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Journal Vol: 80 Journal Issue:
Journal Month: Journal Year: 2000
Article Pages: 38-49

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Entomological Review, Vol. 80, No. 1, 2000, pp. 38–49. Translated from Entomologicheskoe Obozrenie, Vol. 79, No. 1, 2000, pp. 96–106.

Chromosome Numbers and Sex Chromosome Systems in Buprestid Beetles (Coleoptera, Buprestidae)

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Received May 25, 1999

Abstract—Karyotypes of 15 buprestid species of the genera *Julodis* (2 species), *Julodella* (1), *Acmaeoderella* (1), *Capnodis* (2), *Perotis* (2), and *Anthaxia* (7) from Armenia were examined. Five variants of chromosome numbers (14, 16, 18, 20, 26) and 4 sex chromosome systems (*XY*, *neo-XY*, Xy_p, and Xy_r) were revealed. The available karyological data on Buprestidae of the world fauna are summarized in a table. The diploid chromosome numbers in the 77 species examined vary between 12 and 26. Among the diverse sex chromosome systems, the variant Xy_p is the commonest; this state is supposed to be ancestral in the evolution of Coleoptera, having originated in the common ancestor of Coleoptera and Megaloptera.

The family Buprestidae is one of coleopteran families the worst studied from the karyological viewpoint. The karyotypes of two unidentified buprestid species, collected from spruce, were described for the first time by Stevens (1906). By the end of the 1960s, the karyotypes of only 18 species were known (Nichols, 1910; Asana *et al.*, 1942; Smith, 1949, 1958, 1960). Later, Smith and Virkki (1978) studied karyotypes of two more species and summarized all the data available for the family. Quite recently, Mesa and Fontanetti (1984) redescribed the previously studied karyotype of *Euchroma gigantea* L. (Nichols, 1910). In addition, data on the karyotypes of 34 species of the Australian genus *Stigmodera* were published (Gardner, 1988).

The diploid chromosome numbers in the 56 buprestid species studied so far vary between 12 and 26. The mechanisms of sex determination are diverse, even though the information is incomplete for some species (Smith and Virkki, 1978). The system Xy_p was found prevalent in 44 species; 6 species have *neo-XY* mechanism, while the rest of the species have *XY*, *Xy*, or *X0* mechanisms, according to the original descriptions. A complicated set of sex chromosomes was described in *Euchroma gigantea* (Mesa and Fontanetti, 1984).

This work summarizes the karyological information on buprestid beetles, including new data on 15 species from the fauna of Armenia.

MATERIALS AND METHODS

The work was performed at the Institute of Zoology, National Academy of Sciences of Armenia (Yerevan) and the Section of karyosystematics, Zoological Institute, Russian Academy of Sciences (St. Petersburg). All the species investigated, representing 6 genera of 4 tribes and 4 subfamilies, were collected in Armenia. The material is summarized in Table 1. The descriptions follow the standard of Bellamy (1985), with slight modifications.

Chromosome preparations were made using the technique described by Rozek (1994). Male insects were dissected in 1% sodium citrate solution, using a binocular microscope. The testes were placed in the hypotonic colchicine solution (0.005% colchicine in 1% sodium citrate) for 45–60 min and then fixed in ethanol–acetic acid mixture (3 : 1). It was possible to preserve the material in this fixative for a long time at –8°C. Further processing consisted in four successive 30-min rinses in ethanol–acetic acid mixture with increasing acid concentration at 32°C, which resulted in adequate maceration of the tissues. Then, the preparations were squashed between two clean microscope slides in 1–2 drops of 70% acetic acid and frozen on dry ice. After this, the slides were separated using a sharp blade and dried in warm air flow.

Some preparations were stained with 4% phosphate buffered Giemsa solution (pH 6.8) for 10 min, as proposed by Rozek (1994). However, better results were obtained using a somewhat modified technique, described by Grozeva and Nokkala (1996). This technique includes mild hydrolysis of the chromosomal DNA, followed by staining with Schiff's reagent and Giemsa solution. The slides were placed in 1N HCl for

15–20 min at room temperature, after which the material was hydrolyzed in 1N HCl for 8 min at 60°C and stained in Schiff's reagent for 20 min at room temperature. Then, the slides were rinsed in 3 portions of distilled water to remove the excess Schiff's reagent, placed in fresh ethanol–acetic acid mixture (3 : 1) for 30 min, dried in warm air flow, and stained with 4% phosphate-buffered Giemsa solution (pH 6.8) for 10–15 s.

Micrographs were made using a Jenaval microscope at ×800 magnification.

RESULTS

1. ***Julodis faldermanni*** Mnnh., $2n = 26$ (24 + *XY*).

The 2 males examined revealed few cell divisions. The haploid chromosome set in diakinesis–metaphase I is shown in Figs. 1, 2. The haploid karyotype comprises 13 elements, one of which is very large. In each cell, this bivalent has 3 chiasmata: proximal, interstitial, and distal, so that it resembles a figure of eight. One of the bivalents is heteromorphic, consisting of a larger *X*-chromosome and a small *Y*-chromosome. The type of sex chromosome association, determining the type of *XY*-bivalent, remains unknown (probably Xy_p). Therefore, we designate the sex determination mechanism in this species by the traditional symbol *XY*.

The haploid karyotype was identified as $n = 13$ (12 + *XY*); correspondingly, the diploid karyotype is $2n = 26$ (24 + *XY*).

2. ***Julodis andreae*** Ol., $2n = 26$ (24 + *neo-XY*).

Mitoses were observed in one of the 3 males examined. The mitotic metaphases included 26 chromosomes, mostly meta- or submetacentric (Fig. 3). The diploid karyotype includes 3 very large chromosomes: a pair of metacentric autosomes and a single submetacentric *X*-chromosome. Other chromosomes form a gradually decreasing size series. *Y*-chromosome is probably acrocentric, about as large as the medium-sized autosomes, or about half as large as *X*-chromosome. Metaphase I (Fig. 4) reveals 12 autosomal bivalents, including one large bivalent with 3 chiasmata, and a heteromorphic sex bivalent of complicated structure, which undoubtedly belongs to the *neo-XY* type. Other autosomal bivalents have 1 chiasma each. Single cells observed in one specimen had 11 or 12 autosomal bivalents, including the largest one (Figs. 5, 6).

The haploid karyotype was identified as $n = 13$ (12 + *neo-XY*); correspondingly, the diploid karyotype is $2n = 26$ (24 + *neo-XY*).

3. ***Julodella globithorax*** Stev., $2n = 26$ (24 + Xy_p).

Fig. 7 represents a mitotic metaphase of a male specimen. The metaphase comprises 27 chromosomes, including a pair of very large autosomes. One of the chromosomes is probably an accessory, or *B*-chromosome, because most cells in MI reveal 13 elements, including 12 autosomal bivalents and a "parachute"-shaped heteromorphic sex bivalent (Fig. 8). One of the autosomal bivalents is very large and has 3 chiasmata in all the cells examined.

The haploid karyotype of this species was identified as $n = 13$ (12 + Xy_p); correspondingly, the diploid karyotype is $2n = 26$ (24 + Xy_p).

4. ***Acmaeoderella flavofasciata*** Pill. et Mitt., $2n = 18$ (16 + Xy_r).

Eight autosomal bivalents and a large pseudobivalent of sex chromosomes are observed in late diakinesis (Figs. 9, 10). *X*-chromosome is very large, submetacentric. *Y*-chromosome is very small and appears distantly paired with the shorter arm of *X*-chromosome; its morphology remains obscure. According to Smith's (1953) classification, this mechanism belongs to the Xy_r type. The autosomal bivalents form a series with gradually decreasing size, including no particularly large elements. Fig. 11 represents a part of the mitotic metaphase in a female specimen, with 8 chromosomes, of which only one small chromosome is acrocentric, whereas others are meta- or submetacentric. Two of these appear to include nucleolar organizers, because they have satellites. Thus, chromosomes with 2 arms evidently prevail in the karyotype of this species.

The haploid karyotype of this species was identified as $n = 9$ (8 + Xy_r); correspondingly, the diploid karyotype is $2n = 18$ (16 + Xy_r).

5. ***Capnodis tenebrionis*** L., $2n = 14$ (12 + *neo-XY*).

MI stage reveals 6 autosomal bivalents and a large heteromorphic bivalent *neo-XY*, with submetacentric *X*-chromosome and acrocentric *Y*-chromosome (Fig. 12). The autosomal bivalents form a series with gradually decreasing size, including no particularly large elements. Fig. 13 shows anaphase I, with autosomal homologues and sex chromosomes in the process of moving toward the poles.

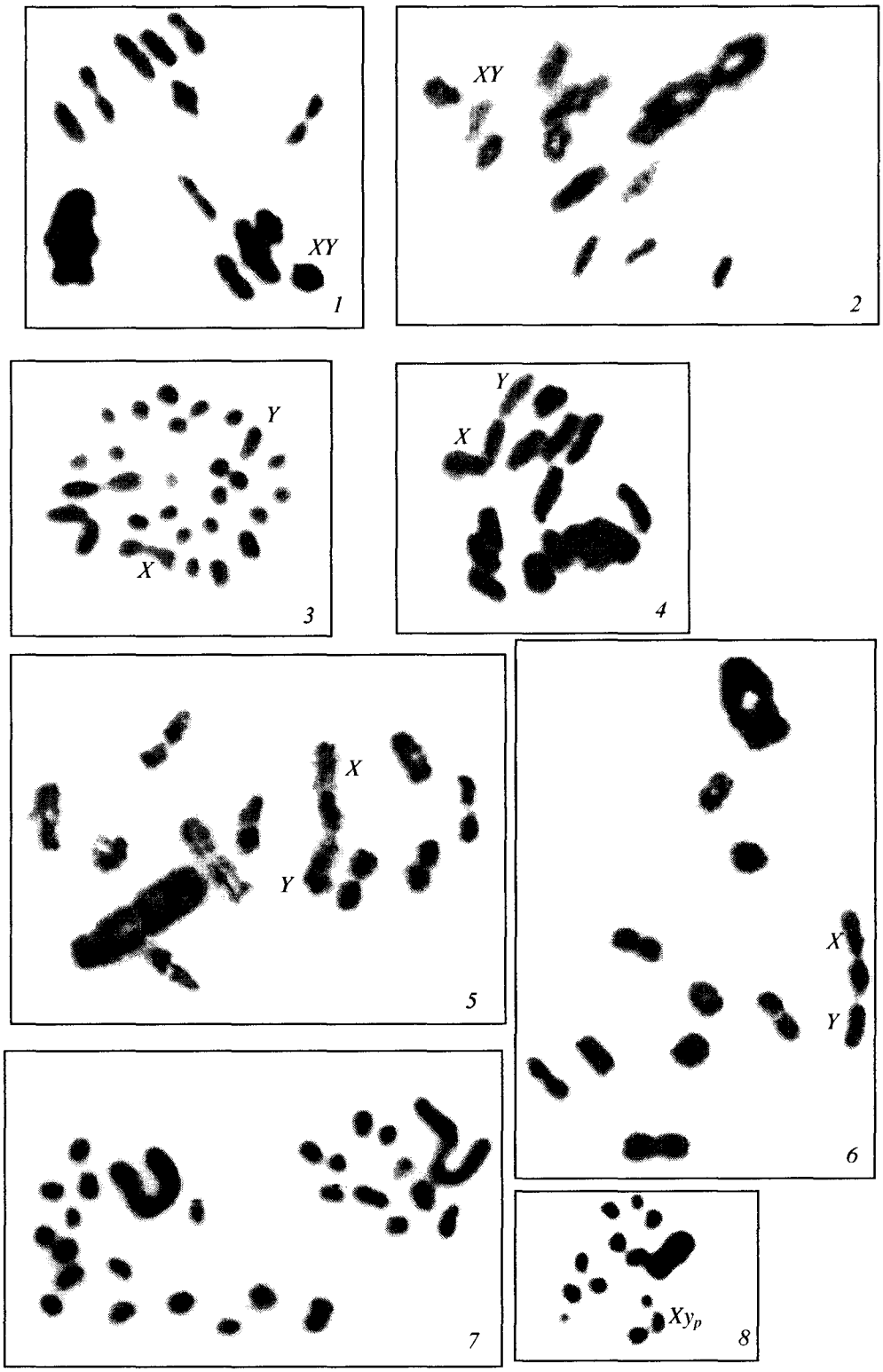
Table 1. The material examined

Species	Collection date and locality	Number of specimens examined, ♂
Genus ***Julodis*** Eschsch.		
J. faldermanni Mnnh.	11.VI.1998, Goravan	2
J. andreae Ol.	12.V.1998, Getap	2
	10.VII.1998, Khosrov	1
Genus ***Julodella*** Sem.		
J. globithorax Stev.	11.VI.1998, Goravan	2
	22.VI.1998, Getap	2
	28.VI.1998, Atsavan	1
Genus ***Acmaeoderella*** Cobos		
A. flavofasciata Pill. & Mitt.	13.VI.1998, Khosrov	2
	22.VI.1998, Lachin-Shushi	1♂, 1♀
	9.VII.1997, Khosrov	2
Genus ***Capnodis*** Eschsch.		
C. tenebrionis L.	10.VIII.1998, Yerevan	6
	28.VII.1997, Yerevan	1
C. miliaris Klug	7.IX.1997, Khorvipan	2
Genus ***Perotis*** Spinola		
P. cuprata Klug	27.IV.1998, Shvanidzor	1
	3.V.1998, Goravan	3
	24.V.1998, Noravank	1
P. lugubris F.	20.VI.1997, Megri	2
	28.IV.1998, Karchevan	2
	11.VI.1998, Megri	1
Genus ***Anthaxia*** Eschsch.		
A. lgockii Obenb.	2–12.V.1998, Getap	2
A. bicolor Fald.	13.VI.1998, Khosrov	2
	12.VII.1998, Khosrov	1
A. podolica Mnnh.	13.VI.1998, Khosrov	2
A. deaurata Gmelin	2.V.1998, Megri	1
A. hungarica Scop.	24.IV.1998, Shvanidzor	2
	28.IV.1998, Kuris	1
A. sponsa Ksw.	27.IV.1998, Shvanidzor	2
A. mirabilis Zhich.	24.V.1998, Noravank	1

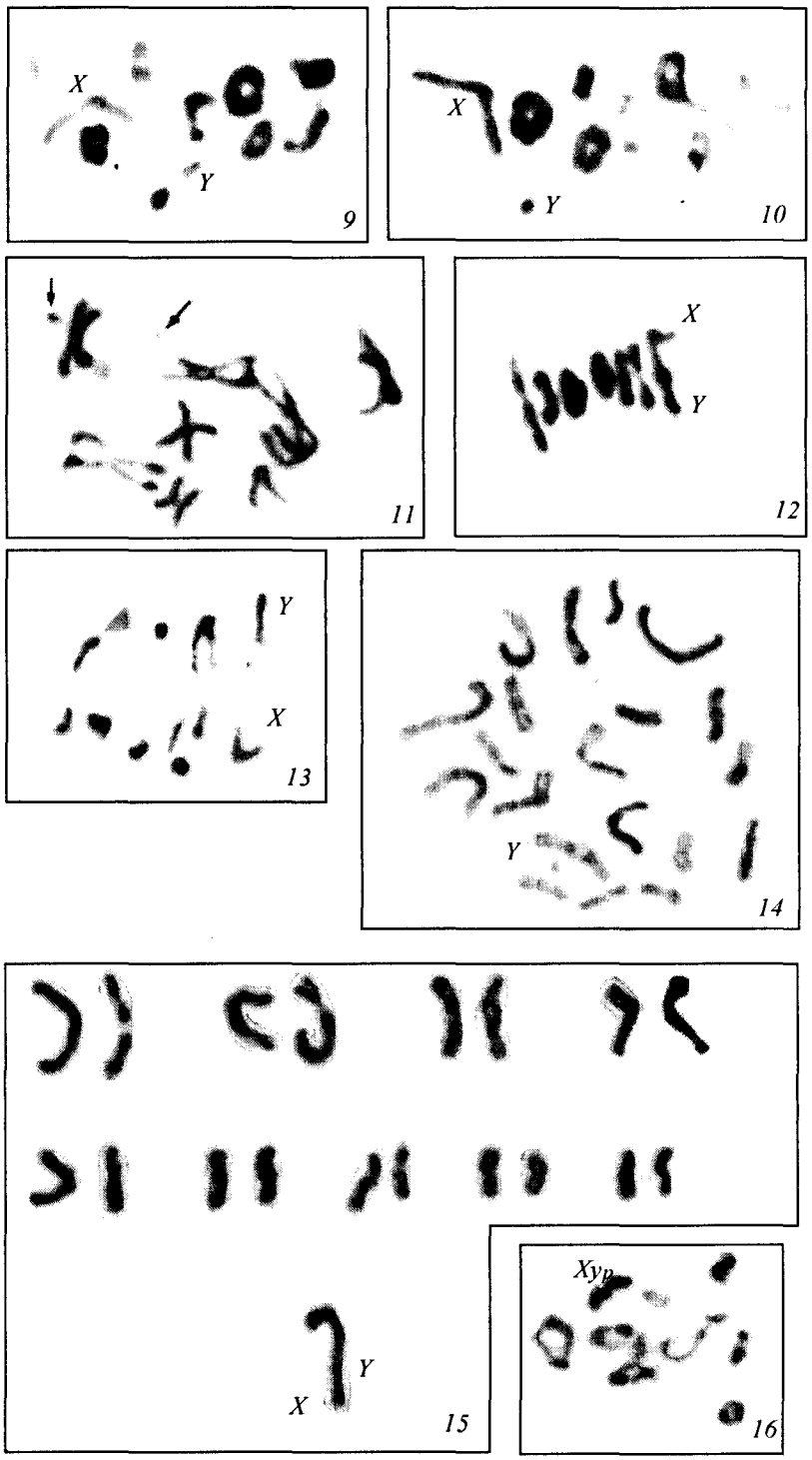
The haploid karyotype of this species was identified as $n = 7$ (6 + *neo-XY*); correspondingly, the diploid karyotype is $2n = 14$ (12 + *neo-XY*).

6. ***Capnodis miliaris*** Klug, $2n = 20$ (18 + Xy_p).

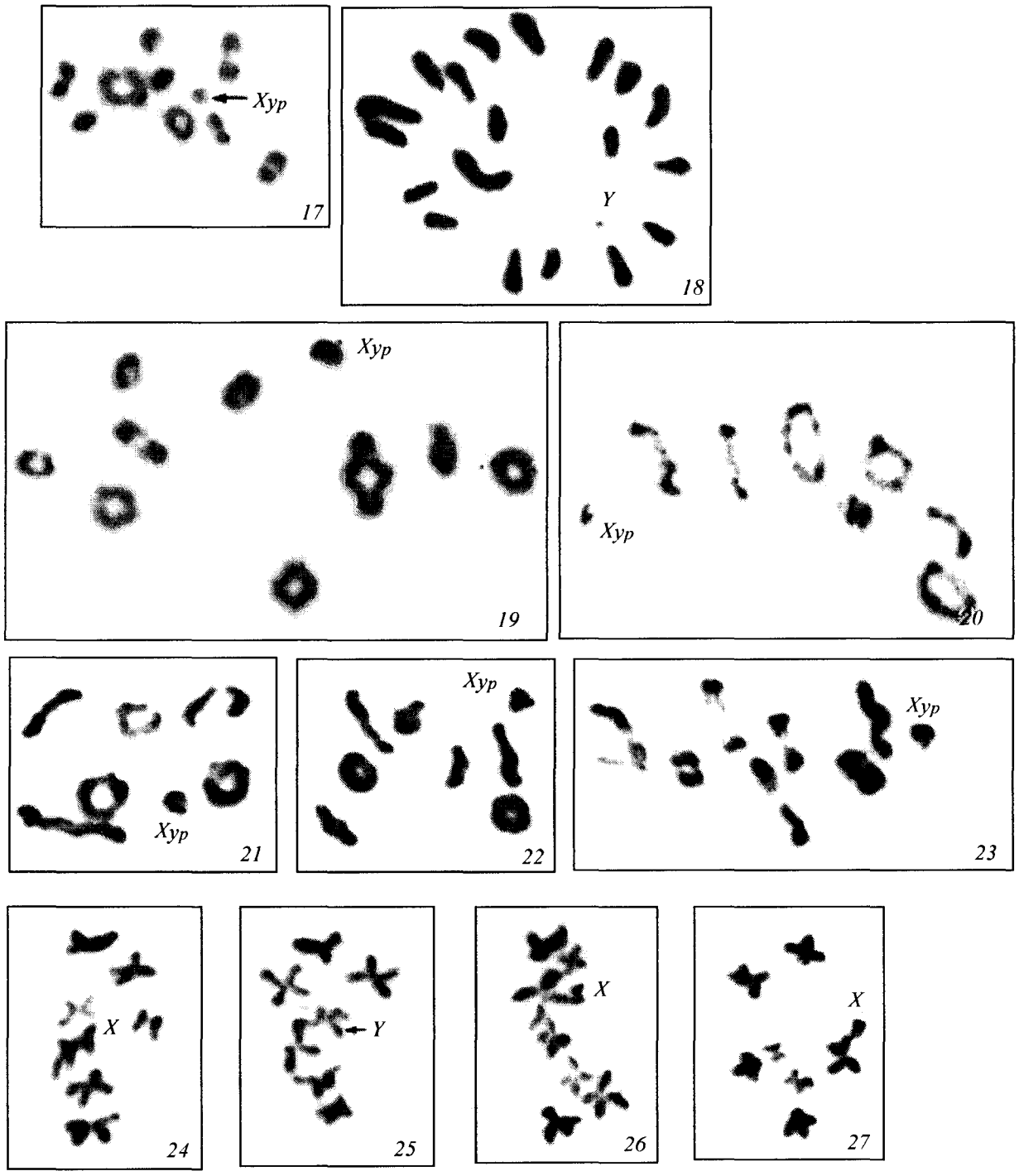
The examined males had numerous mitotic cells and only occasionally revealed meiotic ones. The mitotic metaphase (Fig. 14) comprises 20 chromosomes, including a dot-like *Y*-chromosome. *X*-chromosome is one of the largest elements of the karyotype. All chromosomes (except *Y*, whose morphology was not determined) are metacentric or (less frequently) submetacentric, and gradually decrease in size (Fig. 15). Meiotic MI reveals 9 autosomal bivalents and a parachute-shaped heteromorphic sex bivalent (Fig. 16).



Figs. 1–8. Mitotic and meiotic chromosomes of buprestid males. (*1, 2*) *Julodis faldermanni* Mnnh., n = 13 (12 + *XY*), diakinesis–metaphase I; (*3–5*) *J. andreae* Ol., n = 13 (12 + *neo-XY*) [(*3*) mitotic metaphase; (*4*) MI; (*5, 6*) early and late diakinesis]; (*7, 8*) *Julodella globithorax* Stev., n = 13 (12 + *XY*) [(*7*) mitotic metaphase; (*8*) MI]. *X* and *Y*—sex chromosomes. Scale bar 10 μm.



Figs. 9–16. Mitotic and meiotic chromosomes of buprestids: (*9, 10, 12–16*) males, and (*11*) female. (*9–16*) *Acmaeoderella flavofasciata* Pill. et Mitt., $n = 9$ ($8 + Xy_r$) [(*9, 10*) late diakinesis; (*11*) part of metaphase plate in a female, with arrows pointing at "satellites" of 2 autosomes]; (*12, 13*) *Capnodis tenebrionis* L., $n = 7$ ($6 + neo\text{-}XY$) [(*12*) MI; (*13*) AI]; (*14–16*) *Capnodis miliaris* Klug, $n = 10$ ($9 + Xy_p$) [(*14*) mitotic metaphase; (*15*) karyogram; (*16*) MI]. Designations as in Figs. 1–8.



Figs. 17–27. Mitotic and meiotic chromosomes of buprestid males. (*17*) *Perotis cuprata* Klug, n = 10 (9 + Xy_p), diakinesis–prometaphase; (*18*, *19*) *Perotis lugubris* F., n = 10 (9 + Xy_p) [(*18*) mitotic metaphase; (*19*) MI]; (*20*) *Anthaxia podolica* Mnnh., n = 8 (7 + Xy_p), diakinesis; (*21–25*) *Anthaxia hungarica* Scop., n = 8 (7 + Xy_p) [(*21*) diakinesis; (*22*) prometaphase I; (*23*) late metaphase I; (*24*, *25*) MII [erroneously given as MI in the original text.—Ed.]; (*26*, *27*) *Anthaxia lgockii* Obenb., n = 8 (7 + Xy_p), MII. Designations as in Figs. 1–8.

The haploid karyotype of this species was identified as $n = 10$ (9 + Xy_p); correspondingly, the diploid karyotype is $2n = 20$ (18 + Xy_p).

7. ***Perotis cuprata*** Klug, $2n = 20$ (18 + Xy_p).

In diakinesis–prometaphase I, 10 elements are observed, including 9 autosomal bivalents and a heteromorphic bivalent of sex chromosomes (Fig. 17). Both *X*- and *Y*-chromosome are parachute-shaped at this stage, therefore the mechanism is classified as Xy_p. The autosomal bivalents form a gradually-decreasing-size series, with clearly distinguishable largest element. Even though the morphology of meiotic chromosomes (especially smaller ones) cannot be determined, the larger elements of the karyotype are evidently metacentric.

The haploid karyotype of this species was identified as $n = 10$ (9 + Xy_p); correspondingly, the diploid karyotype is $2n = 20$ (18 + Xy_p).

8. ***Perotis lugubris*** F., $2n = 20$ (18 + Xy_p).

Late mitotic metaphase (Fig. 18) reveals 20 chromosomes, among which the largest pair of autosomes and the dot-like *Y*-chromosome can be easily identified. Other chromosomes gradually decrease in size; their morphology was not determined. *X*-chromosome was not identified in this set. Meiotic MI reveals 10 bivalents, including *X*- and *Y*-chromosome, paired in the form of a "parachute" (Fig. 19). As can be seen at this stage, most chromosomes (including *X*) are meta- or submetacentric.

The haploid karyotype of this species was identified as $n = 10$ (9 + Xy_p); correspondingly, the diploid karyotype is $2n = 20$ (18 + Xy_p).

9–15. ***Anthaxia (Cryptanthaxia) lgockii*** Obenb., ***A.*** (s. str.) ***bicolor*** Fald., ***A.*** (s. str.) ***podolica*** Mnnh., ***A. (Trichocratomerus) deaurata*** Gmelin, ***A. (Cratomerus) hungarica*** Scop., ***A. (Cratomerus) sponsa*** Ksw., and ***A. (Cratomerus) mirabilis*** Zhich., $2n = 16$ (14 + Xy_p).

All these species have the same chromosome number and mechanism of sex determination. In diakinesis, the karyotypes of *A. podolica* and *A. hungarica* (Figs. 20 and 21, respectively) show 8 bivalents, including a pair of sex chromosomes in the parachute-like arrangement. Three large ring bivalents have 2 chiasmata each, whereas the rest of the bivalents have single chiasmata. MI in all the species reveals 7 autosomal bivalents and the bivalent Xy_p, consisting of a relatively small *X*-chromosome and hardly observable, dot-like *Y*-chromosome (Figs. 22, 23). The chromosome morphology was reliably determined only in *A. hungarica, A. lgockii,* and *A. sponsa*, which had numerous cells in MII phase (Figs. 24–27). At this stage, chromatids of each chromosome start to move apart, remaining connected at the centromere, so that the morphology of each chromosome can be determined. Figs. 24 and 25 represent two daughter MII of *A. hungarica*, with *X*- and *Y*-chromosome, respectively; two MII of *A. lgockii*, both with *X*-chromosome, are shown in Figs. 26, 27. The morphology of the dot-like *Y*-chromosome cannot be determined, and *X*-chromosomes are metacentric in all cases. The autosomes are also metacentric, which is especially evident in *A. lgockii* (Fig. 27).

The haploid karyotype of these species was identified as $n = 8$ (7 + Xy_p); correspondingly, the diploid karyotype is $2n = 16$ (14 + Xy_p).

DISCUSSION

Even though the number of species studied is not large, they display a considerable variety of chromosome numbers and mechanisms of sex determination. The chromosome numbers of the diploid karyotype vary between 14 to 26, with the lowest value observed in *Capnodis tenebrionis* and the highest, in *Julodis faldermanni, J. andreae*, and *Julodella globithorax*. The species mentioned have a heteromorphic pair of sex chromosomes *XY*, which belongs to the *neo-XY* type in *C. tenebrionis* and *J. andreae*, and to the Xy_p type in *J. globithorax*. The sex chromosome system in *J. faldermanni* was not identified with any particular type in the usual classification (Smith, 1953) because of the insufficient material analyzed.

All species of the genus *Anthaxia* have $2n = 16$ and the sex chromosome system of the Xy_p type. The same system occurs in 2 species of the genus *Perotis* and in *Capnodis miliaris*, which have $2n = 20$. The sex chromosomes of *Acmaeoderella flavofasciata* ($2n = 18$) belong to the Xy_r type in Smith's (1953) classification.

Beetles are characterized by a unique diversity of the chromosome mechanisms of sex determination (Smith, 1953; White, 1973), even though this diversity is related to morphological, rather than genetical aspects (Blackman, 1995). The type of the heteromor-

Table 2. Chromosome numbers and sex chromosome systems in buprestids

Species	$2n$ ♂*	n**	Author
Subfam. **JULODINAE** Lacord.			
Tribe **Julodini** Lacord.			
Julodis faldermanni Mnnh.	26	12 + *XY****	New data
J. andreae Ol.	26	12 + *neo-XY*	New data
J. whithilli Gray.	24	11 + *neo-XY*	Asana *et al.*, 1942
Julodella globithorax Stev.	26	12 + Xy_p	New data
Sternocera laevigata Ol.	26	12 + *neo-XY*	Asana *et al.*, 1942
S. nitidicollis Laporte & Gory	26	12 + *neo-XY*	Asana *et al.*, 1942
Subfam. **POLYCESTINAE** Lacord.			
Tribe **Acmaeoderini** Kerremans			
Acmaeodera hepburni Lec.	18	8 + *neo-XY*	Smith, 1960
Acmaeoderella flavofasciata Pill. & Mitt.	18	8 + Xy_r	New data
A. gibbulosa Mén.	18	8 + Xy_r	G.A. Karagyan*****
A. vetusta Mén.	18	8 + Xy_r	G.A. Karagyan*****
A. boryi Brullé	18	8 + Xy_r	G.A. Karagyan*****
Subfam. **CHALCOPHORINAE** Lacord.			
Tribe **Chalcophorini** Lacord.			
Chalcophora lacustris Lec.	21♂, 22♀	10 + X	Smith, 1953
Euchroma gigantea L.	26	12 + Xy_r	Nichols, 1910
	24 (2♂) 26 (1♂)****	9 + $X_1X_2X_3Y_1Y_2Y_3$	Mesa, Fontanetti, 1984
Tribe **Sphenopterini** Lacord.			
Sphenoptera scovitzi Fald.	24	–	G.A. Karagyan*****
S. mesopotamica Mars.	24	–	G.A. Karagyan*****
Tribe **Psilopterini** Lacord.			
Capnodis tenebrionis L.	14	6 + *neo-XY*	New data
C. miliaris Klug	20	9 + Xy_p	New data
Perotis cuprata Klug	20	9 + Xy_p	New data
P. lugubris F.	20	9 + Xy_p	New data
Dicerca divaricata Say	20	–	Smith, 1978
D. prolongata Lec.	20	9 + Xy_p	Smith, 1953
D. tenebrosa Kby.	20	9 + Xy_p	Smith, 1953
Subfam. **BUPRESTINAE** Lacord.			
Tribe **Buprestini** Lacord.			
Buprestis fasciata F.	20	–	Smith, 1953
Tribe **Stigmoderini** Lacord.			
Stigmodera cancellata (Donovan)	22	10 + Xy_p	Gardner, 1988
S. goryi Gory & Laporte	22	10 + Xy_p	Gardner, 1988
S. gratiosa Chevrolat	22	10 + Xy_p	Gardner, 1988
S. macularia (Donovan)	22	10 + Xy_p	Gardner, 1988

Table 2. (Contd.)

Species	$2n$ ♂*	n**	Author
S. porosa Carter	22	$10 + Xy_p$	Gardner, 1988
S. roei Saunders	22	$10 + Xy_p$	Gardner, 1988
Themognatha alternata Lumholtz	20	$9 + Xy_p$	Gardner, 1988
Th. barbiventris Carter	22	$10 + Xy_p$	Gardner, 1988
Th. bonvouloiri Saunders	22	$10 + Xy_p$	Gardner, 1988
Th. chalcodera Thomson	22	$10 + Xy_p$	Gardner, 1988
Th. chevrolati Gehin	22	$10 + Xy_p$	Gardner, 1988
Th. donovani Gory & Laporte	22	$10 + Xy_p$	Gardner, 1988
Th. heros Gehin	22	$10 + Xy_p$	Gardner, 1988
Th. mitchelli Hope	22	$10 + Xy_p$	Gardner, 1988
Th. mniszechi Saunders	22	$10 + Xy_p$	Gardner, 1988
Th. nickerli Obenb.	20	$9 + Xy_p$	Gardner, 1988
Th. parvicollis Saunders	22	$10 + Xy_p$	Gardner, 1988
Th. pubicollis Waterhouse	22	$10 + Xy_p$	Gardner, 1988
Th. regia Blackburn	22	$10 + Xy_p$	Gardner, 1988
Th. tricolorata Waterhouse	22	$10 + Xy_p$	Gardner, 1988
Th. variabilis (Donovan)	22	$10 + Xy_p$	Gardner, 1988
Th. viridicincta Waterhouse	22	$10 + Xy_p$	Gardner, 1988
Castiarina adelaidae Hope	22	$10 + Xy_p$	Gardner, 1988
C. argillacea Carter	22	$10 + Xy_p$	Gardner, 1988
C. cupreoflava Saunders	22	$10 + Xy_p$	Gardner, 1988
C. decemmaculata (Kirby)	22	$10 + Xy_p$	Gardner, 1988
C. flavopicta (Boisduval)	22	$10 + Xy_p$	Gardner, 1988
C. grata Saunders	22	$10 + Xy_p$	Gardner, 1988
C. rufipennis (Kirby)	22	$10 + Xy_p$	Gardner, 1988
C. sexplagiata Gory	22	$10 + Xy_p$	Gardner, 1988
C. simulata Gory & Laporte	22	$10 + Xy_p$	Gardner, 1988
C. subnotata Carter	22	$10 + Xy_p$	Gardner, 1988
C. subtincta Carter	22	$10 + Xy_p$	Gardner, 1988
C. triramosa Thomson	22	$10 + Xy_p$	Gardner, 1988
Tribe **Anthaxiini** Gory & Laporte			
Anthaxia viridifrons Gory	16	$7 + Xy_p$	Smith, 1960
A. lgockii Obenb.	16	$7 + Xy_p$	New data
A. bicolor Fald.	16	$7 + Xy_p$	New data
A. podolica Mnnh.	16	$7 + Xy_p$	New data
A. deaurata Gmelin	16	$7 + Xy_p$	New data
A. hungarica Scop.	16	$7 + Xy_p$	New data
A. sponsa Ksw.	16	$7 + Xy_p$	New data
A. mirabilis Zhich.	16	$7 + Xy_p$	New data

Table 2. (Contd.)

Species	$2n$ ♂*	n**	Author
Tribe **Melanophilini** Bedel			
Melanophila acuminata DeG.	12	5 + Xy_p	Smith, 1953
M. drummondi Kby.	16	7 + Xy_p	Smith, 1953, 1960
M. intrusa Horn	16	7 + Xy_p	Smith, 1978
Tribe **Chrysobothrini** Lap. & Gory			
Chrysobothris dentipes Germ.	16	7 + Xy_p	Smith, 1953
Ch. floricola Gory	16	7 + Xy_p	Smith, 1960
Subfam. **AGRILINAE** Lap. & Gory			
Tribe **Agrilini** Lap. & Gory			
Agrilus anxius Gory	22♂,♀	10 + Xy_p/XX	Smith, 1949
A. liragus Berter & Brown	20♂,♀	9 + *neo-XY*/XX	Smith, 1949
A. sp. nr. *pensus* Horn	–	Xy_p	Smith, 1953
A. politus pseudocoryli Fish.	20	9 + *XY*	Smith, 1953
Agrilus sp.	20	9 + *neo-XY*	Smith, 1953
Unidentified species			
"Spruce borer sp. I"	20	9 + *Xy*	Stevens, 1906
"Spruce borer sp. II"	22	10 + *Xy*	Stevens, 1906

* $2n$ ♂—Chromosome number in the diploid male karyotypes (in some cases determined based on the haploid karyotype).

** n—Haploid chromosome number in the spermatogonial MI: autosomal bivalents and sex chromosomes (absence of data is marked with "–").

*** The type of *XY* bivalent (Smith, 1953) was not determined.

**** Spermatogonial MI showed 9 autosomal bivalents, 1 trivalent, and 5 sex chromosomes $X_1X_2X_3Y_1Y_2$.

***** Personal communication.

phic pair of sex chromosomes *XY* in beetles cannot always be reliably classified. This is especially true for a number of *Xy* variants, with the small "*y*" indicating the minute *Y*-chromosome. Each variant is designated by a specific symbol, reflecting the shape and behavior of the *Xy* bivalent during spermatogonial meiosis and especially in the meiotic MI. The commonest variant (especially in Polyphaga) is the so-called "parachute," first described by Stevens (1906) and designated as Xy_p (Smith, 1950). In this type of bivalent, *X*-chromosome in MI resembles the parachute canopy (with spread arms in the case of a metacentric organization, or bent double in the case of a subtelocentric structure), whereas *Y*-chromosome looks like the parachute load. *X*-chromosome may be large, as in *C. miliaris*, or, more frequently, not very large; *Y*-chromosome, on the contrary, is always very small, almost dot-like, and sometimes hardly observable at all in MI. The nature of the Xy_p association is a matter of discussion in the literature. Most frequently, this type of association is explained by the presence of terminal chiasmata between the arms of *X*- and *Y*-chromosomes (Smith, 1951; White, 1973) or by the formation of a nucleolus (Stevens, 1905, 1906; John and Lewis, 1960). However, recent investigations (Virkki *et al.*, 1991) did not confirm these hypotheses. Some argyrophilous material, resembling that of the synaptonemal complex of autosomes and possibly proteinous, was discovered between the *X*- and *y*-chromosomes. It was shown that this material plays some role in the formation of *Xy* bivalent and facilitates the regular segregation of sex chromosomes during AI phase, but does not participate in the nucleolus formation.

As shown in the same publication (Virkki *et al.*, 1991), *X*- and *y*-chromosomes form a terminal association of the "end-to-end" type during early meiotic prophase until pachytene, even though in MI they resemble a parachute figure. However, the mechanism in

which the sex chromosomes form an end-to-end association in MI is considered to belong to a separate category and is designated as Xy_r, with "*r*" indicating the rod-shaped bivalent (Smith, 1953). Thus, the mechanisms Xy_p and Xy_r cannot be reliably discriminated. Well-documented cases of the Xy_r mechanism are rare, and many species for which this type was reported probably have the Xy_p system (White, 1973). In our material for *Acmaeoderella flavofasciata*, *X*- and *y*-chromosomes formed no parachute figure in late prophase and MI, but showed the "distant pairing" of the end-to-end type. Therefore, after a prolonged discussion, this mechanism was designated as Xy_r. It should be noted that the same mechanism was also revealed in *A. gibbulosa*, *A. vetusta*, and *A. boryi*, confirming the close relations among these species.

A special case among the diverse *XY* mechanisms known in beetles is represented by those termed *neo-XY*. These mechanisms are always of secondary nature, being the result of various translocations between autosomes and sex chromosomes (White, 1973; Blackman, 1995). One of such systems with a large *Y*-chromosome, probably resulting from *X*–autosomal fusion in the *X0* system (Blackman, 1995), was observed in *C. tenebrionis* ($2n = 14$) and *J. andreae* ($2n = 26$). In this type, *neo-X* includes the original *X*-chromosome and an autosomal part, while *neo-Y* is in fact a homologue of the autosome which has fused with *X*. It is possible that some species of the genera *Capnodis* and *Julodis* have the *X0* mechanism.

Analysis of published data shows that the sex determination mechanisms found in the 15 buprestid species studied represent almost the entire spectrum known for this family (Table 2). The mechanisms considered above appear to be the most typical of Buprestidae. The other two systems, namely *X0* and the so-called multiple sex chromosomes, have been described only in 2 species: *Chalcophora lacustris* (Smith, 1953) and *Euchroma gigantea* (Mesa and Fontanetti, 1984), respectively.

With addition of the 15 species investigated in this work and the 5 species examined by the Ag-banding method, karyotypes have been studied in a total of 77 species, belonging to 19 genera, 10 tribes, and 5 subfamilies of Buprestidae (Table 2). The chromosome numbers vary between 12 and 26. The prevalent karyotype $2n = 22$ ($20 + Xy_p$) was found in 34 species; however, 32 of these species belong to the genera *Stigmodera*, *Themognatha*, and *Castiarina*, which were previously treated as subgenera within a single genus *Stigmodera* (Gardner, 1989). In the mentioned genera, this karyotype represents the absolute modal state, probably inherited from the common ancestor of the tribe Stigmoderini (Gardner, 1988). Although the available data are insufficient for determining the prevalent number of chromosomes (in fact, gene linkage groups) in Buprestidae, the most typical sex determination mechanism in this group is probably Xy_p, reported so far in 54 species. The absence of this system in some genera and even subfamilies (Julodinae and Polycestinae) is probably explained by the insufficient material on these groups. The Xy_p mechanism is considered to be the feature ancestral to the entire Coleoptera (Smith and Virkki, 1978; Virkki *et al.*, 1991; Blackman, 1995). This is confirmed by the prevalence of this system in Polyphaga, where it occurs in nearly 2/3 of over 2000 species examined, and by its presence, though very rare, in Adephaga (Smith and Virkki, 1978) and Myxophaga (Mesa and Fontanetti, 1985). The Xy_p mechanism is known, except Coleoptera, only in Megaloptera (Hughes-Schrader, 1980), confirming the hypothesis that this system is a primitive character for Coleoptera, which originated in the common ancestor of the two orders (Virkki *et al.*, 1991).

As stated above, the available karyological data on Buprestidae are by no means sufficient for any taxonomic conclusions to be made. However, some preliminary estimations can be drawn.

The closely related buprestid species usually have similar karyotypes. For example, all 6 studied species of *Stigmodera*, all 12 species of *Castiarina*, and 14 of the 16 studied species of *Themognatha* (tribe Stigmoderini) have $2n = 22$ ($20 + Xy_p$). Eight species of the genus *Anthaxia* have the karyotype $2n = 16$ ($14+ Xy_p$), 4 species of *Acmaeoderella* have $2n = 18$ ($16 + Xy_r$), 4 species of *Dicerca* have $2n = 20$ ($18 + Xy_p$), and 2 species of *Sternocera* have $2n = 26$ ($24 +$ *neo-XY*). These data indicate that karyotypes can be used for characterizing supraspecific taxa of Buprestidae.

The closely related species occasionally show insignificant differences in the chromosome number (*Themognatha*, *Melanophila*), which in *Themognatha* are explained by Robertsonian translocations (Gardner, 1988). In other cases, closely related species differ in the sex determination mechanism (*Julodis*), or in both characters mentioned (*Capnodis*, *Agrilus*). These differences may be of varied origin, to be elucidated

upon addition of new data and methods of investigation.

Species of the related genera *Julodis* and *Julodella* are of special interest. These species are not similar in karyotypes, differing in the chromosome number or the sex determination mechanism. However, they have a pair of very large autosomes, which obviously represent a synapomorphic character clearly distinguishing them from other buprestid genera.

ACKNOWLEDGMENTS

The authors cordially thank M.Yu. Kalashian (Institute of Zoology, National Academy of Sciences of Armenia, Yerevan) and M.G. Volkovitsh (Zoological Institute, Russian Academy of Sciences, St. Petersburg) for their help with collection and identification of the material and for advice on the buprestid macrotaxonomy, and C. Nokkala (Laboratory of Genetics, University of Turku, Finland) for valuable help in interpreting the karyotype of *Capnodis tenebrionis*.

The work was financially supported by the Russian Foundation for Basic Research, grant no. 99-04-49770.

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