digitatus* (Chironinae) has 2 acrocentric autosomes, whereas *Hybosorus orientalis* (Hybosorinae) has none.

Family : CHRYSOMELIDAE

8. *Lema* sp.

Karyotype formula : (2n = 16; 7AA + Xyp.)

Morphologically this beetle is found to be very different from the other known species of the genus *Lema*.

16 metacentric chromosomes have been counted in 20 well spread spermatogonial metaphases (Fig. 21). Autosome pair 1 is 19.1% and 3 and 4 are almost equal, being 12.6% and 12.0% respectively.

The smallest pair is No. 7 which is 6.4%. The X chromosome is fairly large and measures 15.5%. The Y chromosome is one of the smallest members of the complement measuring about 6.7 % (Fig. 44 & Table II). The course of meiosis is the same as that already described in a general way. Early prophase cells show blocks of heterochromatin.

Metaphase I shows 7 autosomal bivalents each having single chiasma. The 8th

bivalent is formed by the large X and small Y chromosomes (Fig. 22). A few bivalents still contain unterminalized chiasmata.

The first meiotic division is reductional. Metaphase II cells are of two kinds with X or with Y

The metacentric nature of the chromosomes is quite clear in second metaphases (Fig. 23 & 24). The X chromosome can be easily identified.

9. *Cryptocephalus sexsignatus* Fabricius

Karyotype formula : ($2n = 30$; 14AA + Xy)

The genus *Cryptocephalus* can readily be recognized by its reniform eyes and retractable head. Only two male adults were captured by light trapping. Meiosis was almost over in the testicular follicles but still contained some metaphase I and II. Spermatogonial metaphases were also absent, so that, the diploid number was ascertained from first metaphases which contained 14 autosomal and one sex bivalent (Fig. 25).

Early prophases show chromocentres distributed through the nucleus. One distinct, bivalent like structure, was deeply stained and is the presumed 'XY' complex. It always occupies a peripheral position.

The most frequently encountered stage is first metaphase. The bivalents have a single chiasma each and the chromosomes appear to be rod-like except the X and Y which are both large, near equal metacentrics.

10. *Paridea* sp.

Karyotype formula : ($2n = 40$; 19AA + Xy)

This beetle closely resembles *Paridea octomaculata* but differs markedly in elytral markings and general colour.

The diploid number determined from 30 spermatogonial metaphase plates from the testes of 7 individuals, is 40, which includes a large X and a small dot-like Y chromosome (Fig. 26). Owing to the small size of the autosomes, the positions of the centromeres could not be precisely determined. However, from early mitotic anaphase cell at least 5 or 6 pairs appear acrocentric. The largest pair of autosomes is 8.2% which is similar to the length of the X. Pairs I through 14th are probably metacentric, the remainder acrocentric. The relative lengths of the chromosomes vary little (Fig. 45 & Table II).

First metaphases reveal 20 bivalents, each having a single terminalized chiasma. The sex bivalent is almost indistinguishable in most cells, but could be

distinguished with difficulty in a few cells. Some of the bivalents are precociously **disjoined** at this stage (Fig. 27).

11. *Oides bipunctata* (Fabricius)

Karyotype formula : ($2n = 17$; 8AA + XO)

This species has the lowest number of chromosomes so far recorded in **Galerucinae**. Four males were examined and found to have $2n = 17$, including single X chromosome (Fig. 28). Six pairs of chromosomes are metacentric but **uncertainty** exists about the remaining pairs. Pair 1 has a mean relative length of **16.2%** and pair 8, 7.3%. The X is the smallest chromosome (Fig. 46 & Table II) **being 4.6%**.

Early meiotic stages are very similar to what has been found in other **chrysomelids**.

At first metaphase, there are 8 rod-like bivalents, each with a single chiasma (Fig. 29).

First anaphase results in the production of two types of metaphase II cells, one **with a 8 autosomes** plus the X and the other with only 8 autosomes (figs. 30 & 31).

12. *Hyphasoma* sp.

Karyotype formula : ($2n = 22$; 10AA + neo-XY.)

Two males were produced from Gangtok (Sikkim). First meiotic stages were **plentiful** but only two spermatogonial cells both prometaphases were countable. The **diploid number** proved to be 22 (Fig. 32), of which the largest chromosome is **presumably the X**.

At first metaphase, there are 10 rather small dumb-bell shaped bivalents. The **sex-determining mechanism** appears to be neo-Xy type, because, the autosomal part, which has presumably been translocated to the original X chromosome, remains **isopycnotic** with the autosomes. Whereas the original X portion is more deeply **stained** (Fig. 33). The neo-Y is associated terminally with the isopycnotic arm of the X. No clear evidence of the heteropycnotic nature of the former has been found. This is system in the sub-family Alticinae, although Smith (1960a) lists a species of *Disonycha* as neo-XY

13. *Lacoptera quadrimaculata* Thunberg

Karyotype formula : ($2n = 18$; 8AA + Xyp.)

Three specimens were collected from Sikkim for this study.

The spermatogonial number is 18 and all chromosomes except perhaps the

minute Y are metacentric (Fig. 34). Measurement of the chromosome reveal that the autosomes are graded from pair 1 at 15.4% down to pair 8, which is only 8% of the total haploid set. The X chromosome is almost equal in size to the smallest pair of autosomes and Y is the smallest in the complement measuring 1.5% (Fig. 47 & Table II).

At diakinesis the 8 autosomal bivalents each have a single chiasma. The chiasmata are localized near the centromere, the sex chromosomes form a typical parachute (Fig. 35). At a later stage, the bivalents are somewhat more condensed and the sex bivalent is situated slightly off the equatorial plate.

Remaining meiotic stage are similar to those of the species in this family already described.

14. *Dactylispa atkinsoni* Gestro.

Karyotype formula : ($2n = 16$; 7AA + Xyp.)

These beetles are mostly pests of rice. Although only 2 males were available, they however, gave a clear picture of its chromosomes. Morphometric analysis was not possible because of much size overlap of chromosomes. Nevertheless, the mitotic number was clearly 16 with a relatively large X and small Y chromosome (Fig. 36). The autosomes as well as the X chromosome are mediocentric.

First meiotic metaphase cells had 7 autosomal bivalents which always appear rod-shaped. The sex chromosomes form a well defined parachute (Fig. 37.).

Unfortunately, second meiotic metaphases were not seen but presumably they do not depart from the general rule of pre-reduction.

Remarks : The eight chrysomelid species studied belong to 5 different subfamilies : Criocerinae, Galerucinae, Alticinae, Hispinae and Cassidinae. They show a chromosomal range from $2n = 16$ to 57, with such kind of sex determining mechanism as Xy, XO, neo-XY, XY, XXY. In all, cytological information is available on more than 400 species including one parthenogen. The Chrysomelidae is the family in which the most bisexual species are known cytologically in the whole of the Coleoptera. Chromosome number range from 8 to 59, in addition to which the sex determining mechanism is highly variable.

In the Donaciinae, of the 3 known species, one, *Donacia biimpressa*, has a complement of 14AA + Xyp and two *D. hirticollis* and *D. subtilis* 13AA + Xy. The Criocerinae also presents two types of karyotypes : *Lema trilineata* is 15AA + Xy (Stevens 1909), while an unidentified species *Lema* sp. has only 7 pairs of autosomes (present report) and thus a karyotype resembling that of *Crioceris asparagi* (Smith 1960a). Since Stevens reported short rod-like chromosomes in *Lema trilineata*, therefore, it is presumed that fusion translocation must have been involved in production of the metacentrics including the Y

In the Cryptocephalinae, the Pachybrachini has $7AA + Xy$ in its 3 species, but the Cryptocephalini includes *Cryptocephalus quadruplex* with $11AA + Xyp$ (Smith 1960a) and *C. sexsignatus* with $14AA + XY$ (present report) along with another two species having similar karyotype (Yadav 1977).

In the Eumolpinae, 27 species have been investigated (Stevens 1909; Smith 1960a; Virkki 1964; Yadav 1971; Yadav & Pillai 1976; Dasgupta 1973; Dasgupta and Chakravarty 1972; Takenouchi & Shiitsu 1972) including the parthenogenetic *Adoxus obscurus* (Suomalainen 1958a). There are two trends in the evolution of the karyotypes, one towards lower numbers such as 5 to 7 pairs of autosomes, i.e. in *Brachypnoea*, *Talurus*, *Deuteronoda* and *Nodonota*, the other towards higher numbers from 11 to 12 pairs, as in *Maecolaspis*, *Chalcophana*. The primitive $9AA + Xy$ or Xy has been retained by *Glyptoscelis*, *Phanaeta* and *Chrysodinopsis* (Virkki 1964).

In Galerucinae, more than 100 species examined cytologically, reveal similar trends. Entities with the consisting of highest chromosome number are associated with multiple sex chromosomes, as is evident by *Rhaphidopalpa femoralis* having $28AA + XXy$ (Goto and Yosida 1953) and *Aulacophora intermedia* having $27AA + XXy$ (Kacker 1976).

The karyotype of $19AA + Xy$ in *Paridea* sp. reported in this paper, also indicates a similar trend. The category having a lower chromosome number is well represented by *Diabrotica* wherein over 30 species show $9AA + XO$ (Smith). The lowest number reported in Galerucinae is for *Oides bipunctata* (present report), with $8AA + XO$.

The Chrysomelinae is characterised by higher chromosome numbers, ranging between $9AA + XO$ and $23AA + Xy$. approximately 70 (64 + 6) species are known cytologically (Smith 1953a, 1960a; Virkki 1964; Robertson 1966; Petitpierre 1970, 1975; Takenouchi and Shiitsu 1972). The most uniform constituted genus is *Calligrapha* in which almost all the 18 species studied (Stevens 1909; Robertson 1966) have the formula $11AA + XO$ or else are parthenogenetic tetraploid. Higher numbers are found in *Labidomera*, *Leptinotarasa*, four species of *Chrysomela* spp. *Melasoma* and *Phytodecta* (Smith 1953a, 1960a).

Cytologically the most interesting subfamily is the Alticinae, of which about 110 species are known chromosomally. *Homoshema nigriventre* has the lowest chromosome formula of $3AA + XY$ and *Disonycha alternata* has the highest chromosome number, viz., $24AA + neo-Xy$ (Smith 1960a; Virkki 1970; Virkki and Purcell 1965 a,b). This family also has various type of sex chromosomes, from a simple XY to $X1 X2 Y1 Y2$ and even post-reductional gaint-size sex chromosomes, as in *Alagoasa* and *Walterianella* (Virkki 1970). Like most of the Alticines the primitive *Forsterita* has $11AA + Xy$. Increase in chromosome number has occurred in such genera as *Disonycha*, *Walterianella*, *Argopus*, *Blephirida* and *Macrohaltica*,

where it ranges from 12 to 24 pairs of autosomes; a decrease in number appears in *Alagoasa*, *Omphoita*, *Apraea*, *Syphraea*, *Homoschema*, from 10 to 3 pairs. During the present investigation, *Hyphasoma* sp. has been found to have 10AA + neo-XY. This probably is the only sp. occurring in India and constitutes a second example of an Alticinae having a neo-XY.

The subfamily Hispinae has not been studied in detail. About ten species, including *Dactylispa atkinsoni* (present report), are known cytologically. Three species viz. *Anoplistis inaequalis*, *Anoplistis* sp. *Baliosus californicus*, have 8AA + Xyp (Smith 1950, 1960a) and two species, *Chalepus dorsalis* (Stevens 1909) and *Dactylispa atkinsoni*, have 7AA + Xyp.

In Cassadini twenty three species are known chromosomally, including the *Lacoptera quadrimaculata* studied in the present paper. Except in *Botanochara angulata*, which shows a very high diploid number in male, of 51 and XpneoXneoYp sex chromosome complex (Vaio & Postiglioni 1974), most of the species have 8AA + Xyp and to lesser extent 10AA + Xyp (Smith & Virkki 1978).

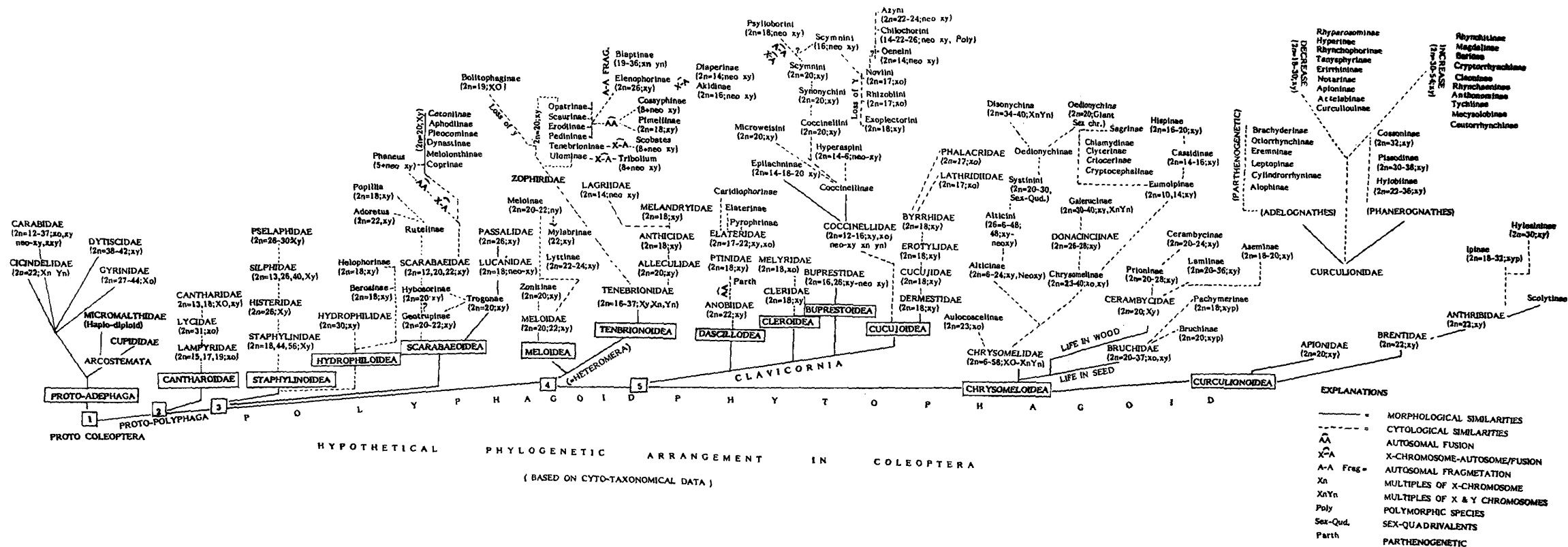
In subfamily Aulacoscelinae, only one species, *Aulacoscelis melanocera* having 11AA + XO, is known cytologically (Virkki 1964).

PHYLOGENY AND INTERRELATIONSHIPS IN COLEOPTERA

Studies on the chromosomes of Coleoptera, particularly in relation to taxonomy and evolution, were of course initiated much later than the studies based on morphology. Whatever theories or explanations have been advanced with regard to its phylogeny, they are based mainly on morphological characters, both adult and larval, supplemented by embryological and anatomical evidence. In order to trace the possible interrelationships between different taxa in the group an attempt has been made here to incorporate available cytological information with current knowledge of the classification of Coleoptera.

Unfortunately, fossil records do not provide a comprehensive picture that permits an understanding of the origin and evolution of beetles; we have, therefore, to depend only on the evidences obtainable from extant beetles. It is generally held that the Coleoptera evolved from Megaloptera like ancestors during the Permian time (Crowson 1960).

A hypothetical phylogenetic tree has been constructed in which relationships at the superfamily level are based on larval and adult characters. Each point of bifurcation in the tree indicates changes that occurred in the prototype of the branches which represents a superfamily. The evolutionary sequence within each superfamily has been discussed only for those families studied cytologically; unfortunately, these data are limited to the number of chromosomes and the sex-



determining mechanism and the conclusions are consequently to be taken only as first approximations.

Very early in evolution, the coleopterans branched out into two main suborders 'Adephaga' and 'Polyphaga' mainly on their feeding habits. The Adephaga in turn adopted two different ways of life, one on land and the other in water. The former comprises the Carabidae and Cicindelidae, the latter, the Gyrinidae and Dytiscidae. These groupings can also be supported on a chromosomal basis. The Geoadephagoids have comparatively lower chromosome number, viz., $2n = 8-37$ in Carabidae and $2n = 22$ in Cicindelidae, while the Hydradephagoids have higher chromosome number viz., $2n = 38-42$ in Dytiscidae and $2n = 27-44$ in Gyrinidae. The Carabidae and Cicindelidae are also chromosomally distinct, the latter alone having a multiple sex chromosome complex.

We have no information about the chromosomes of Cupedidae. The Micromalthidae is cytogenetically almost unique in having a haplo-diploid system of sex determination (Scott 1936) and therefore its separation possibly along with Gupedidae into a distinct sub-order Archostemata (Forbes, 1926) is justified cytogenetically.

The hypothetical ancestors of Polyphaga (point 2) have undergone several morphological changes to give rise to a large number of superfamilies. The changes undergone are : fusion of tibia and tarsus, claws becoming single at larval stage, concealment of propleural plates by the flanks of the pronotum, reduction of cross veins; testes becoming follicular and sessile and arranged around the vas deferens, and ovarioles becoming telotrophic.

The superfamily Cantharoidea does not depart from the archetype of Polyphaga except that the larvae have become terrestrial and have lost the segmentation of pseudocerci. This superfamily includes three families, namely Lampyridae, Lycidae and Cantharidae, which are known cytologically. The most striking common cytological feature in these families is XO type of sex determining mechanism found in the 14 species so far studied. However, in Autillean lycid beetle, *Thonalmus chevrolati* segregation of X is pre-reductional (Virkki 1978). The families differ in having different autosomal number (*vide*, phylogenetic tree).

At the stem of the staphylinoida and Scarabaeoidea (point 3), the 2nd sternite becomes invaginated, absent medially, but distinctly visible at the sides. Antennae are clevate (in Staphylinoida) and larvae remain aquatic. In the Scarabaeoidea, which itself is a specialized and clear cut group, the antennal club is asymmetrical and lamelliform. The testes are also of a special type, not occurring in any other family, but somewhat acquired by phytophaga. The male genitalia are modified and unlike any other Coleoptera. Chromosomally also these two superfamilies seem to be distinct. According to Jeannel and Paulian's (1944) arrangement, five chromosomally known families, viz., Staphylinidae, Silphidae, Pselaphidae,

Histeridae and Hydrophilidae, are included under one superfamily the Staphylinioidea. But Crowson (1955) suggests three separate superfamilies, namely (1) Staphylinioidea retaining the families Staphylinidae, Silphidae and Pselaphidae, (2) Histeroidea comprising the family Histeridae, and (3) Hydrophiloides. Chromosomally, the Staphylinioidea of Jeannel and Paulian, minus Hydrophilidae, show similarities in having higher diploid numbers which are $2n = 18-44-56$ in Staphylinidae, $2n = 13-26-40$ in Silphidae and $2n = 28-30$ in Pselaphidae. The Histeridae also has a high diploid number like that of the Staphylinidae. The Hydrophilidae, on the other hand, shows two types of chromosome number $2n = 18$ and $2n = 30$ (see phylogenetic tree). It would be preferred, at the present state of cytological knowledge, to accept two superfamilies, Staphylinioidea and Hydrophiloides.

The superfamily Scarabaeoidea consisting of Lucanidae, Passalidae and Scarabaeidae (*sensu stricto*) whose chromosomes have been studied. Scarabaeidae has been studied in detail. The lucanidae has a karyotype of $9AA + XO$ in *Psalidoremus inclinatus* and of $8AA + Neo-XY$ in *Dorcus paralleliopipedus* (Virkki 1959). The latter karyotype has arisen, most likely by, A-A fusion. Passalidae are comparatively better known cytologically (Virkki & Reyes-Castillo 1972). There seems to be two trends in karyotypic evolution. The tribe passalini is characterized by $12AA + XO$ whereas the tribe proculini is heterogeneous with karyotype of $8AA + Neo-XY$ to $18AA + Xy$. X-A fusion is probably the cause of autosomal-reduction. Crowson (1960) suggests that the Lucanidae themselves are related to the Scarabaeidae indirectly through Troginae, and that the Passalidae are direct offshoots of the Lucanidae. Cytologically no serious contradiction to this relationship is suggested. The Scarabaeidae (*sensu stricto*) has many subfamilies and more than 90% of their species have a uniform karyotype of $9AA + Xy$. Evolution within the family seems to have proceeded mainly through gene mutation and minute structural rearrangements. The role of structural arrangements in speciation in this group can only be determined when data on the karyotypes, such as relative length of chromosomes, their centromeric indices, etc., are known. Relative heterochromatin content and distribution by C-banding and also studies on G-banding if available would be of paramount importance.

On the basis of the primitive structure of their genitalia, Sharp and Muir (1912) consider the Troginae and Geotrupinae, especially the former as the most primitive of all Scarabaeid subfamilies. Two Troginae genera, *Trox* and *Glaresis*, are considered critical in this respect, and it is thought that all scarabaeids are derived from forms similar to them. Crowson (1960), however, favours the view that the Geotrupinae is the most primitive scarabaeid subfamily based on fossil evidence and the presence of 11-segmented antennae. Cytologically, both these groups have about equal claim to be primitive. The two above mentioned genera of Troginae, are known chromosomally and both have $9AA + Xy$, which of course is the modal

formula for the Coleoptera as a whole, and, therefore, indicates the Troginae as the more primitive. Geotrupinae has chromosomally two distinct tribes viz., Bolbocerinae with conservative $9AA + Xy$ and Geotrupini with $10AA + Xy$ (Smith and Virkki 1978). It appears that Troginae is cytologically more conservative. According to Crowson (1960), the Hybosorinae is the connecting link between the Geotrupinae and the Scarabaeidae (*Sensu Stricto*). The chromosomes are known of only one species, namely, *Ilybosorus orientalis* (Kacker 1970), and its formula is the same as that of the two Troginae, indicating that, cytologically, scarabaeids can be derived as well from it as from the Hybosorinae.

Returning to the main stem (at point 4), two main changes have taken place in the morphology of the group : First, the distal ends of the Malpighian tubules have become concealed in the membrane that surrounds the proctodaeum (*i.e.* Cryptonephridism), and second, the pseudocerci have become one-segmented and hook-like in the larvae. Crowson (1960), recognises Cucujoidea as a large superfamily divided into two major sections, Heteromera and Clavicornia. Heteromera, as the name indicates, have the tarsal formula 5-5-4, wings with more than four anal veins, and maxillae with two lobes. The Clavicornia have the tarsal formula 5-5-5 or 3-3-3, antennae clubbed, wings often with 5 anal veins, and maxillae with single lobe. Taxonomically the Cucujoidea presents formidable difficulties in arriving at a workable natural classification, hence it is not proposed to follow the system of Crowson in the strict sense.

In the so called Heteromera, the two main families Tenebrionidae and Meloidae (Superfamilies according to Jeannel and Paulian 1944), have evolved in two different ways : The Tenebrionidae by having invaginated genitalia with phallobase (Tegman) forming a sheath, and Meloidae by having differentiated characteristic hypermetamorphosis in larvae. After the differentiation of meloids, there occurred a loss of the 2nd sternite, giving rise to the other relatives of tenebrionids.

The Tenebrionidae has diploid numbers ranging from 16 to 37 together with various types of sex chromosomes. The basic chromosome formula of the family nevertheless remains $9AA + Xy$. The different chromosome numbers have been derived through X-A fusion, A-A fusion, and autosomal fusion (Smith 1952). The chromosomal relationships at the subfamily level are indicated in the hypothetical phylogenetic tree. The Anthicidae, Lagriidae and Melandryidae have cytological similarities in that all have a low diploid numbers that can be derived from the basic number in Alleculidae through centric fusion.

The Meloidae has three chromosomally known subfamilies : The Meloinae has a karyotype of $9AA + Xy$, (although one of its tribes, viz., Mylabrini, has $10AA + Xy$), whereas the subfamily Lyttinae retains the typical karyotype of $9AA + Xyp$ in most of its species. Zonitinae is also $9AA + Xy$ in its sole species known cytologically.

At point 5 we find similar morphological changes that have taken place in the Tenebrionidae i.e., loss of 2nd sternite, but not accompanied by the changes in the genitalia. At this point a tremendous amount of diversity appeared during evolution, and it becomes extremely difficult to arrive at a proper natural classification and decide from what common trunk the various superfamilies arose. However, it is assumed that the Cucujoidea (corresponding to Clavicornia of Crowson 1960), Dascilloidea, Cleroidea, Buprestoidea and Phytophagoid families have been evolved from here. Only the cucujoids have retained the primitive three lobed coleopteran type of genitalia, whereas the remainder have evolved with specialised one.

Among the Dascilloidea, the families Elateridae, Ptinidae and Anobiidae are known cytologically. Morphologically the Elateridae are related to the Cantharoidea. The predacious habits of some elaterid larvae suggest their affinity with such primitive Coleoptera as Caraboids, Staphylinoids, Hydrophyloids and Cantharoids. Characters such as presence of luminous organs in some pyrophorine elaterids, wing venation, structure of metendosternite also suggest a relationship with Lampyridae (Cantharoidea). Cytological data on about 75 species reveal that 48 species possess XO sex chromosomes, similar to Lampyridae in particular and other Cantharoids in general. These overall similarities suggest that if the Elateridae is to be merged with any superfamily it should be the Cantharoidea. Other Dascilloidea such as Ptinidae and Anobiidae are poorly known chromosomally. It may be recalled here that at least one Ptinid is gynogenetic.

The Superfamily Euprestoidea consists of a single family the Buprestidae, which is considered closely related to the Elateridae but differs essentially in the structure of the aedeagus and metasternum. Cytologically, the Buprestidae have predominantly Xy or neo-XY sex chromosomes as against the Xyp and XO of Elateridae. Thus, the cytological findings do not conflict radically with the taxonomic grouping

The superfamily Cleroidea, though taxonomically complicated, has a uniform karyotype of $8AA + Xyp$ in the family Cleridae.

The Cucujoidea (section Clavicornia of Crowson) Comprises the Coccinellidae, Dermestidae, Byrrhidae, Cucujidae, Erotylidae, Lathridiidae and Phalacridae. Except for the first and the last two families, all have the formula $8AA + Xy$ or neo-XY

The Coccinellidae, which has been studied extensively, presents a wide range of chromosome numbers and also much variation in its sex chromosome systems. The family is divided into two subfamilies, viz., Epilachninae and Coccinellinae, the phylogeny of which has been discussed in detail by kapur (1970). According to Boving and Craighead 1931) the larvae of *Hyperaspis* (Hyperaspini) are primitive, and typically have a $6AA + X + y$ karyotype (Smith 1960a). Contrary to earlier findings the primitive karyotype of $9AA + Xy$ is infact represented in the Epilachninae, just as in some tribes of the Coccinellinae, for example, coccinellini,

Synonychini and Scymnini. The Noviini and Rhizobiini have 8AA + XO. This karyotype seems to have evolved by way of loss of Y chromosome. Further reduction in the chromosome number has been found in the Oeneini (6AA + neo-XY) and is probably due to joint X-A and A-A fusion. The Chilacorini, whose cytology is known in detail, has one distinctly polymorphic XXY species (Smith 1957a, c, 1958, 1959, 1965). All other species of this tribe, so far worked out cytologically, are neo-XY type. In *Chilocorus* due to centric fusion there has been a gradual decrease in number from 11 pairs of autosomes in *C. stigma* to 6 pairs in *C. hexacyclus*. This is a unique tribe in which translocations have played a very important role in speciation. A less extreme situation is met within the Psylloborinae, which seems to have arisen from some Scymnini type of karyotypes.

Such a wide diversity of chromosomal numbers and sex-determining mechanism in between tribes suggests that the Coccinellidae should be given superfamily rank, so that the lower taxonomic categories could be accommodated in a natural system of phylogeny.

The final branch of the tree, viz. Phytophaga, is a highly specialized group. Adults of the families included under the Phytophagoidea have in common cryptopentamerous tarsi with bristles beneath; follicles of testes with 1-2 pedunculate testiculi and no ejaculatory duct. Male genitalia are saddleshaped. Jeannel and Paulian (1944) have placed the Chrysomelidae, Cerambycidae, Bruchidae, Curculionidae, Brentidae, Anthribidae and Scolytidae in the Phytophagoidea, but Crowson (1955) favours grouping them into two superfamilies, Chrysomeloidea, comprising the first three families, and Curculionoidea, embracing the remainder.

The Chrysomeloidea seems to be a natural superfamily and has similarities with the allied Curculionoidea. Some earlier authorities have advocated derivation of Curculionidae from Chrysomelidae through Bruchidae (Ganglbauer, 1889).

Cytologically, the Chrysomelidae presents a miniature replica of the whole of the Coleoptera, in showing the complete range of chromosome numbers and types of sex chromosomes. Even parthenogenesis occurs in *Adoxus obscurus* and *Calligrapha*.

The Eumolpinae and Galerucinae appear to be cytologically complicated. In the Eumolpinae the karyotype has evolved in two directions ; one towards higher and the other towards lower diploid numbers. Although the Galerucinae has attained the highest chromosome numbers in the order as a whole, the genus *Diabrotica* has remained cytologically conservative (Ennis 1972a). The Donaciinae has not been studied in detail, but it shows $2n = 30$ in all three species studied. Karyological affinities, corresponding with larval affinities, are evident in the Hispinae and Cassidinae, both of which have 9AA + Xy. Details on the chromosomal distribution in each subfamily have already been presented.

The Bruchidae is considered very closely related to the Chrysomelidae morphologically, but the conclusion cannot be supported by cytological data. The Bruchidae shows two distinct karyotypes, one of $9AA + Xyp$ and another $18AA + XO$. A detailed cytological study may reveal some important and interesting facts.

The Cerambycidae is markedly conservative chromosomally. About 150 species in 4 subfamilies, have in all Xy or Xyp sex determining mechanism. More than 70% of species studied chromosomally show $2n = 20$, having $9AA + Xy$. This may be due to their peculiar habitat creating a potential barrier for genetical reshuffling.

The Curculionidae out numbers the Chrysomelidae in total numbers of constituted species and is regarded as one of the most specialized families of Coleoptera second only to the Scolytidae. It has morphological features in common with the Cerambycidae, e.g. both lack side margins to the prothorax. The cytological implications in concerning the apparent relatedness must await further detailed studies.

On the basis of external characters the Curculionidae can be conveniently subdivided into two groups, namely, the Phanerognathes and Adelognathes. The former have a long rostrum and exposed maxillae, the latter, a comparatively short rostrum and maxillae hidden beneath the expanded mentum (Emden & von 1938).

Among the Phanerognathes, members of the subfamilies Pissodinae and Hylobinae have been studied cytologically in detail. The genus *Pissodes* contains some polymorphic species taxa and different species, $2n = 24$ to 34 (Manna and Smith 1959). However, the basic diploid number remains constant at 34 . *Hylobius* on the other hand has many species showing far greater numerical diversity, i.e., $2n = 20, 28, 36, 40$ and 48 (Smith 1956b; Takenouchi 1954, 1955b, 1958a, b); of these *H. warreni* is almost certainly a fusion pericentric inversion neo-homogygote deprived from $2n = 40$ (Smith 1956b). *Hylobius warreni* ($2n = 32$), *H. pinicola*, *H. piceus*, *H. albosparsus* (all $2n = 40$) and *H. elongatus* ($2n = 48$) can be grouped together on the basis of the external characters (Wood 1957).

In adelognathes curculionids, the subfamily Otiorrhynchinae is particularly well studied, doubtless, because of the interest its parthenogens have attracted Mikulska (1951), Suomalainen (1954). To a lesser degree the same is true of subfamilies Leptopinae, Cylindrorrhynae, Alophinae, etc. (*vide*, phylogenetic tree).

Cytological data are available in more than 300 species of Curculionids covering about 34 subfamilies. The karyotypes reveal two trends, one towards decrease in chromosome number and another towards increase. They are placed only approximately on the phylogenetic tree.

Other families of Cuculionoidea are the Brentidae, Anthribidae and Scolytidae. The Brentidae has an uniform karyotype of $10AA + Xy$ in the 5 species so far

studied, as also in 2 species of Anthribidae (Virkki 1965). These two families can be grouped together chromosomally. The Scolytidae shows wide chromosomal variation. One of its subfamilies the Ipinae, has some arrhenotomus (Xyloborini) and gynogenetic (Ipinii) parthenotes; and the other the Hylesininae has a uniform diploid number of 30. Crowson (1955) regards the Scolytidae as a subfamily Scolytinae, of the Curculionidae. Cytological data are insufficient to merit comments on this.

It is evident from the above discussion that Phylogenetic relationships within the higher taxon can but rarely be substantiated by chromosome number alone. The details of longitudinal differences along the chromosome length ultimately may provide some answers to the cytotaxonomy of coleopteran insects. Presence of heterochromatin in some coleopterans have resulted in variety of chromosomal abnormalities such as deletions, translocation or even emergence of an entire new arm. Position of centromere may also vary within the chromosomes. Significantly the genus *Chilocorus* shows some differential chromosomal condensation in its two arms. The euchromatic arm condenses earlier than the heterochromatic arm, when treated with Colchicine. This has proved to be of great practical significance in the analysis of heterochromatin relationship in chilocorinae karyotype (Smith 1966b). Similar differential staining is achieved by the techniques of C-banding developed by Arrighi & Hsu (1974) which basically provide differential segments of chromosomes. Application of quinacrine mustard or other fluorochromes often give quite similar results, though useful, but non-infallible in identification of chromosomes (Zech 1973). Although theoretically the C-banded (Constitutive heterochromatin) arms could be dispensable without significant genetic effect but it does play a role in the evolution of chromosome number and form. On the other hand G-banding produced by Giemsa staining of euchromatic arm does provide a great deal of information for chromosomal comparison in various groups of animals specially in the mammals. In coleoptera, however, data are not available in plenty to venture into its applicability except by Angus (1982,83) who has separated the species in the genus *Helophorus* (family Hydrophilidae) with the help of G-banded karyotype. The two species in the genus differ because of translocations in some chromosomes hitherto merged as one species.

Therefore, the cytotaxonomists need more precise step to study the banding pattern. In Coleopteran cytogenetics, this area has not yet opened to the extent of realising its significance sufficiently, nonetheless, some efforts have been made. Unless the banding data are available in Coleoptera one will have to continue to depend on the older type of conventional cytogenetical studies.

White (1954) has rightly stated that.....“Cytology is certainly a tool that deserves more attention by animal taxonomist than it has received in the past; but it is not a magic key that will unlock all taxonomic problems as some have supposed’

TABLE—II
Comparative Measurements of Karyotypes

SPECIES	MEAN RELATIVE LENGTH IN PER CENT OF EACH PAIR OF CHROMOSOME																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	X	Y
1. <i>Cyaneolytta</i> sp. nov.	12.5	11.5	11.4	11.0	10.1	9.8	9.3	8.9	7.3	—	—	—	—	—	—	—	—	—	—	8.3	4.5
2. <i>Psalydolytta</i> sp.nr. <i>rouxi</i>	13.0	11.6	11.4	10.4	9.9	9.8	9.1	8.9	7.1	—	—	—	—	—	—	—	—	—	—	8.8	4.9
3. <i>Adelocera colonicus</i>	14.0	12.7	12.1	10.4	10.2	9.9	9.3	8.1	—	—	—	—	—	—	—	—	—	—	—	13.0	—
4. <i>Afissa parvula</i>	13.7	12.3	11.0	10.5	9.3	8.6	7.9	7.1	—	—	—	—	—	—	—	—	—	—	—	19.4	2.1
5. <i>Platynotus punctatipennis</i>	12.9	11.6	10.7	10.5	10.4	9.9	8.8	8.5	7.7	—	—	—	—	—	—	—	—	—	—	8.7	3.2
6. <i>Gymnopleurus cyaneus</i>	16.4	12.0	11.6	10.6	10.1	8.3	7.8	7.7	6.7	—	—	—	—	—	—	—	—	—	—	8.7	1.9
7. <i>Lema</i> sp. nov.	19.1	15.3	12.6	12.0	10.6	8.6	6.4	—	—	—	—	—	—	—	—	—	—	—	—	15.5	6.7
8. <i>Paridea</i> sp. nov.	8.2	6.5	6.1	5.8	5.5	5.5	5.3	5.1	4.7	4.6	4.5	4.3	4.1	4.1	3.8	3.7	3.5	3.4	3.1	8.2	1.9
9. <i>Oides bipunctata</i>	16.2	15.3	13.7	12.6	11.9	9.7	8.7	7.3	—	—	—	—	—	—	—	—	—	—	—	4.6	—
10. <i>Laccoptera quadrimaculata</i>	15.4	13.7	12.6	11.9	11.1	10.6	9.3	8.0	—	—	—	—	—	—	—	—	—	—	—	7.4	1.5

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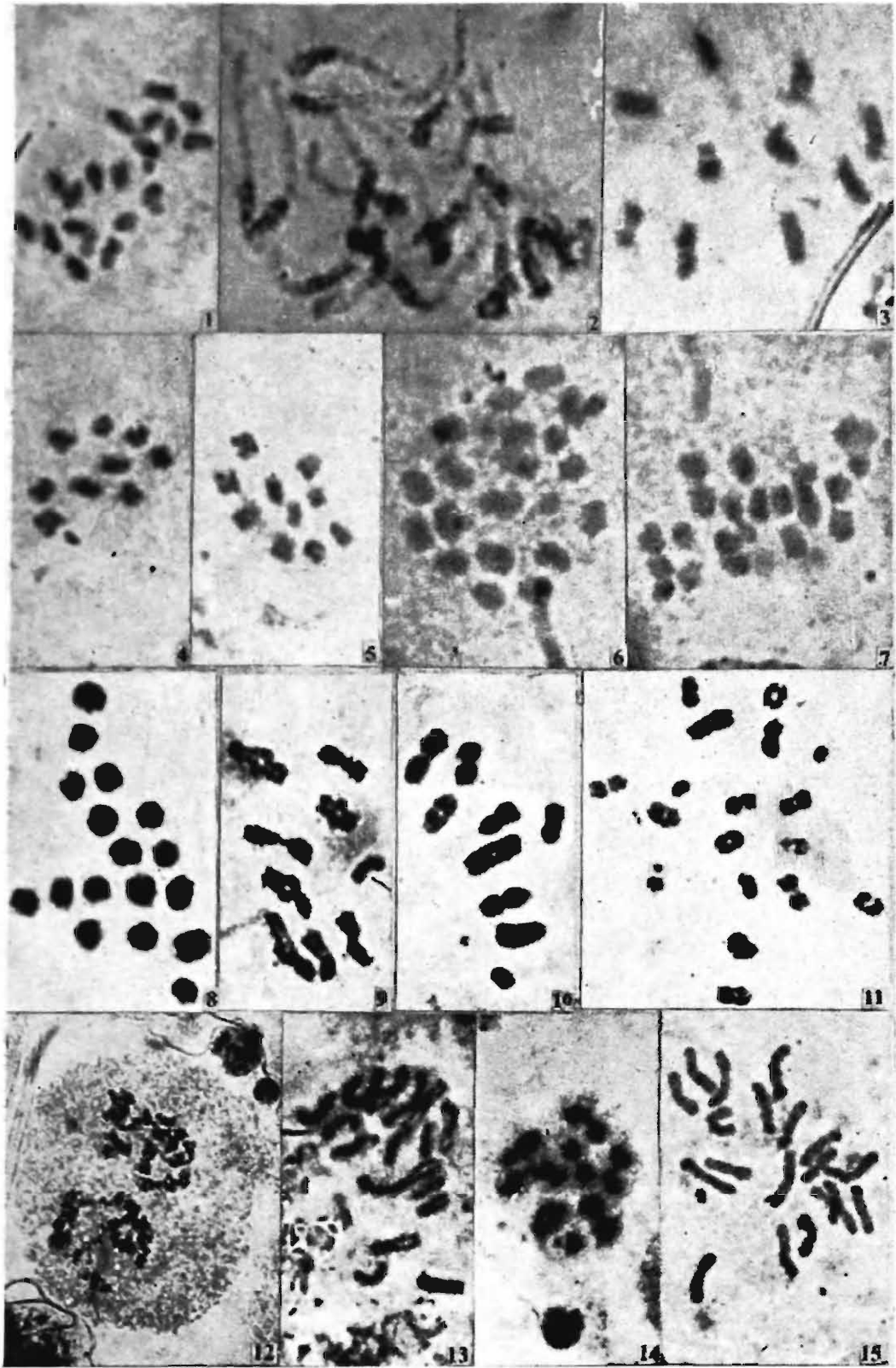
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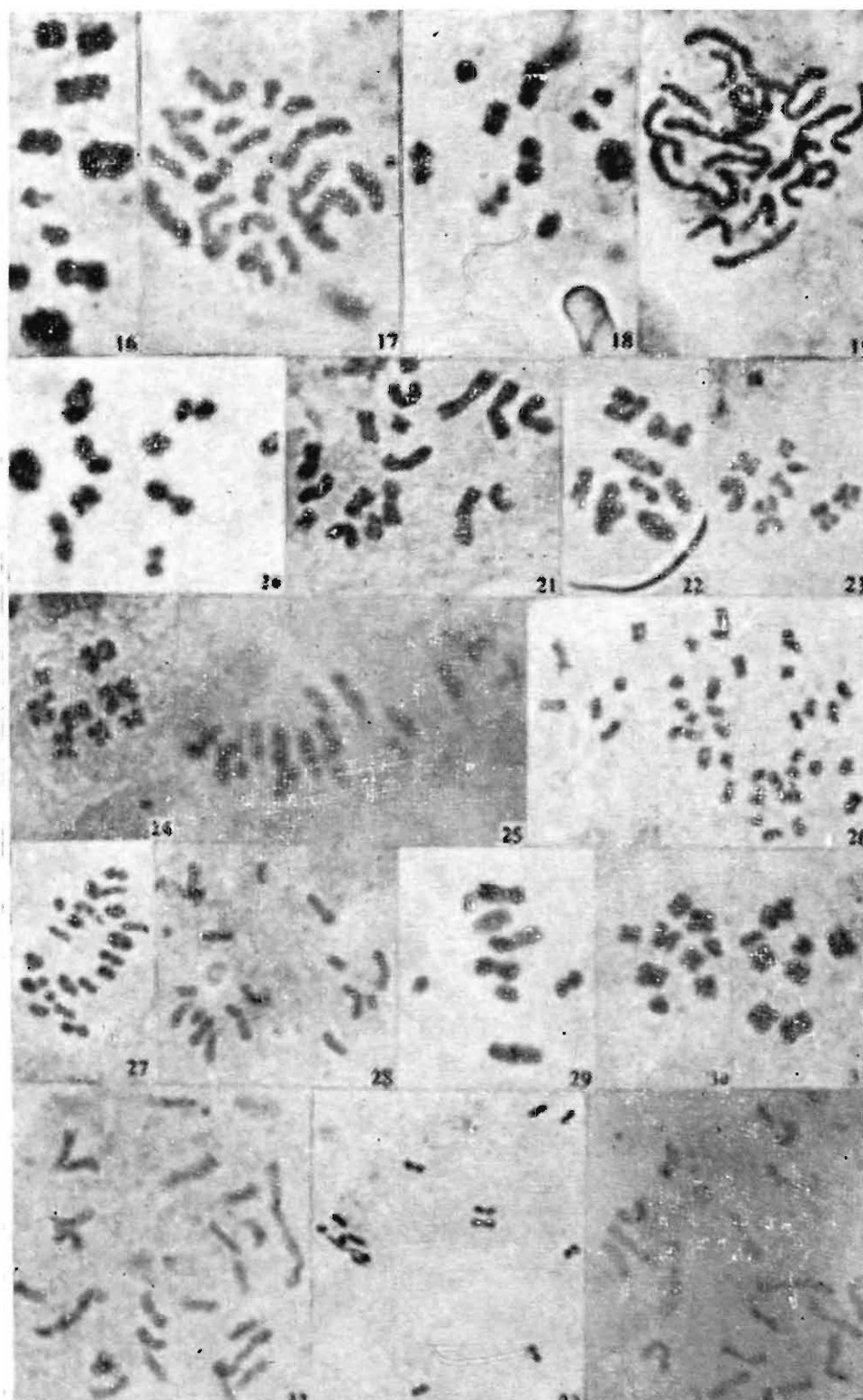
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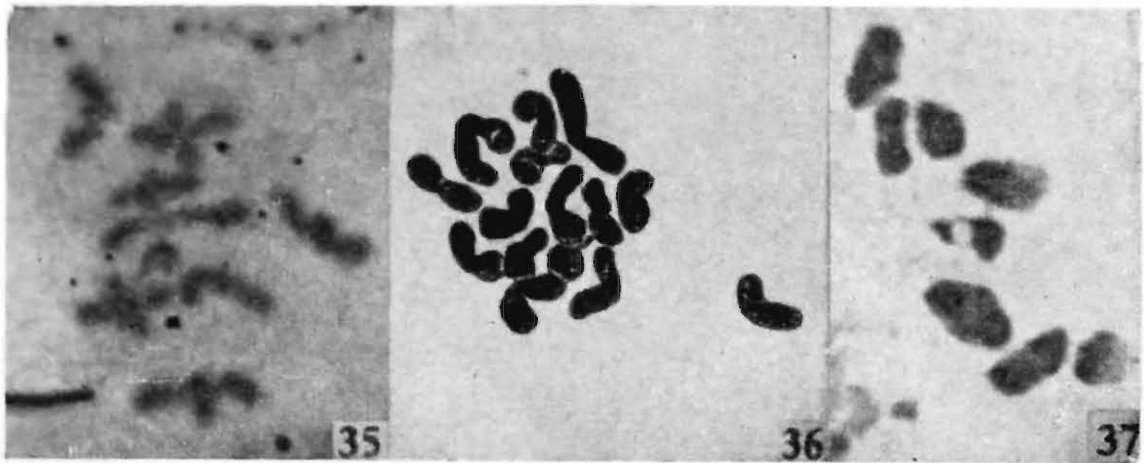
Figs. 1—15

Spermatogonial metaphase in *Cyaneolytta* Sp. (1) Spermatogonial metaphase showing deeply stained regions (2), metaphase I in *Cyaneolytta* Sp. (3), metaphase II in *Cyaneolytta* Sp. (4 & 5), Spermatogonial metaphase in *Psalydolytta* Sp. nr *rouxi* (6), metaphase I in *P. sp. nr rouxi* (7), Spermatogonial metaphase in *Adelocera colonicus* (8), Diakinesis in *A. colonicus* (9), metaphase I in *A. colonicus* (10), Tetraploid and binucleate cells in *A. colonicus* (11 & 12), Spermatogonial metaphase in *Afissa parvula* (13), metaphase I in *A. parvula* (14), Spermatogonial metaphase in *Platynotus punctatipennis* (15).



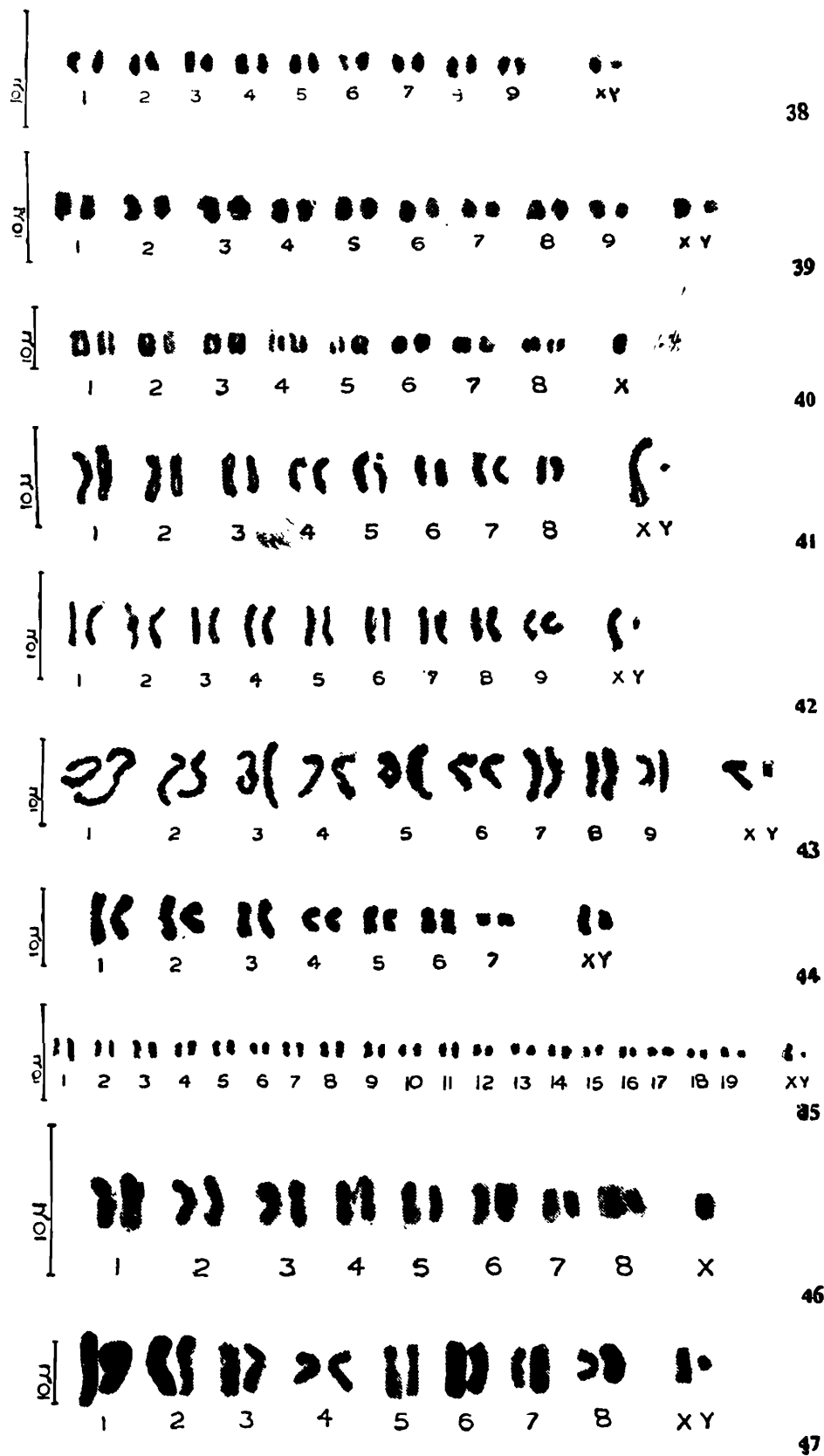
Figs. 16—34

Metaphase I in *Platynotus punctatipennis* (16), Spermatogonial metaphase in *Sphenarlopsis tristis* (17), metaphase I in *S. tristis* (18), spermatogonial metaphase in *Gymnopleurus cyaneus* (19), metaphase I in *G. cyaneus* (20), Spermatogonial metaphase in *Lema* Sp. (21), metaphase I in *Lema* Sp. (22), metaphase II in *Lema* Sp. (23 & 24), metaphase I in *Cryptocephalus sexsignatus* (25), Spermatogonial metaphase in *Paridea* Sp. (26), metaphase I in *Paridea* Sp. (27), Spermatogonial metaphase in *Oldes bipunctata* (28) metaphase I in *O. bipunctata* (22), metaphase II in *O. bipunctata* (30 & 31), Spermatogonial metaphase in *Hyphasoma* Sp. (32), metaphase I in *Hyphasoma* Sp. (33). Spermatogonial metaphase in *Laccoptera quadrimaculata* (34).



Figs. 35--37

Diakinesis in *Lacoptera quadrimaculata* (35), Spermatogonial metaphase in *Dactylispa atkinsoni* (camera lucida) (36), metaphase I in *D. atkinsoni* (37)



Figs. 38—47

Karyotypes of *Cyaneolytta* Sp. (38). *Psalydolytta* Sp. nr. *rouxi* (39), *Adelocera colonicus* (40), *Afissa parvula* (41), *Platynotus punctatipinnis* (42), *Gymnopleurus cyaneus* (43), *Lema* Sp. (44), *Paridea* Sp. (45), *Oldes bipunctata* (46), *Laccoptera quadrimaculata* (47).