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Cytogenetic analysis, karyotype evolution and phylogenetic study of family Scarabaeidae (Coleoptera: Insecta)

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ABSTRACT

The family Scarabaeidae comprises 25, 000 described species and is known cytologically by 404 species of 123 genera and 18 subfamilies. The present investigations recorded an account of 33 species representing 6 subfamilies, of which 17 species are new additions to this family. Scarabaeidae is conservative family in having the chromosome number 2n=20, sex determining mechanism 'Xyp' and metacentric chromosomes. Most of the cytogenetically known species have a chromosome number varying from 2n=8 in *Eurysternus caribaeus* to 2n= 36 in *Gymnopleurus miliaris* race-II (present study). The most prevalent sex determining mechanism is Xyp. The most common karyotype possessed by 175 species belonging to 18 subfamilies is 9AA+Xyp male, the most prevalent condition in Coleoptera as a whole. As many as 302 species showed a haploid number of 10. So, this can be very well designated as the 'modal number' for Scarabaeidae.

1. Introduction

The Polyphagan beetles possess 2n=20 as the 'modal number' of chromosomes. Structural changes in the chromosomes, distribution patterns of constitutive heterochromatin and localization of nucleolar organizer region on the chromosomes are equally important in the speciation of beetles and in other group of insects. Detailed analytical studies on the lines of a large number of workers Bickham and Baker (1976), Smith and Virkki (1978) Yadav and Pillai (1979), Bengtsson (1980), Bickham (1981), Angus (1983), Bickham *et al.* (1983), Lyapunova *et al.* (1983), Vorontsov *et al.* (1984), Virkki (1984, 1988), Petitpierre (1987), Yadav *et al.* (1991), Colomba *et al.* (2000) and Bione *et al.* (2005a, b) are essential for proper understanding of interrelationships and evolutionary processes in this group.

The order Coleoptera has the highest species diversity within the animal kingdom, yet cytogenetic data using specific banding techniques are still scarce. C-banding data have revealed a preferential localisation of constitutive heterochromatin (CH) in centromeric area and less so observed in interstitial and telomeric areas. Sex chromosomes also show a variable CH distribution, as it has been observed in the pericentric region or along the entire chromosome. Major contributions in using C-banding technique for the cytological analysis of Polyphaga are of Ennis (1975), Colomba *et al.* (2000, 2004), Mafei *et al.* (2000, 2004), Rozek and Holecova (2002), Petitpierre and Garneria (2003),Vitturi *et al.* (2003), Petitpierre *et al.* (2004), Wilson and Angus (2004 a, b, 2005 a, b, 2006), Bione *et al.* (2005 a, b), Beauchamp and Angus (2006), Angus *et al.* (2007), Holecova *et al.* (2008), Arcanjo *et al.* (2009) and Oliveira *et al.* (2010), Carbal *et al.* 2011.

Silver nitrate staining of meiotic chromosomes of eukaryotic species has been a very useful approach for the analysis of the structure and variability of nucleoli, nucleolar organiser region and kinetochores (Goodpasture and Bloom 1975; Virkki and Denton 1987; Virkki *et al.* 1991). NOR activity at the bigning of the meiotic prophase is widely observed in a large number of organisms, including Coleoptera species. However, this activity was observed during a restricted period of time only, declining rapidly and disappearing in the middle of the diplotene phase. Nevertheless, the nucleolar masses produced can persist for a longer period of time, especially in species with prolonged diplotene (Virkki and Denton 1987; Virkki *et al.* 1991).

The cosmopolitan beetle family Scarabaeidae comprises approximately 2000 genera and 25000 species (Arcanjo *et al.* 2009). Despite of the large number of species, there are few studies about the chromosomal diversity of Scarabaeidae representatives and approximately, only 390 species have been analysed, predominantly using conventional staining (Arcanjo *et al.* 2009). About 70 Scarabaeidae species have been studied using differential or molecular cytogenetic technique, such as C-banding, base specific fluorochromes, silver niterate staining or fluorescence *in situ* hybridisation by Moura *et al.* (2003), Wilson and Angus (2004 a, b, 2005 a, b, 2006), Bione *et al.* (2005 a, b), Angus *et al.* (2007) and Dutrillaux *et al.* (2007 a, b). The constitutive heterochromatin in this family is predominantly located in the pericentric region of the chromosomes and this genomic component shows wide heterogeneity regarding A-T richness and G-C richness. However, the nucleolar organiser region (NORs) is predominantly located either in a single autosomal pair or in the X chromosome or more than one rDNA site clustered in different chromosome pairs (Moura *et al.* 2003; Bione *et al.* 2005 a, b; Macaisne *et al.*2006).

2. Variation of chromosome number

The family Scarabaeidae comprises 25, 000 described species and is known cytologically by 397 species of 123 genera and 18 subfamilies (Table 1). The major contributors are Yosida (1949b, 1951), Virkki (1951, 1954a, 1967a), Manna and Lahiri (1972), Salamanna (1972), Kudho *et al.* (1973), Yadav and Pillai (1975a, 1976a, b, 1978, 1979), Vidal *et al.* (1977), Smith and Virkki (1978), Vidal (1984), Yadav and Dange (1988b, 1989, 1991), Yadav *et al.* (1989), Hanski and

Cambefort (1991), Colomba *et al.* (1996, 2000, 2004, 2006), Moura *et al.* (2003), Bione *et al.* (2005a,b), Angus *et al.* (2007), Carbal de Mello *et al.* (2007, 2008, 2010, 2011) and Silva *et al.* (2009), The present investigations recorded an account of 33 species representing 6 subfamilies, of which 17 species are new additions.

Scarabaeidae is conservative family in having the chromosome number 2n=20, sex determining mechanism 'Xyp' and metacentric chromosomes (Smith and Virkki 1978, Yadav and Pillai 1979, Colomba *et al.* 1996, Moura *et al.* 2003, Bione *et al.* 2005 a, b). Most of the cytogenetically known species have a chromosome number varying from 2n=8 in *Eurysternus caribaeus* (Carbal de Mello *et al*. 2007 and Arcanjo *et al.* 2009) to 2n= 36 in *Gymnopleurus miliaris* race-II (present study). The most prevalent sex determining mechanism is Xyp (Smith and Virkki 1978, Vidal 1984, Colomba *et al.* 2000) . The most common karyotype possessed by 175 species belonging to 18 subfamilies is 9AA+Xyp male, the most prevalent condition in Coleoptera as a whole. As many as 302 species (Table 1) show a haploid number of 10. As such this can be very well designated as the 'modal number' for Scarabaeidae.

All the karyologically known species of subfamilies Pleocominae and Troginae have the basic karyotype 9AA+Xyp with 2n=20 (Purcella and Virkki 1966, Virkki 1967a, Yadav and Pillai 1976b, 1978, 1979, Yadav and Dange 1988b, 1989, Yadav *et al*. 1989). In subfamily Geotrupinae eight species of genus *Geotrupes* (Virkki 1951, 1960, Smith 1960a, Salamanna 1966, 1972), *Thorectes intermedius* and *Anoplotrupes stercosus* (Colomba *et al.* 2004) have 2n=22, while *Bolbelasmus arcuatus* and *Athyreus excavates* (Virkki 1967a, Smith and Virkki 1978) and two species of *Bolboceras* viz. *B. quadridens* and *B. indicum* (Yadav and Pillai 1979, Yadav 1983, Yadav *et al.* 1990 and present report) possessed the modal number of scarabs. In *Bolbocerus indicum* both the sex chromosomes were found associated to a nucleolar body during first meiotic division. Subfamilies Orphinae, Hybosorinae, Chironinae, Glyphyrinae, Aegialiinae, Trichiinae, Acanthocerinae and Cetoniinae are uniform in having 20 chromosomes in the diploid set, while subfamily Dynamopinae with only one species *Dynamopus athleta* possess 2n=22: 10AA+Xyp (Yosida 1949b, 1951, Virkki 1951, 1954a, 1954b, 1967a, Smith 1960a, Kacker 1970, Manna and Lahiri 1972, Salamanna 1972, Kudho *et al.* 1973, Vidal *et al.* 1977, Yadav and Pillai 1977a, 1979, Smith and Virkki 1978, Vidal 1984 and Mascaine *et al.* 2006 and present reports). In the present investigations, meioformula 2n= 9AA+Xyp, lampbrush like fibres in bivalents of first prophase and high chiasma frequency of *Hybosorus orientalis* confirmed the earlier reports given by Kacker (1970) and Yadav *et al.* (1990).

Out of 40 chromosomally known species of subfamily Aphodiinae only *Aphodius moestus* (Yadav 1973; present report) has a diploid number of 22, whereas remaining all species possess the modal number 2n=20. The Scarabaeinae constitutes a highly diverse subfamily that comprises about 5000 described species belonging to 234 genera spread widely in the world (Hanski and Cambefort, 1991). This subfamily shows maximum variation in the number, morphology and size of chromosomes. Cytologically, 162 Scarabaeinae species are known and chromosome number varies from 2n=8 in *Eurysternus caribaeus* to 2n= 24 in *Oniticellus spinipes*, with the Xyp being the most prevalent sex chromosome mechanism (Smith and Virkki 1978; Yadav and Malik 1978; Vidal 1984; Colomba *et al.* 2000). The other variations falling between the two extremes are 2n=12: 5+neoXy in five species of *Phanaeus* (Hayden 1925; Virkki 1959; Smith and Virkki 1978 and Carbal de Mello *et al.* 2008), 2n = 14: 6+neoXy in five species of *Deltochilum* (Carbal de Mello *et al.* 2008, 2010), *Gymnopleurus mundus* with 6+Xyp (present report) , *Copris incertus* (Virkki 1960), *Copris sinicus* (Angus *et al.* 2007), *Copris* species (Manna and Lahiri 1972) while *Sisyphus neglectus* possess 2n=16 : 7+Xyp (present report) , 32 species : *Anomiopsoides heteteroclyta, Euranium arachnoids, Glyphoderus sterquilinus, Isocopris inhiata, Bubas bubalus, Gymnopleurus sinuatus, G. parvus, Copris signatus, Paracopris ramosiceps, Canthidium breve,* three species of *Canthon, Canthochilum* spp., *Catharsius* sp., *Onthophagus* spp. and 15 species of *Dichotomius* have 2n=18 with 8+Xyp (Manna and Lahiri 1972; Vidal 1984; Colomba *et al.* 1996; Bione *et al.* 2005b; Angus *et al.* 2007; Carbal de Mello *et al.* 2008, 2011; Silva *et al.* 2009; present report), whereas *Copris hispanus cavolinii* has 2n=19 (Salamanna 1972) and remaining 110 species possess 2n=20 : 9+Xyp which was the most common number in this family (Yosida 1951; Virkki 1951, 1954a, 1967a; Joneja 1960; Dasgupta 1963; Kacker 1970; Yadav and Pillai 1977b, 1978, 1979; Yadav and Malik 1978; Vidal 1984; Yadav and Dange 1988 a-b, 1989; Yadav *et al.* 1993b; Colomba *et al.* 1996, 2000, 2006; Bione *et al.* 2005b; Angus *et al.* 2007), while *Copris fricator* possess 2n=21: 10+X (Joneja 1960).

Two types of diploid configurations 2n= 20 : 9+Xyp and 2n=36: 17+Xyp were encountered during the present investigations in two races of *Gymnopleurus miliaris* which depict dimorphic nature of this species.

Subfamily Sericinae is cytogenetically known by 14 species. All of the ten species belonging to genus *Serica* and *Maladera* depict 2n=20: 9+Xyp (Smith 1950; Joneja 1960; Virkki 1960, 1967a; Manna and Lahiri 1972; Yadav and Pillai 1974a, 1979; Yadav and Dange 1988b, 1991; Yadav *et al.* 1989). A single unidentified species of *Aserica* possessed 2n = 19 (Yadav and Pillai 1979), whereas one unidentified *Autoserica* species (Dua and Kacker 1975) and *Ophthalmosarica karafutensis* (Kudoh *et al.* 1973) have 2n=18. The highest diploid number of the family Scarabaeidae, 2n= 30 (Dasgupta 1977; Yadav *et al.* 1979; Arcanjo *et al.* 2009) is represented by *Autoserica assemensis* of this subfamily. The variation in the number of chromosomes in subfamily Melolonthinae is much less than Scarabaeinae. As many as 37 species belonging to 13 genera are known to cytology (Shaffer1920; Virkki 1951; Smith 1960a; Duff 1970; Kacker 1970; Manna and Lahiri 1972; Saha 1973; Yadav and Pillai 1974a, 1976c, 1979; Yadav and Dange 1988b; Moura *et al.* 2003) Whereas 33 species possess the 'modal number' 2n=20:9+Xyp, three species of *Apogonia* (Kacker 1970; Yadav and Pillai 1974a, 1976c) show 2n=19: 9+XO and one unidentified species of *Apogonia* possess 2n= 21: 10+X (Saha 1973), however, *Haplidia etrusca* depict 2n= 18 : 8+neoXY (Salamanna 1972) . So the basic diploid number of this subfamily is 20.

In subfamily Rutelinae diploid number varies from 16 to 22 in 52 cytologically known species, out of which all 13 species of genus *Adoretus* and one species of *Adorrhinyptia* possess the higher number 2n=22: 10+Xyp (Joneja 1960; Kacker 1970, 1971; Yadav and Pillai 1975a, 1976 a, b, 1979; Mittal *et al.* 1987; Yadav and Dange 1988b; Yadav *et al.* 1989; present report), whereas one unidentified species of genus *Adorrhinyptia* show polymorphic nature (Saha and Manna 1971; Saha 1973). Although most of the species of genus *Anomala* (Yosida 1949b; Joneja 1960; Agarwal 1960, 1962; Lahiri and Manna 1969; Manna and Lahiri 1972; Kudoh *et al.* 1973; Yadav and Pillai 1974a, 1975a, 1979; Smith and Virkki 1978; Mittal *et al.* 1985) depicted basic karyotype 2n=20, yet two types of diploid number 2n=18 and 20 were reported in *Anomala bengalensis* (present report) and *A. rufocuprea* (Saha and Manna 1971; Yadav *et al.* 1993a; Kudoh *et al.* 1973; Yosida 1949b) explicating dimorphic nature of both the species.

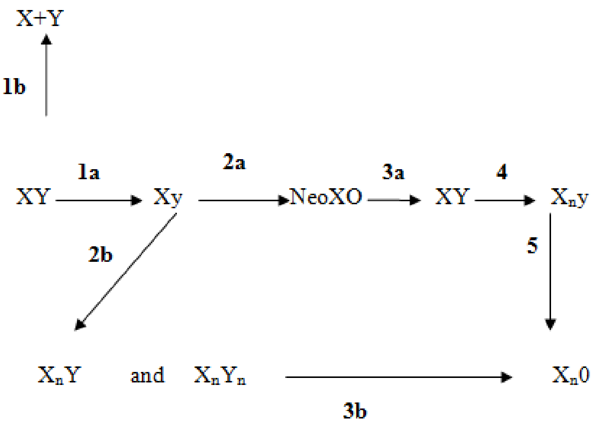
Cytological data belonging to 35 species of subfamily Dynastinae is known. The commonest number is 2n=20 possessed by 21 species belonging to the genus *Cyclocephala, Dyscinetus, Diloboderus, Euetheola, Ligyrus, Bothynus, Ligyroides, Phylloganthus, Pentodon, Eophileurus, Allomyrina* and *Lycomedes* ((Joneja 1960; Virkki 1967a; Kodoh *et al.* 1970, 1973; Vidal *et al.* 1977; Yadav and Pillai 1977a, 1979; Smith and Virkki 1978; Vidal 1984; Bione 2005a). Variations are 2n= 16 :7+neoXY in *Arcophileurus vervex vervex* (Vidal 1984) , 2n=18 : 8+neoXY in eight species: *Cyclocephala tridentate, C. maffafa, Enema pan, Dynastea hercules hercules* , *Ligyrus cuniculus* , *Phylloganthus sinensis, Strategus syphax* and *Megasoma actaeon* (Virkki 1951; Salamanna 1972; Vidal and Giacomozzi 1978; Vidal 1984; Dutrillaux *et al.* 2007 a, b), 2n=19: 9+XO in three species of *Pentodon* (Joneja 1960; Salamanna 1966), whereas *Oryctes nasicornis* depicts the dimorphic configuration with 2n= 12: 5+XY and 2n= 18: 9II (Virkki 1951, 1954b) and X-chromosome diphasism in *Coeloxis bicornis* was reported by Martins (1989).

3. Evolution of karyotype

It is very difficult to establish the evolutionary history of more remotely related cytological extremes, with certainty. But some light must be shed on how these have occurred by a study of the principles operating in the present day species, because similar processes must have prevailed in the past. On the basis of the known karyotypes found among closely related species, mainly four types of chromosome changes have been implicated in this order Coleoptera (John and Shaw 1967).

These are:

I. Centric Fusion (*Chilocorus* and *Exochomus*) and fission (*Pissodes*) given by (Smith 1959, 1965a).
II. Pericentric Inversion (*Hylobius*) (Smith 1962a), *Trox* (Purcell and Virkki 1966) and *Timarcha* (Petitpierre 1970).
III. Polyploidy (Blaps) (Lewis and John 1957)
IV. Erosion and replacement of the y chromosome according to the sequecnce given below



Steps 3a and 4 in this sequence themselves depict upon the redeployment of autosomal material into new sex chromosome system by centric fusion (Smith 1962a).

I (a). Centric fusion- represents as a major mechanism in the karyotype evolution of many groups of animals. In the genus *Drosophila* (Patterson and Stone 1952, Stone 1955) acridid grasshopper (White 1951, Yadav *et al.* 1981, Yadav and Yadav 1990), it is strongly believed that evolution has proceeded from the higher to the lower number by centric fusion. Two types of centric fusion has been observed in Coleoptera: Autosome – Autosome fusion occurred in species, in which there is decrease in chromosome number without any change in X chromosome e.g. *Gymnopleurus parvus* and *Copris signatus* (2n=18), *Sisyphus neglectus* (2n=16), Copris sp. *Gymnopleurus mundus*, *Phaenaeus yucatamus* (2n= 14) and *Phanaeus igneus* (2n=12). Autosome – X fusion observed in species in which sex chromosome system Xy changed to neo-XY system with reduction of chromosome number e.g. *Sulcophanaeus* spp. (9+neoXY), *Deltochilum valgum* (6+neo XY), *Phanaeus* spp. (5+neoXY) and *Eurysternun caribaeus* (3+neoXY).

I (b). Centric fission- also called 'dissociation' is the opposite process of centric fusion and results in increased chromosome number. But it is very difficult to envision cytologically, since it implies the formation of two telocentric chromosomes from a metacentric, or the occurrence of centromere 'donors' in the form of supernumerary chromosomes seems rarer than fusion (Mathey 1973). John and Lewis (1968) and Southern (1969) suggested that the evolutionary replacement of a metacentric chromosome by two rod-shaped elements (acrocentrics) is always due to 'dissociation'. These authors contend that simple fission through the centromere of a metacentric may sometimes give rise to two stable telocentrics. It is observed that the 'dissociation' played a major role in the chromosome polymorphism in many beetles. Manna and Smith (1959) reported a case of polymorphism in bark weevils *Pissodes*. A metacentric chromosome A in *Pissodes* is represented by the acrocentric A^{l} and A^{R}. Though Manna and Smith (1959) tentatively suggested that the metacentric A A represents the primitive condition, they could not give any evidence to rule out the possibility of fusion of two acrocentrics. This condition is also observed in *Dynamopus athleta*, *Geotrupes* spp., *Oniticellus spinipes*, *Thorecetes intermedius* and *Gymnopleurus miliaris* (Bione *et al.* 2005 a, b, present investigations). Most frequently fission results in the supernumerary chromosomes. In certain exotic species of *Chilocorus*, the chromosome number has increased from the basic 18 to 22 by means of two fissions mediated by the presence of floating supernumerary chromosomes (Smith 1962b).

II. Inversions- are of two types, pericentric and paracentric- the latter has very little evolutionary significance. Stone (1955) has listed 32 pericentric inversions which have occurred during the fixation of karyotypes of the genus *Drosophila*, of which the best known is the one that established itself in the second chromosome of the Montana section of the virilise group, converting the elements from an acrocentric to metacentric. The exact number of paracentromeric inversions that the karyotypes have undergone in the genus is not known. The role of pericentromeric inversion in the speciation has been reported in many grasshopper species by White (1949, 1951, 1969), White and Andrew (1960, 1962), White *et al.* (1964), in mantids by White (1941, 1965) and in beetles by Smith (1958, 1962b, Manna and Smith (1959), Smith (1970), Petitpierre (1970).

III. Polyploidy- In Coleoptera polypoidy is common only in Curculionidae, in which a number of parthenogenetic forms are known (Suomalainin 1955, 1969, Takenouchi 1964, 1972). This phenomenon has arisen in many forms from the diploid bisexual species by automixis or a similar fusion of two diploid nuclei. The aberrant Balptinae from Tenebrionids is also reported to have undergone through polyploidisation coupled with hybridisation and successive allosome/ autosome translocation (Lewis and John 1957). In family Scarabaeidae, *Gymnopleurus mundus* (2n= 14 and 28), showed the polyploidy under present investigations.

IV. The erosion of y chromosome and its replacement or total loss has been discussed under evolution of sex chromosome mechanism in *Apogonia* spp. and *Copris fricator*.

In family Scarabaeidae, Of the 397 cytologically known species, sex chromosomes are known in 359 species (Table 1). The most common karyotype in Scarabaeidae is 9AA+Xyp, possessed by 175 species. A clear predominance of 2n=20 and Xyp sex chromosome system in the Scarabaeidae is a strong evidence that those possessing different complements are derived forms. A review of literature reveals that atleast four types of major changes have been involved in the evolution of karyotype which contributed to the chromosomal diversity of the family (Fig. 1).

Bolobocerus quadridens and *B. indicum* with 2n= 9AA+Xyp (Yadav *et al.* 1990 and present report) link Geotrupinae which possess 2n=22. Virkki (1959) assigned the increase to the fragmentation of two metacentrics. The presence of four acrocentrics in *Geotrupes* spp. and *Thorectes intermedius* further supports this hypothesis. But presence of two pairs of acrocentrics in *Bolbocerus* spp. (9AA+ Xyp) and small y chromosome in *B. indicum* makes the present situation complicated i.e. a fresh decrease after initial increase in the number of chromosomes. Presence of a large metacentric X-chromosome suggests the neo X-Y origin of decrease followed by erosion of the y chromosome resulting in the present situation. *Hybosorus orientalis*, 2n=20 (Kacker 1970, Yadav *et al.* 1990 and present report), represents Hybosorinae. Cytologically it shows closeness with *Bolboceras*, in possessing a similar diploid complement. The size and morphology of chromosomes, however vary to a great extent. Further, y chromosome is large in comparison with its Geotrupinae counterpart. Dynamopinae is chromosomally known by *Dynamopus athleta* having 2n=22 (10AA+Xyp) and showing a karyological kinship with *Geotrupes* spp. and *Thorectes intermedius*.

The range of diploid chromosome number in Scarabaeinae is very wide (Fig. 2). It ranges from 8 in *Eurysternun caribaeus* (Carbal de Mello *et al.* 2007) to 36 in *Gymnopleurus miliaris* race I (present report) which indicates a series of rearrangements in the evolution of this subfamily. Arcanjo *et al.* (2009) presumed that the decrease in the number of *Eurysternun caribaeus* is due to X-autosome fusion which brought the number from 2n= 12 in *Phanaeus vindex* to 2n=8, neo-XY. Whereas Virkki (1959) rightly suspected repeated neo-XY formation causing decrease from 2n=20 to 2n=12 via *Haplidia etrusca* and *Phyllognathus silensis* (8+ neo XY) → *Acrophileurus vervex vervex* (7+neoXY)→*Deltochilum valgum* (6+ neo XY) → *Phanaeus spp.* (5+ neo XY) to finally *Eurysternun caribaeus* (3+ neo XY). The chromosome number 21 with 9+ XO in *Copris fricator*, however, suggest that the karyotype evolution took place in two steps, firstly one pair of autosomes has undergone dissociation as observed in *Geotrupes* spp. *Thorectes intermedius Dynamopus athleta, Adoretus* spp. and *Adorrhinyptia dorsalis* and *Aphodius moestus* with 2n = 22 representing different subfamilies, secondly 'excretion' of one of the sex chromosome, the y has taken place resulting finally XO condition. This is probable that 2n=21 (XO) in *Copris fricator* may have secondarily been evolved through Geotrupinae karyotype 2n=22 (Xyp). Since Geotrupinae is anatomically close to Scarabaeinae than any other subfamily, this hypothesis gets enough support (Virkki 1957).

In contrast to it Autosome – Autosome fusion occurred in species, in which there is decrease in chromosome number without any change in X chromosome e.g. *Gymnopleurus parvus* and *Copris signatus* (2n=18: 8+Xyp), *Sisyphus neglectus* (2n=16: 7+Xyp), *Copris* sp. *Gymnopleurus mundus*, *Phaenaeus yucatamus* (2n= 14: 6+Xyp) and *Phanaeus igneus* (2n=12: 5+Xy) (Hayden 1925, Manna and Lahiri 1972, Smith and Virkki 1978, present report).

In comparison with Scarabaeinae, Melolonthinae presents cytologically uniform picture. The variation of chromosome number is least in 37 species belonging to 13 genera known cytologically (Fig. 2). Except three species of *Apogonia* and *Haplida etrusca*, all the species possessed 2n=20. Three species of *Apogonia* with 2n= 19: 9+XO involves loss of y chromosome. One unidentified species of *Apogonia* with 2n= 21: 10+XO involves autosome dissociation followed by loss of y chromosome. This has both genetic and mechanical implications. From the gentic point of view the possibility of y being translocated on to some other member of karyotype cannot be ruled out. The mechanical properties of y are, however of considerable importance in ensuring a regular segregation of the X chromosome. But as suggested by Smith (1952), once X has achieved independence of mobility (as in

XO species), it never appears to have surrendered it. This hypothesis is compatible with the discovery of two types of karyotypes, 9+Xyp (Kacker 1970) and 9+XO (Manna and Lahiri 1972) in *Apogonia nigricans*. It takes some time for the X chromosome to get stabilised and thus to synchronise with autosomes during Anaphase-I. So, differential behaviour of X chromosome can be observed at different stages in the congenric species of *Apogonia*. Therefore, the karyotype of *Apogonia* is not at all to be considered as rigid with regard to new genetic recombinations and reshuffling of the karyotype.

Highest diploid number 2n=36 in the family Scarbaeidae is from subfamily Scarabaeinae, in which *Gymnopleurus miliaris* race-I represents this diploid number (present report). This may be due to the centric fission, as acrocentric autosomes are present in this species. However, of 13 cytologically known species of this subfamily, 10 species exhibited 2n=20 (9+Xyp), the modal number of this subfamily. Whereas variation within 2n= 19 (XO) in *Ascaria* sp. involve the loss of y chromosome and 2n=18 (Xyp) in *Ophthalmoserica karafutus* showed the involvement of autosome fusion without changing the Xyp sex determining mechanism.

As we know that in subfamily Rutelinae diploid number varies from 16 to 22 in 51 cytologically known species, so the variations has taken place towards decrease and increase in chromosome number. 13 species of genus *Adoretus* and one species of *Adorrhinyptia* with higher diploid number 2n=22: 10+Xyp (Joneja 1960; Kacker 1970, 1971; Yadav and Pillai 1974a, 1976 a, b, 1979; Mittal *et al.* 1987; Yadav and Dange 1988b; Yadav *et al.* 1989; present report), suggested the autosome dissociation, whereas on the other hand one unidentified species of genus *Adorrhinyptia* show polymorphic nature with 2n= 16/ 18/ 20 (Xyr) (Saha and Manna 1971; Saha 1973) and *Popillia japonica*, *Macraspis* spp and *Anomala corpulenta* with 2n= 18 (Xyp) suggested the involvement of autosome – autosome fusion in karyotype rearrangements. Although most of the species of genus *Anomala* depicted basic karyotype 2n=20, yet two types of diploid number 2n=18 and 20 were reported in *Anomala bengalensis* (present report) and *A. rufocuprea* (Saha and Manna 1971; Yadav *et al.* 1993a; Kudoh *et al.* 1973; Yosida 1949b) explicating dimorphic nature of both the species. Thus it seems probable that the trend of evolution in the genus is towards increasing asymmetry in the karyotype.

Out of the 34 species chromosomally known from Dynastinae, 21 species with 2n=20 suggested this to be the 'modal number' of this subfamily. Chromosome number 18 and 16 with the formation of neo XY sex determining mechanism in 9 species confirmed that autosome-X fusion is responsible for the reduction of diploid number (Virkki 1959) whreas alteration of chromosome number and sex determining mechanism 9+XO in *Pentodon* spp. involve the loss of y chromosome. *Oryctes nasicornis* depicts the dimorphic configuration with 2n=12 and 18, which shows chromosomal rearrangements in the species towards the increase or decrease the chromosome number.

Finally in subfamily Trichiinae all species represent modal number of chromosomes, whereas in Cetoniinae 19 speceis exhibited 'modal number' of Scrabaeidae except *Oxythyrea funesta* with 2n=20 (Xy)/ 19 (XO) showed dimorphic nature and involvement of loss of y chromosome in chromosomal rearrangements.

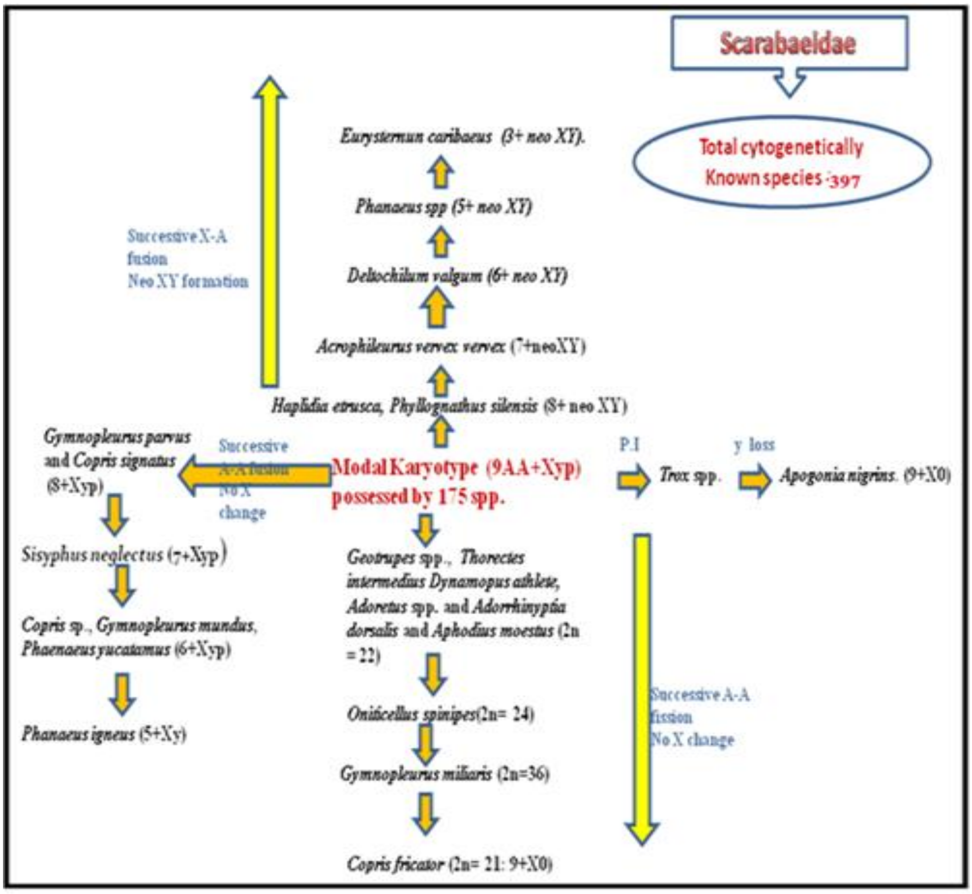


Fig. 1: Evolution of diploid number of chromosomes and sex chromosomal mechanism in family Scarabaeidae

During the present investigations cytological account of 33 species belonging to 14 genera and six subfamilies viz.: Geotrupinae, Dynamopinae, Hybosorinae, Aphodiinae, Scarabaeinae and Rutelinae of family Scarabaeidae is presentedin few papers given by Kaur and Yadav (2011, 2013, 2014 a-d). Out of these 17 species are new additions, while C-banding technique has been applied on 19 species. Constitutive heterochromatin has been localised at pericentromeric regions in two species of *Bolbocerus*, *Aphodius testaceus, Catharcius pithecius, Copris signatus, Gymnopleurus miliaris, Oniticellus pallipes, Oniticellus pallens, Onthophagus fasciatus, Onthophagus unifasciatus* and *Sisyphus neglectus,* agreed with the earlier reports given by Vidal and Giacomozzi (1978), while centromeric C-bands in *Gymnopleurus mundus* corroborated the results of Colomba *et al.* (2000). In other spceis C-bands were observed only at metaphase I stages with approximate two C-blocks on each autosomal bivalent.

4. Evolution of sex chromosomes

Of the 397 cytologically known species sex chromosomes are known in 359 species (Table 1 and 2). Both ‘Orthodox’ and ‘Unorthodox’ systems of Smith and Virkki (1978) are found in this family.

The most common male sex chromosome system in Scarabaeidae is the Xyp, possessed by 231 species amounting to about 65% of total species for which the sex chromosome mechanism is known. The other types are Xy (93 species), neo XY (13 species), XO (10 species), Xyr (8 species). This however includes many Xyp. XY is possessed by 3 species whereas X+Y is present in *Gymnopleurus sinuatus* (Manna and Lahiri 1972). The XY system is exhibited by *Phanaeus igneus, P. vindex* and *Apogonia* unistriata (Hayden 1925, Lahiri and Manna 1969). In *P. vindex* Virkki (1959), on reinvestigation, found neo-XY type of male sex chromosome system. Chironinae, cytologically represented by single species, is the only subfamily that lacks Xyp system. XO mechanism is reported for Scarabaeinae, Melolonthinae and Dynastinae only. Xy mechanism is, however, more common and is met within subfamilies Geotrupinae, Chironinae, Aphodiinae, Scarabaeinae, Melolonthinae, Rutelinae, Trichiinae and Cetoniinae.

A clear predominance of 2n=20 : 9+Xyp species in the Scarabaeidae is a strong evidence that those possessing different complements are derived forms. A review of literature reveals at least four types of major changes as follows:

i. **Centric fusion: a.** Autosome –Autosome fusion in which reduction of diploid number is there without changing the X chromosome e.g in *Oryctes nasicornis, Gymnopleurus parvus, Canthochilum* spp., *Copirs* spp. *Gymnopeurus mundus, Sisyphus neglectus, Phanaeus igneus.* **b.** Autosome – X fusion and formation of Neo XY, is depicted by *Sulcophanaeus* spp., *Haplidia etrusca*, *Phyllognathus silensis*, *Acrophileusus vervex vervex*, *Deltochilum valgum* and *Phanaeus* spp. Along with X- autosome fusion, autosome- autosome fission (*Sulcophaenus* spp.), autosome – autosome fusion (*Phanaeus* spp., *Deltochilum valgum* and *Acrophileusus vervex vervex*) and no autosome autosome fusion (*Haplidia etrusca* and *Phyllognathus silensis*) were observed

ii. **Centric fission** or dissociation involve increase in chromosome number without changing the sex chromosomes as studied in *Dynamopus athlete, Geotrupes* spp. and *Adoretus* spp.

iii. **Pericentric inversion:** In which the change of karyotype occurred from metacentry to acrocentry without changing the sex chromosomes e.g. *Trox* spp.

iv. **Elimination of y chromosome:** XO sex chromosome mechanism, in which there is elimination of y chromosome from Xy to acquire XO sex chromosom system. It is reported in *Apogonia* spp. and *Copris fricator.*

So, the sex chromosome mechanism evolved as follows in the family Scarabaeidae

Xyp ——→ Xy ——→ neo XY ——→ XO
(primitive form) (---------derived forms-----------)

5. Cytotaxomony and phylogenetic relationships

Phylogenetic classification reflects the best estimate of the evolutionary history of organisms. It is well known that chromosomal data can be used to establish interrelationships among related species for taxonomic purpose. On the other hand, the pattern of chromosomal divergence within a group may not necessarily parallel those of morphological features.

In early 1908, Mclung in an address “Cytology and Taxonomy” stressed out the importance of chromosome studies to clarify the taxonomic relationships. Based on the difference in the morphology of a single chromosome, he divided the orthopteran species *Mermeria bivittata* into two groups. The correlations between morphologic and karyologic evolution are very hard to understand. Benazzi (1957) opined that some phylogenetic trends are associated with chromosome variations, but we cannot establish at least at present, to what extent and how these two events are linked to each other.

Helwig (1958) pointed out some interesting parallels that exist between morphological characters and chromosome morphology and the use of latter in indicating taxonomic and phylogenetic relationships. John (1981) pointed out that morphologically primitive traits do not frequently correlates with karyological ones. Stebbins (1971) infers, “the chromosomal differences have a meaning entirely different from morphological, physiological and ecological differences”. The latter represents the end products of long sequences of interaction between primary, secondary genes modified by the effects of environment development.

The comparison of karyotypes can be useful in establishing the phylogenetic relations within taxonomic groups. This, however, needs the assumption that divergence in karyotype structure increases with the time separations of the two species, which means that two closely related species should show less differences in number and structure of chromosomes than do two widely, separated species (Boer 1972). But, when karyological transformations are considered, it should be clear that they cannot reflect phylogenetic evolution in a suitable way.

Actually a closer look makes it clear that the taxonomic grouping should ideally be based on natural relationship of several groups at different levels. Therefore, the question of speciation cannot be considered in isolation from the phylogenetic relationships. The modern or synthetic view of organic evolution regards speciation as a special and perhaps usually brief stage in evolutionary divergence, during which genetic isolating mechanisms develop to a level which makes the phyletic separation of incipient species irreversible (White, 1968).

Structure of the chromosomes and their behaviour and hybridisation experiments have been well utilised to clarify certain puzzling relationships in Cleoptera. The puzzling status of Curculinoid genera *Hylobius* and *Pissodes* was finally settled on the basis of chromosome studies by Smith (1956c, 1959, 1962b). Drouin *et al.* (1963) identified a weevil of the genus *Pissodes* as *P. terminalis* only on cytogenetic basis. They remark “Although specimens from Saskatwan were grossly different in elytra pattern from California, it was identified as *terminalis* on cytogenetic basis”.

The eastern North American Ladybird beetle *Chilocorus stigma* of the subfamily Coccinellinae of Coccinellidae has been shown to comprise an assemblage of subunits display sequential chromosomal polymorphism through incorporation of centric fusion (Smith 1956b, 1957 a, b, 1959). Similar situation has been further clarified in genus *Exochomus*, from India and Pakistan, and established at least five species in an assemblage which has classified into two species on the basis of external morphology (Smith 1965a, 1966)

Although Scarabaeidae is well defined group of Coleoptera yet the origin and interrelationship of scarabs had been a matter of controversy from the very beginning and the matter is still unresolved.

Gangalbaur (1903) included all the Lamellicornia under the general term of ‘Scarabaeidae’ in the suborder Polyphaga. Erichson (1848) on the basis of posterior abdominal spiracles divided this group into two sections- the ‘Scarabaeides-Laprosticti’ and the ‘Scarabeides- Pleurosticti’. Arrow (1909) pointed out that this division did not correspond with any natural line of cleavage as several intermediate forms exist. Yet Arrow (1909, 1910) allowed this distinction for Indian fauna as no intermediate forms exist and two divisions may safely be used. Arrow (1910) grouped Lucanids, Pasilids and Scarabaeids in a common division ‘Lamellicornia’ by taking into consideration their lamellate antennae. Many taxonomists trace the ancestry of scarabs in Lucanids (Fowler 1912). While Lameere (1900) declined to accept this view, since Lucanids possess five visible ventral abdominal segments instead of six found in Scarabs. But Gangalbaur (1903) did not attach much phylogenetic significance to the number of abdominal segments, as it is the result of varying length of elytra. When the elytra entirely cover the abdomen, segments are five in number, but if the apex of the abdomen in uncovered, they are more than five in number.

Sharp and Muir (1912) find close affinity between the scarab genus *Trox* and lucanids, based on an extensive study of male genetalia. They consider Troginae as the ancestral stock from which passalids, scarabids and lucanids evolved. However, Crowson (1955) support the age old view of considering lucanids as a common ancestor for passalids and scarabaeids. Possibly, Passalidae is a direct offshoot of the luccanid stem, specialised for a peculiar mode of life. The lucanids themselves would seem to be related to the remaining scaraboids indirectly through Troginae (Crowson 1960).

The available cytological data on Lucanids presents a wide spectrum of karyotypes, the haploid number ranging from 5 in *Nipponodorcus rubrofemoratus* (Abe *et al.* 1969) to 13 in *Lucans maculifemoratus* (Toshioka and Yamamoto 1937, Virkki 1959, 1967a). None of the Lucanids is reported to have the basic haploid number 10 (9+Xyp), which is the only number known in different species of *Trox* (Purcell and Virkki 1966, Virkki 1967a, Yadav and Pillai 1976b). It can, therefore, be said with reasonable certaininty that lucanids show scarcely any karyological relationship with trogines.

Another primitive group, Geotrupinae enjoys an isolated position among scarabs. Morphologically, presence of 11 segmented antennae (only exception with *Plecoma*) keeps them apart from other scarabs. Anatomically, broad and septate testicular follicles are unlike other laparostictean species (Virkki 1957). Cytologically, 2n= 22 in different species of *Geotrupes* and *Thorectes intermedius*, possibly with some acrocentric chromosomes (Virkki 1960, Bione *et al.* 2005 a) is a notable deviation from the ‘modal’ karyotype 2n=20 all metacentrics. Thus, lucanids, trogines and geotrupines share species with basic scarab karyotype.

It seems that evolution has taken place in both these groups independently along different lines. In trogines, a series of pericentric inversions or ‘centromeric shift’ changed the morphology in different species without altering the number of chromosome number (Purcell and Virkki 1966, Virkki 1967a). On the contrary in Geotrupinae, the evolution has progressed towards an increase in the number of chromosomes from 2n=20 in *Bolboceras indicum* and *B. quadridens* (present report) to *Geotrupes* (Virkki 1960), *Thorectes intermedius* (Bione *et al.* 2005a). Virkki (1959) assigned this increase to the fragmentation of two metacentrics. In view of the presence of acrocenrics in *Geotrupes* spp. and *Thorectes intermedius*, this seems to be a credible hypothesis. The cytological observations seem to support Medvedev (1976) who on the basis of larval characters maintains that Troginae and Geotrupinae have diverged earliest from other Laprosticti.

Dynamopus, a primitive genus with limited species, was variously classified with Hybosorinae and Orphinae. Arrow (1911) separated these beetles and created a new subfamily Dynamopinae. On the cytological grounds, in having a common chromosome number 2n= 22, these beetles seem to be more closely related to Geotrupinae than to Hybosorinae or Orphinae. Paulian (1941) proposed Hybosorinae as a connecting link between Geotrupinae and rest of the scarabs. Since cytological knowledge of Hybosorinae is limited to only one species Hybosorus orientalis (present report), nothing definite can be said in this regard.

The dung beetles (Scarabaeinae) include 5000 species and exhibit a diverse array of morphologies and behaviours. This variation presumably reflects the adaptation to a diversity of food types and the different strategies used to avoid competition for vertebrate dung, which is the primary breeding environment for most species. Monaghan *et al.* (2007), presented a molecular phylogenetic analysis of 214 species of Scarabaeinae, representing all 12 traditionally recognized tribes and six biogeographical regions, using partial gene sequences from one nuclear (28S) and two mitochondrial (cox1, rrnL) genes. Length variation in 28S (588–621 bp) and rrnL (514–523 bp) was subjected to a thorough evaluation of alternative alignments, gap-coding methods, and tree searches using model-based (Bayesian and likelihood), maximum parsimony, and direct optimization analyses. It has been suggested that the Scarabaeinae arose from mycetophagous ancestors (Scholtz and Chown, 1995). The other basal member recovered consistently was Sarophorus, thought to be a detritus feeder (old dung and carrion remains). Frolov (2004) also considered Sarophorus and Coptorhina to be sister taxa. The phylogenetic tree given by Monaghan *et al.* (2007) revealed that tribe Gymnopleurini is more close to Phanaeini and tribe Scarabaeini is close to Coprini whereas some members of Onthophagini are close to Oniticellini and others are close to tribe Onitini. Decrease in the chromosome number both in some species of *Gymnopleurus* and *Phaenus* support the phylogentic relationship given by Monaghan *et al.* (2007), similarly dominance of diploid number 20 and XO sex mechanism in some of the species of tribes Scarabaeini and Coprini bring them more closer, whereas tribes Onthophagini, Oniticellini and Onitini have predominantly 20 chromosome number and Xyp sex mechanism.

Peringuey (1904), in the description catalogue of Coleoptera of South Africa, presented an elaborate account of subfamilies Pleurostict Scarabaeidae and retained Melolonthinae, Sericinae, Rutelinae, Dynastinae and Cetniinae as its subfamilies.

Fowler (1912) placed Melolonthinae along with Glaphyrinae and Oncerinae between the laprostict scarabids. His view is almost in conformity with the classification adopted earlier by Leconte and Horn (1883) placing the first tribe under Pleurostict Melolonthinae and last two under Laprostict Melolonthinae. Arrow (1910), however, Melolonthinae in Pleurosticti and placed it at the bottom of the group. On the basis of available data, Melolonthinae has cytological closeness with higher laprosticti viz. Aphodiinae in which all chromosomaly known species except *Aphodius moestus* (present report, Yadav *et al.* 1993b) possess the 'modal number'. The chromosomal relationships with Coprinae (Scarabaeinae), another laprostict group, is however, obscure.

Anomalini and Adoritini, the two tribes of the subfamily Rutelinae, share same common characteristics, but they are sharply divided by their mode of feeding (Arrow 1917). In old classification they were out at opposite ends of the subfamily separated by the tribe Parastasiini. Arrow (1917), however, brought these together and added a new tribe Adorhinyptini which is constituted by three species (originally described as species of *Rhinayptia* belonging to Anomalini) that exhibit a remarkable combination of characteristic features of Anomalini and Adoritini. In possessing a flat horizontal labrum *Adorrinayptia* is typically similar to anomaline, but the elytra do not have membranous margins which is an invariable mark of the Anomalini. Resemblance with Adoretini is in the presence of last abdominal spiracle being situated close to the hinder margins of penultimate segment, the sculpture of elytra and form of claws. On the cytological level, Adorrhinyptini should be considered as closely related to Adoretini, since both groups have a uniform karyotype 2n=22 (10+Xyp). The evolutionary line in these groups must have progressed towards an increase in chromosome number, probably through dissociation. Kacker (1970) ruled out the above possibility as he could not observe any acrocentrics in *Adoretus incurvatus* and *A. versutus* (Yadav and Pillai 1976a) and *Adoretus* sp. (present report), however, is suggestive of their origin through fragmentation. In other species secondary structural rearrangements like pericentric inversions might have accompanied dissociation. Similar observation were made in Geotrupinae genera *Geotrupes* and *Thorectes* and Dynamopinae genus *Dynamopus* where all cytologically known species have uniform 2n=22, but there does not exist any taxonomic closeness between these groups. This situation has a similarity in mammalian order Carnivora when Wurster and Benirschke (1968) reported these species belonging to three different families possessing very similar karyotypes. These are cases of parallelism in karyotype evolution in completely independent groups.

Cetoniinae considered being the most advanced subfamily among Pleurosticti (Medvedev 1976). The karyotype, being composed of comparatively very small chromosomes (Yadav and Pillai 1977a), considered to be an advanced character (Stebbins 1971), supports this view. As such the modal number in this case may have secondary origin.

Phylogenetic relationships like connecting link *Hybosorus orientalis* between subfamilies Geotrupinae and Scarabaeinae was confirmed on the basis similarities and dissimilarities in the karyotypes of the species. 21 species are new records ions in the cytological data of the Coleoptera.

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Tables & Figures

Table-1: Chromosomal analysis of Scarabaeidae

Sr. No.	Species with classification	Diloid number	Meioformula	Reference
	Subfamily: PLEOCOMINAE			
1	*Pleocoma crinite* Lins.			
2	*P. dubitalis* Davis	20	9+Xyp	51
3	*P. simi* Leach	-	9+Xyp	51
4	*P. minor* Lins.	20	9+Xyp	51
		20	9+Xyp	51
	TROGINAE			
5	*Glaresis* sp.	-	9+Xyp	51
6	*Trox aricensis* Gut.	20	-	51
7	*T. borrei* (Harold)	20	9+Xyp	43
8	*T. costatus* Wied.	20	9+Xyp	76, 64
9	*T. faveicolis* Har.	20	9+Xyp	32, 51
10	*T. indicus* F.	20	9+Xyp	68
11	*T. monachus* Herbst	-	9+Xyp	51
12	*T. omacanthus* Har.	20	9+Xyp	70, 73, 74
13	*T. punctatus* Germar	20	-	32
14	*T. scaber* L.	20	9+Xyp	51
15	*T. scutellaris* Say	-	9+Xyp	51
16	*T. spinulosus* dentibius Rob.	20	9+Xyp	51
17	*T.* sp.	20	9+Xyp	68
	GEOTRUPINAE			
18	*Thorectes intermedius*	22	-	54, 12
19	*Athyreus excavates* Cast.	20	9+Xyp or Xy	51
20	*Bolbelasmus arcuatus* Bates	-	9+Xyp	42
21	*Bolboceras indicum* Westw.	20	9+Xyp	61, 74, PR
22	*B. quadridens* F.	20	9+Xyp	61, 74, PR
23	*Geotrupes balvi* Jek.	22	10+Xy	40
24	*G. hypocrita* Serv.	22	10+Xy	47
25	*G. intermedius* Costa	22	10+Xy	35, 36
26	*G. mutator* Mars.	22	-	46
27	*G. spiniger* Mars.	-	11 II	36
28	*G. splendidus* F.	22	? + Xy	50
29	*G. stercorarius* L.	22	11 II	46
30	*G. stercorosus* Scriba	22	11 II	46
	ORPHINAE			
31	*Orphnus mysoriensis* Westw**.**	20	9+Xyp	25
32	*O. impressus* Westw.	20	9+Xyp	61, 74
	HYBOSORINAE			

33	*Hybosorus orientalis* westw.	20	9+Xyp	20, 61, 74, PR
	DYNAMOPINAE			
34	*Dynamopus athleta* Sem.	22	10+Xyp	61, 74, PR
	CHIRONINAE			
35	*Chiron digitatus* (F.)	20	9+Xyp	20
	AEGIALIINAE			
36	*Aegialia arenaria* F.	20	10 II	46
37	*A. blanchardi* Horn	-	9+Xyp	51
	APHODIINAE			
38	*Aphodius ater* DeG.	20	-	46, 59
39	*A. depressus* Kug.	20	-	46, 59
40	*A. distinctus* Mull	20	?+Xy	50, 56
41	*A. elevates* Ol.	20	-	47
42	*A. erraticus* L.	20	9+Xyp	47, 58
43	*A. fimetarius* L.	20	9+Xy	46
44	*A. fimetarius* L.	20	9+Xyp	40
45	*A. feotens* F.	20	10 II	46
46	*A. feotens* F.	20	9+Xy	46
47	*A. fossor* L.	20	9+Xy	46, 58
48	*A. haemorrhoidalis* L.	-	9+Xy	46, 58
49	*A. merdarius* f.	20	9+Xyp	46
50	*A. moestus* F.	22	10+Xyp	60, 74, PR
51	*A. pusillus pusillus* Herbst	20	-	76, 62, 64
52	*A. rufipes* L.	20	9+Xy	46, 56
53	*A. rufus* Moll	20	10 II	46, 59
54	*A. scrutator* Herbst	20	9+Xy	47, 58
55	*A. subterraeneus* L.	-	10 II	46
56	*A. luridus*	20	9+Xy	56
57	*A. contaminates*	20	9+Xy	56
58	*A. obliterates*	20	9+Xy	56
59	*A. conspurcatus*	20	9+Xy	56
60	*A. haemorrhoidalis*	20	9+Xy	58
61	*A. lineolatus*	20	9+Xy	56
62	*A. testaceus* (Germ.)	20	9+Xyp	PR
63	*A. paykulli*	20	9+Xy	56
64	*A. sticticus*	20	9+Xy	56
65	*A. lapponum*	20	9+Xy	59
66	*A. constans*	20	9+Xy	59
67	*A. nemoralis*	20	9+Xy	59
68	*A. borealis*	20	9+Xy	59
69	*A. fasciatus*	20	9+Xy	59
70	*A. vittatus mundus*	20	9+Xy	59
71	*Ataenius spretulus* Hald.	20	-	40
72	*Psammodius oregonensis* Hald.	-	9+Xyp	51
	SCARABAEINAE			
73	*Canthochilum andyi* Chap.	-	8+Xyp	51
74	*C. hispidium* Chap.	-	8+Xyp	51
75	*C. histeroides* Har.	-	8+Xyp	51
76	*C. oakleyi* Chap.	-	8+Xyp	51
77	*Canthon indigaceus* Chevr.	-	8+Xyp	51
78	*C. muticus* Harold.	20	9+Xyp	43
79	*C. septemmaculatus* (Latreille)	20	9+Xyp	43
80	*Canthidium breve* (Germar)	-	8+Xyp	43
81	*Deltochilum valgum* Burm.	14	6+neo Xy	43
82	*D.* aff *morbillosm*	14	6+neo Xy	9
83	*D.* aff *amazonicum*	14	6+neo Xy	8
84	*D. calcaratum*	14	6+neo Xy	9
85	*D. verruciferum*	20	9+Xyp	9

86	*Anomiopsoides heteteroclyta* (Blanch.)	18	-	43
87	*Autoserica assamensis*	30	-	7
88	*Euranium arachnoids* Brulle	18	8+Xyp	43
89	*Eurysternum caribaeus* Herbst.	8	3+Xy	4
90	*Glyphoderus sterquilinus* Westw.	18	8+Xyp	43, 10
91	*Ontherus sulcator* (F.)	20	9+Xyp	43
92	*Isocopris inhiata*	18	8+Xyp	5
93	*Diabroctis mimas*	20	9+Xyp	5, 8
94	*Dichotomius anaglypticus* (Mannerheim)	18	8+Xyp	43
95	*D. geminatus*	18	8+Xyp	8
96	*D. nisus*	18	8+Xyp	38
97	*D. semisquamosus*	18	8+Xyp	38
98	*D. sericeus*	18	8+Xyr	38
99	*D. carolinus*	20	9+Xyp	42, 43
100	*D. bosqui*	20	9+Xyp	42, 43
101	*Gromphas lacordairei* Brulle	20	9+Xyp	43
102	*Bolbites onitoides* Harold	20	9+Xy	43
103	*Bubas bubalus*	18	8+Xy	3
104	*B. bison*	20	9+Xy	3, 10
105	*B. bubaloides*	20	9+Xy	3
106	*Gymnopleurus cyaneus* F.	20	9+Xyp	21
107	*G. koenigi* F.	-	n=10	14
108	*G. sinuatus* Ol.	18	8+X+Y	25
109	*G. geoffroyi*	20	9+Xyp	3
110	*G. sturmi*	20	9+Xyp	11
111	*G.miliaris*	36	17+Xyp	PR
112	*G. parvus*	18	8+Xyp	PR
113	*G. mundus*	14	6+Xyp	PR
114	*Scarabaeus laticollis* L. (*Ateuchus laticollis* L.)	20	9+Xyp	46, 3
115	*S. sacer* L.	20	9+Xyp	36
116	*S. semipunctatus* F.	20	9+Xyp	36
1171	*S. cristatus*	20	9+Xyp	3
18	*Sisyphus schaefferri* L.	20	9+Xy	47
1191	*S. neglectus* Gory	16	7+Xyp	PR
20	*Caccobius schreberi* L.	20	9+Xy	47
121	*C. ultor* Sharp	20	9+Xyp	PR
122	*C. vulcanus* (F.)	20	9+Xyp	PR
123	*Catharsius molossus* L.	20	9+Xyp	19, 25, 72, PR
			9+Xy	20
124	*C. pithecius* F.	20	9+Xyp	19, 25, 72, 74, PR
125	*C. sagax* Quens.	20	9+Xyp	25
126	*C.* sp.	20	9+Xyp	25
1271	*C.* sp.	18	8+Xyp	25
28	*C.* sp.	20	9+Xyp	19
129	*C.* sp.	20	9+Xyp	34
130	*Copris fricator* F.	21	10+X	19
131	*C. hispanus*	20	9+Xy	3
132	*C. hispanus cavolinii* Pet.	19	-	35, 36
133	*C. incertus* Say	14	-	50
134	*C. lugubris* Boh.	-	6+Xyp	51
135	*C. lunaris* L.	20	-	3, 47
136	*C. tullius* Ol.	20	-	50
137	*C. sinicus*	14	6+Xyp	3
138	*C. signatus* Walker	20	9+Xyp	PR
139	*C.* sp.	14	6+Xyp	25
140	*Paracopris ramosiceps*	18	8+Xyp	3
141	*Microcopris doriae*	20	9+Xyp	3
142	*M. hidakai*	20	9+Xyp	3
143	*Helicopris bucephalus* F.	20	9+Xy	25
144	*H. gigas*	20	9+Xyp	3
145	*Oniticellus fulvus* Goeze	-	10II	47
146	*O. pallipes* F.	20	9+Xyp	62, 64, 65, PR
147	*O. pallens*	20	9+Xyp	PR
148	*O. cinctus*	20	9+Xyp	PR
149	*O. spinipes*	24	11+Xyp	PR
150	*Chironitis furcifer* Rossi	20	9+Xy	36
151	*Onitis philemon* F.	20	9+Xyp	19, 72, 79, PR

152	*O. belial*	20	9+Xy	3
153	*O. ion*	20	9+Xy	3
154	*O. crassus* Sharp	20	9+Xyp	74
155	*Onthophagus amyntas* Ol.	20	-	46
156	*O. andalusicus italicus* Goid.	20	-	36
157	*O. bonasus* F.	20	9+Xyp	62, 64, PR
			9+Xyr	19
158	*O. bifasiatus* F.	20	9+Xyp	62, 76
159	*O. fasiatus*	20	9+Xyp	PR
160	*O. unifasiatus*	20	9+Xyp	PR
161	*O. catta* F.	20	9+Xyp	20, 25, 72, PR
			9+Xyr	19
162	*O. dama* F.	20	9+Xyr	20, PR
163	*O. fractiornis* Prey.	20	-	46
164	*O. furcatus* prey	-	9+Xy	47
165	*O. hecate* Panz	-	9+Xyp	41, 50
166	*O. hirculus* Mannerheim	20	9+Xyp	43
167	*O. illyricus* S. DeG.	-	9+Xy	47
168	*O. lemur* F.	20	-	46, 47
169	*O. marginicollis* Har.	-	9+Xyp	42
170	*O. mopsus* (F.)	20	9+Xyp	72
171	*O. mopsus gracilicornis* Germar	20	9+Xyp	25
172	*O. nuchicornis* L.	20	-	46, 47
173	*O. falsus* (Gill.)	20	9+Xyp	PR
174	*O. bangelensis* (Har.)	20	9+Xyp	PR
175	*O. spinifex* (F.)	20	9+Xyp	PR
176	*O. ovatus* F.	20	-	47
177	*O. pacificus* Lansb.	20	9+Xyp	62, 64, 76
178	*O. pennsylvanicus* Har.	-	9+Xyp	62
179	*O. punctatus* Ill.	-	10II	46
180	*O. quaestus* Sharp	-	9+Xyp	72, 74
181	*O. ramosellus* Bates	20	9+Xyp	25, 72, 74, PR
182	*O. rufiesiens* Bates	-	9+Xyp	42
183	*O. ruficapillus* Br.	20	9+Xy	46
184	*O. taurus* Schreb.	20	9+Xy	46
185	*O. vacca* L.	20	-	46, 47
186	*O. verticicornis* Laich.	20	-	47
187	*O.* sp. 1	20	9+Xyp	25
188	*O.* sp. 2	20	9+Xyp	25
1891	*O.* sp. 3	18	8+Xyp	25
90	*O.* sp. 4	18	8+Xyp	25
191	*Phanaeus daphnis* Har.	-	5+neo XY	42
192	*P. igneus* MacL.	12	5+XY	18
193	*P. mexicanus* Har.	-	5+neo XY	42
194	*P. vindex* MacL.	-	5+XY	18
		12	5+neo XY	49
195	*P.* near *yucatanus* Bates	-	6+Xyp	42
196	*P. chalcomelas*	12	5+XY	8
197	*Pinoteus carolinus* L.	-	9+Xyp	42
198	*Sulcophanaeus menelas* (Castelnau)	20	9+neoXY	43
199	*S. imperator* (Chevr.)			
200	*Oruscatus davus* (Erichson)	20	9+neoXY	43
201	*Coprophanaeus ensifer*	20	-	43
202	*C. cyanescenss*			
203	*C. dardanus*	20	9+Xyp	30
204	*Canthon chalybaeus*	20	9+Xyp	30
205	*C.* aff *carbonarius*	20	9+Xyp	8
		20	9+Xyp	8
	GLAPHYRINAE	20	9+Xyp	8
206	*Lichananthe rathvoni* Lec.	20	9+Xyp	51
	ACANTHOCERINAE			
207	*Cloeotus globosus* Say	-	9+Xyp	42
	SERICINAE			
208	*Aserica pilula* Sharp	20	9+Xyp	66, 74
209	*A.* sp.	19	9+X	74

210	*Autoserica* sp.	20	9+Xyr	19
211	Genus nr. *Autoserica & Neoserica*	20	9+Xyp	25
212	*Opthalmoserica karafutoensis*	18	9II	23
213	*Serica assamensis* Bk.	20	9+Xyp	63, 76
214	*S. falli* Dawson	-	9+Xyp	51
215	*S. sericea* Ill.	-	9+Xyp	50
216	*S. tristis* Lec.	20	9+Xyp	39
217	*S. umbrinella* Bk.	20	9+Xyp	63, 76
218	*Maladera alcocki* Bk.	20	9+Xyp	63, 76
219	*M. truncates* Mittal	20	9+Xyp	80
	MELOLONTHINAE			
220	*Costelytra zealandica* White	20	9+Xyp	15
221	*Odontria silvatica* Brown	20	9+Xyp	15
222	*Amphimallon solstitiale* L.	20	-	46
223	*Apogonia carinata*	-	9+Xyp	63, 76
224	*A. ferruginea* watr.	19	9+X	74
225	*A. nigricans* Hope	20	9+Xyp	20
		19	9+X	25
226	*A. proxima* Watr.	20	9+Xyp	63, 76
227	*A. unistriata* Bk.	20	9+Xy	24
228	*A.* sp.	20	9+Xyp	24
229	*A.* sp.	21	10+X	33
230	*A.* sp.	19	9+X	66
231	*Chlaenobia aequata* Bates	-	9+Xyp	42
232	*C. tumulosa* Bates	-	9+Xyp	42
233	*Diplotaxis anqustula* Moser	-	9+Xyp	42
234	*D. obscura* Lec.	-	9+Xyp	51
235	*D. sierrae* Fall	-	9+Xyp	51
236	*D.* sp.	20	9+Xyp	40
237	*Haplidia etrusca* Kr.	18	8+neoXY	36
238	*Holotrichia longipennis* Blanch.	20	9+Xyp	63, 76
239	*H. problematica* Bk.	20	9+Xyp	63, 76
240	*H. serrata* F.	20	9+Xyp	69, 74
241	*Melolontha hippocastoini* F.	-	9+Xy	46
242	*Phyllophaga anxia* Lec.	20	-	50
243	*P. dasypoda* Bates	-	9+Xyp	42
244	*P. delata*	20	9+Xy	37
245	*P. drakki* Kby.	20	?+Xy	50
246	*P. fusca*	20	9+Xy	37
247	*P. gracilis*	20	9+Xy	37
248	*P. rostripyga* Bates	-	9+Xyp	42
249	*P. tristis*	20	9+Xy	37
250	*P. yucateca* Bates	-	9+Xyp	42
251	*P. vestita*	20	9+Xyp	29
252	*P. aff capillata*	20	9+Xyp	29
253	*Lysogenys fuscus*	20	9+Xyp	29
254	*Schizonycha fuscesens* Blanch.	20	9+Xyp	25
255	*S. ruficollis* F.	20	9+Xyp	66, 74
256	*Microtricha cotesi* Bk.	20	9+Xyp	80
	RUTAELINAE			
257	*Adorrhinyptia dorsalis* (Burm.)	22	10+Xyp	69, 74
	A. sp.		7/8/9+Xyr	
258	*Anomala bengalensis* Blanch.	16/18/20	8+Xy	33
259	*A. biharensis* Arrow	18	9+Xyp	34
260	*A.* sp. nr. *Bilobata* Arrow	20	9+Xyp	28
261	*A. cincta polychalca* Bates	20	9+Xy	24
262	*A. corpulenta* Mots.	20	-	42
263	*A. cuprea*	20	8+Xy	78
264	*A. dorsalis* F.	18	10II	23
265	*A. lucens*	20	9+Xyp	1, 2, 68, 74
266	*A. vestigator* Arrow	20	9+Xyr	23
267	*A. polita* Blanch.	20	9+Xyp	68, 74
268	*A. ruficapilla* Burm.	20	9+Xyp	66, 68, 74
269	*A. rufocuprea* Mots	20	9+Xyp	66, 68, 74
270	*A. superflua* Arrow	20	8+Xy	23
271	*A. varicolor* Gyll.	18	10II	78
272	*A.* sp.	20	9+Xyp	19

273	*A.* sp.	20	9+Xyp	68, 74
274	*Rhinyptia indica* Burm.	20	9+Xyp	21
275	*Mimela glabra* Hope	-	9+Xyp	25
276	*Mimela* sp.	20	9+Xyp	76
277	*Macraspis dichroa* ssp. Cribata	-	9+Xyp	63, 76
	Watr.	20	9+Xyp	19
278	*Popillia japonica* Newn.	20	8+Xyp	43
279	*Strigodermella protea* (Burm.)	-	8+Xy	78
280	*Adoretus birmanus* Arrow	18	9+Xyr	42
281	*A. bombinator* Burm.	-	10+Xyp	66
282	*A. decanus* Ohaus	22	10+Xyp	63, 76
283	*A. duvaceli* Blanch.	-	10+Xyp	69, 74
284	*A. epipleuralis* Arrow	-	10+Xyp	69, 74
285	*A. incurvatus* Ohaus	22	10+Xyp	63, 76
286	*A. lasiopyqus* Burm.	22	10+Xyp	69, 74
287	*A. limbatus* Blanch	22	10+Xyp	69, 74
288	*A. minutus* Bk.	-	10+Xyp	69, 74
289	*A. simplex* Sharp	22	10+Xyp	28
290	*A. versutus* Har.	22	10+Xyp	66
291	*A.* sp.	22	10+Xyp	20, 69, 74
292	*A.* sp.	22	10+Xyp	19
293	*Catalpa lanigera* L.	22	10+Xyp	69, 74
294	*Ectinohoplia rufipes*	22	9+Xy	37
295	*Hoplia communis*	20	9+Xyp	37
296	*Pelidnota punctata*	-	9+Xyr	23
297	*P. virescens aurescens* Latr.	-	10II	23
298	*Phyllopertha campestris* Latr.	20	9+Xy	37
299	*Pocalta ursine* Horn	-	9+Xyp	42
300	*Geniates borelli*	20	9+Xy	47
301	*Macraspis festiva*	20	9+Xyp	50
302	*M. tristis*	20	9+Xyp	6
303	*Pelidnota pallidipennis*	18	8+Xyp	6
		18	8+Xyp	38
		20	9+Xyp	6
	DYNASTINAE			
304	*Cyclocephala dimidiate* Burm.	-	9+Xyp	42
305	*C. tridentate*	18	9+Xy	
306	*C. maffafa*	18	9+Xy	16
307	*C. lutea* Endroedi	20	9+Xyp	16
308	*C. putrida* Burm.	20	9+Xyp	43
309	*Dyscinetus bidentatus* Burm.	-	9+Xyp	43
310	*D. rugifrons* (Burm.)	20	-	42, 43
311	*Diloboderus abderus* (Sturm)	20	9+Xyp	43
312	*Dynastea hercules hercules*	18	8+neo XY	43
313	*Euetheola humilis* (Burm.)	20	9+Xyp	17
314	*Enema pan* (F.)	18	8+Xyp	43
315	*Arcophileurus vervex vervex* Burm.	16	7+neoXY	43
316	*Ligyrus gibbosus* ssp.	-	9+Xyp	43
317	*L. ebenus*	20	9+Xyp	43
318	*L. cuniculus*	18	8+Xy	6
319	*L. burmeisteri* Steinheil	-	9+Xyp	16
320	*Bothynus striatellus* Fairm.	-	9+Xyp	43
322	*B. nasutus* Burm.	-	9+Xyp	43
323	*Ligyrodes relictus* Say	20	9+Xyp	42
324	*Orizabus cultripes* Fairm	-	8+Xyp	51
325	*Oryctes nasicornis* L.	12	5+XY	51
		18	$9II^{+ss}$	31
326	*Phylloganthus dionysius* F.	20	9+Xyp	46, 48
327	*P. silenius* F.	18	8+neoXY	71, 74
328	*Pentodon bisoinifrons* Reit.	20	9+Xyp	36
329	*P. punctatus* Vill.	19	9+X	19
330	*P. bidens punctatum*	20/19	9+X0/XX	35
331	*P.* sp.	19	9+X	55
332	*Eophileurus chinensis*	20	10II	19
333	*E. platypterus* (Wied.)	20	9+Xyp	23
334	*Allomyrina dichotoma* L.	-	9+Xyp	71, 74
335	*Lycomedes mniszechi* Thomson	-	9+Xyp	22
336	*Strategus surinamensis*			42
337	*S. syphax*	20	9+Xyp	
338	*Megasoma actaeon*	18	8+Xy	6

		18	8+Xy	16
	TRICHIINAE			16
339	*Trichiotinus assililis* Kby.	-	9+Xyp	40
340	*Trichius fasciatus* L.	20	9+Xy	47, 78, 79
341	*T. succinctus*	20	9+Xy	23
342	*T. zonatus* Germar	-	9+Xy	47
	CETONIINAE			
343	*Rhomborrhina polita*	-	10II	23
344	*R. unicolor*	-	10II	23
345	*Cotinis mutabilis* G. & P.	-	9+Xyp	42
346	*Gymnetis kerremansi* V. de P.	-	9+Xyp	42
347	*Cetonia aurata* L.	20	9+Xy	46, 47
348	*C. roelofsi*	20	10II	23
349	*Clinteria spilota* (Hope)	20	-	71, 74
350	*Coenochilus trabecula* Schaum	-	9+Xyp	71, 74
351	*Epicometis hirta* Poda	20	9+Xy	46, 47
		-	$9+Xy^{+ss}$	48
352	*E. squalida* Scop.	20	$9+Xy^{+ss}$	36
353	*Euphoria inda* L.	20	9+Xy	40
354	*E. lurida* Fab.	20	9+Xyp	43
355	*Glycyphana fulvistemma* Mots.	20	9+Xy	78
356	*Oxycetonia albopunctata* F.	20	9+Xy	66
357	*Oxythyrea funesta* Poda	20	9+Xy	46, 47
358	*Potosia cuprea* F.	20	9+Xy	46, 47
359	*P. morio* F.	-	9+Xy	47
360	*Ceremestocheilus armatus* Wlk	20	-	51

Table 2: Distribution of species, genera and subfamilies according to male sex chromosome mechanism in Scarabaeidae

Subfamily	Male sex chromosome mechanism								Total
	X0	Xy	Xyp	neoXY	Xyr	XY	X+Y	UK	
Pleocominae	-	-	4	-	-	-	-	-	4
Troginae	-	-	11	-	-	-	-	2	13
Geotrupinae	-	5	4	-	-	-	-	5	14
Orphinae	-	-	2	-	-	-	-	-	2
Hybosorinae	-	-	1	-	-	-	-	-	1
Dynamopinae	-	-	1	-	-	-	-	-	1
Chironinae	-	-	1	-	-	-	-	-	1
Aegialiinae	-	-	1	-	-	-	-	1	2
Aphodiinae	1	25	6	-	-	-	-	8	40
Scarabaeinae	-	30	102	9	4	3	1	18	167
Glaphyrinae	-	-	1	-	-	-	-	-	1
Acanthocerinae	-	-	1	-	-	-	-	-	1
Sericinae	1	-	10	-	1	-	-	2	14
Melolonthinae	4	7	24	1	-	-	-	2	38
Rutaelinae	-	8	36	-	3	-	-	4	51
Dynastinae	3	6	20	3	-	-	-	1	33
Trichiinae	-	3	1	-	-	-	-	-	4
Cetoniinae	1	9	5	-	-	-	-	2	17
Species	10	93	231	13	8	3	1	45	404
Genera	5	36	87	7	6	1	1	23	166
Subfamilies	5	8	18	3	3	1	1	10	49

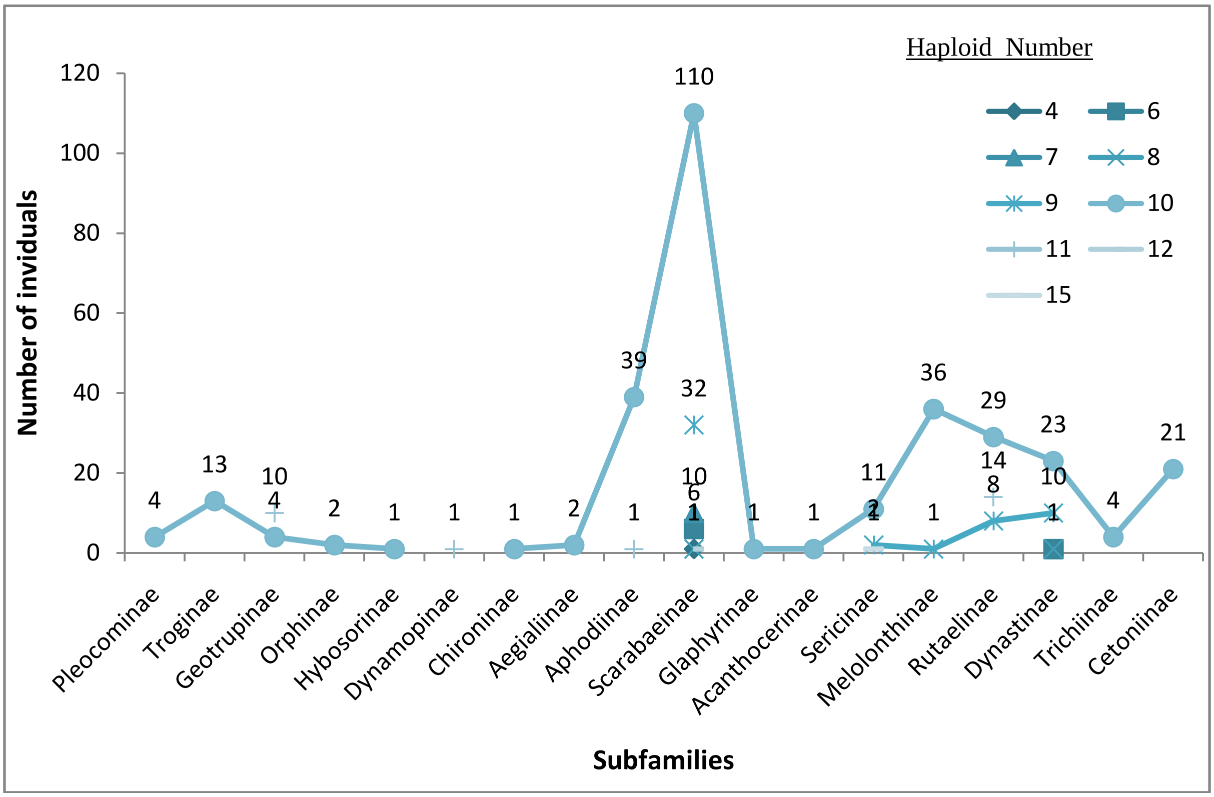

Fig. 2: Distribution of haploid number of chromosomes in different subfamilies of Scarabaeidae