PL-ISSN 0015-5497 (print), ISSN 1734-9168 (online)
© Institute of Systematics and Evolution of Animals, PAS, Kraków, 2013
Folia Biologica (Kraków), vol. 61 (2013), No 3-4
doi:10.3409/fb61_3-4.193

A Chromosomal Analysis of Twelve Species of the Subfamily Chrysomelinae (Coleoptera, Chrysomelidae)

Eduard PETITPIERRE and Yuri E. MIKHAILOV

Accepted May 15, 2013

PETITPIERRE E., MIKHAILOV Y. E. 2013. A chromosomal analysis of twelve species of the subfamily Chrysomelinae (Coleoptera, Chrysomelidae). Folia Biologica (Kraków) **61**: 193-198.

Twelve species of chrysomelines, all but one from the Palaearctic region, have been cytogenetically analyzed, mostly through their male meiotic metaphases I. *Ambrostoma superbum* has 2n = 40 (Xy_p), *Chrysolina colasi, Oreina fairmairiana* and the Neotropical *Platyphora spectabilis* have 2n = 24 (Xy_p), *Chrysolina gebleri* 2n = 26 (XY_p), *Colaspidema barbarum* 2n = 28 (Xy_p), *Crosita altaica* and *C. rugulosa* 2n = 30 (Xy_p), *Phratora polaris, Ph. vitellinae* and *Ph. vulgatissima* 2n = 34 (Xy_p), and the karyotype of *Chrysolina marginata,* consisting of 40 chromosomes, is also described. These results are discussed with those previously obtained in related genera and congeneric species, giving further support and extending the high chromosomal variability so far found in this subfamily of leaf beetles.

Key words: Coleoptera, Chrysomelidae, karyotypes, sex-chromosome systems, cytotaxonomy, evolution.

Eduard PETITPIERRE, Lab. of Genetics, Dept. of Biology, University of Balearic Islands, 07122 Palma de Mallorca, Spain.
E-mail: eduard.petitpierre@uib.es
Yuri E. MIKHAILOV, Dept. of Ecology, Ural Federal University, 620083 Ekaterinburg, Russia / Dept. of Botany and Forest Protection, Ural State Forest Engineering University, 620100 Ekaterinburg, Russia.
E-mail: yuri.mikhailov@usu.ru

The subfamily Chrysomelinae is a large group of leaf beetles consisting of roughly 3000 species (REID *et al.* 2009) in 175 genera (DACCORDI 1982) which were later reduced to 133 (DACCORDI 1994). The number of tribes and subtribes is variable depending on the particular opinions of the different authors, but the majority consider two tribes, Timarchini and Chrysomelini, the former with only one subtribe and the latter with five, Entomoscelina (= Phyllocharitina), Chrysolinina, Doryphorina (sometimes included within the previous one), Gonioctenina (= Paropsina), and Chrysomelina (DACCORDI 1994; RILEY *et al.* 2002; REID 2002; PETITPIERRE 2011).

The Chrysomelinae are relatively well-known cytogenetically, with 180 surveyed taxa 25 years ago (PETITPIERRE *et al.* 1988), a figure updated to 260 taxa recently (PETITPIERRE 2011), that is 8.7% of the total described species in 41 genera or 23.3% to 30.8% of all known genera, depending on how many are recognized. Herein we have analyzed ten new species, and we have augmented cytogenetic data in two further species either by meiotic or by mitotic metaphase analyses.

Material and Methods

Collection sites

The list of examined species and their geographical sources are given in Table I.

The number of analyzed adult male specimens was as follows: *Ambrostoma superbum* (1), *Chrysolina marginata* (1), *Chrysolina gebleri* (1), *Chrysolina colasi* (3), *Oreina fairmairiana* (3), *Colaspidema barbarum* (2), *Crosita altaica* (1), *Crosita rugulosa* (1), *Phratora polaris* (1), *Phratora vitellinae* (2), *Phratora vulgatissima* (1), *Platyphora spectabilis* (1).

Chromosome preparations

The cytogenetic data were obtained by testis dissection of adult male specimens which were fixed in 45% acetic acid, later on teased into small pieces for five minutes, squashed under a coverslip, immediately frozen in liquid nitrogen to remove the coverslip, and finally treated using conventional Giemsa staining procedures. Most examined cells

Table I

Cytogenetically analysed species of leaf-beetles and their geographical sources

Ambrostoma superbum (Thunberg, 1787)	Badaling at Great Wall, 50 km north Beijing (China)
Chrysolina (*Chalcoidea*) *marginata* (Linnaeus, 1758)	La Sagra, Granada, Andalucia (Southeast Spain)
Chrysolina (*Pleurosticha*) *gebleri* L. Medvedev, 1979	Charysh distr., Altai Province (Russia)
Chrysolina (*Stichoptera*) *colasi* (Cobos, 1952)	Pico Veleta, around 3000 m alt., Granada (Spain)
Colaspidema barbarum (Fabricius, 1792)	La Sagra, Granada, Andalucia (Southeast Spain)
Crosita altaica (Gebler, 1823)	Mugojary mts., Aktyubinsk reg. (West Kazakhstan)
Crosita rugulosa (Gebler, 1841)	South-Chuya mt. range, Republic of Altai (Russia)
Oreina (*Chrysochloa*) *fairmairiana* (Gozis, 1882)	Gausac, Val d'Aran, Pyrenees of Lleida, Catalonia (Spain)
Phratora (*Phyllodecta*) *vitellinae* (Linnaeus, 1758)	Kevo (North Finland)
Phratora (*Phratora*) *vulgatissima* (Linnaeus,1758)	Alpthal (Switzerland)
Platyphora spectabilis (Baly, 1858)	P.N. Brenes (Costa Rica)

were in meiotic metaphases I, providing the male meioformulas, thus the number of autosomal bivalents plus male sex-chromosome systems. Three among the twelve surveyed species gave spermatogonial meta- or prometaphase cells, from which we obtained results on their chromosomal architecture.

Results

Subtribe Chrysolinina

Ambrostoma superbum

Several metaphase I cells were screened in this species showing a $19 + Xy_p$ meioformula, composed of similar medium sized autosomal bivalents and the Xy_p ("parachute-type") sex-chromosome system, with a large X and a small y-chromosome (Fig. 1). A spermatogonial mitotic prometaphase displays mostly meta- and submetacentric medium or small chromosomes out of a large autosomal pair (Fig. 2).

Chrysolina marginata

The meioformula of this species, $19 + Xy_p$, was studied previously (PETITPIERRE 1981), but not its karyotype comprised of 2n = 40 chromosomes from spermatogonial metaphases. This karyotype has two pairs of large metacentric autosomes, seven pairs of medium sized ones of which three are acrocentrics ($3^{th.}$, 4^{th} and 9^{th}) and the remaining are metacentrics, and ten other pairs of medium-small, four of them clearly smaller than the other three, plus a rather large submetacentric X-chromosome and a tiny y-chromosome (Figs 3 and 4). Therefore, the number of large chromosome arms or "fundamental number" (FN) in *Ch. marginata,* is FN = 74.

Chrysolina gebleri

This species exhibits a $12 + XY_p$ meioformula (Fig. 5), that is 2n = 26 chromosomes. The autosomal bivalents are relatively small and the male sex-chromosome system is a "parachute-type" XY_p, constituted by two elements, the X and Y chromosomes of similar sizes.

Chrysolina colasi

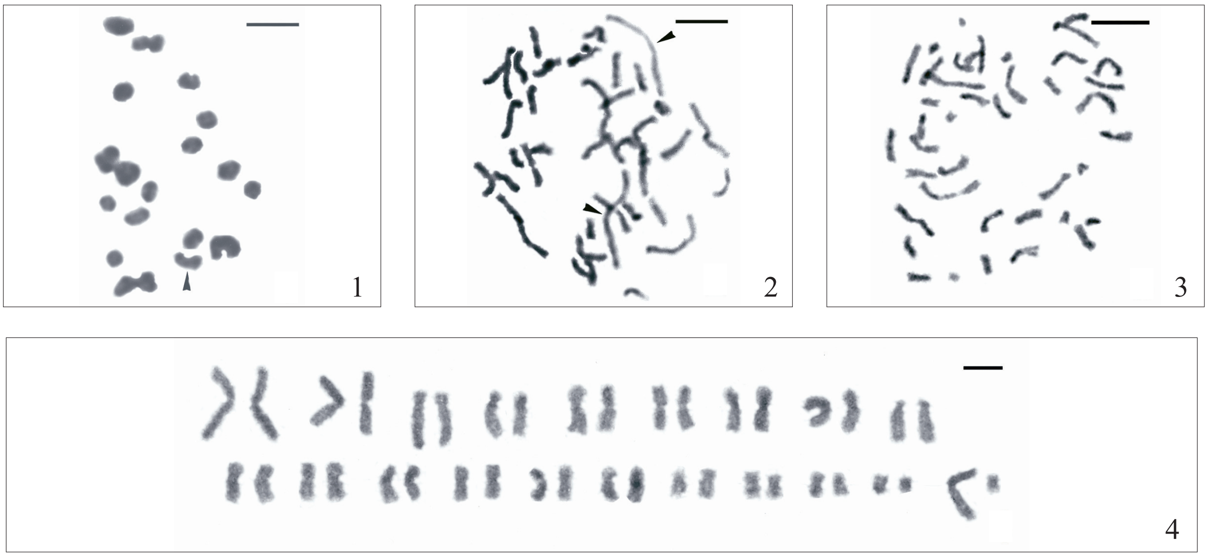
The mitotic metaphases of *Ch. colasi*, with 2n = 24 chromosomes, have been studied before (PETITPIERRE 1981). Herein, we provide a metaphase I showing a $11 + Xy_p$ meioformula (2n = 24), with four large bichiasmate autosomal bivalents, seven medium sized unichiasmate ones, and the Xy_p sex-chromosome system (Fig. 6).

Oreina fairmairiana

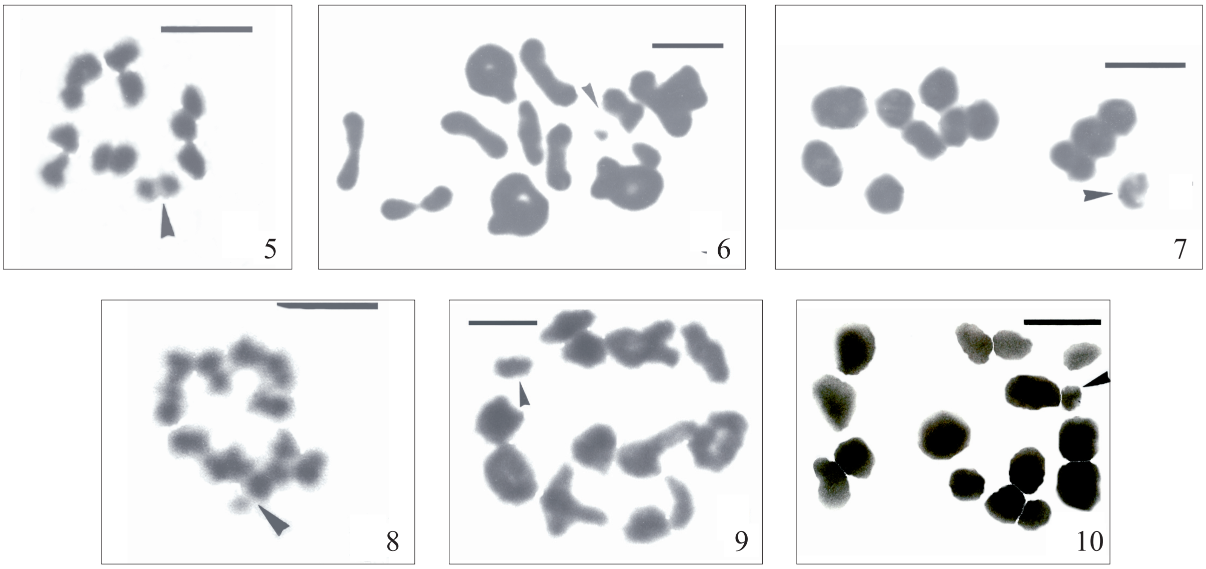
Similar to the former species, this one has metaphases I with a $11 + Xy_p$ meioformula (2n = 24) that consists of similar medium sized and mostly round autosomal bivalents out of the Xy_p sex-chromosome system (Fig. 7).

Colaspidema barbarum

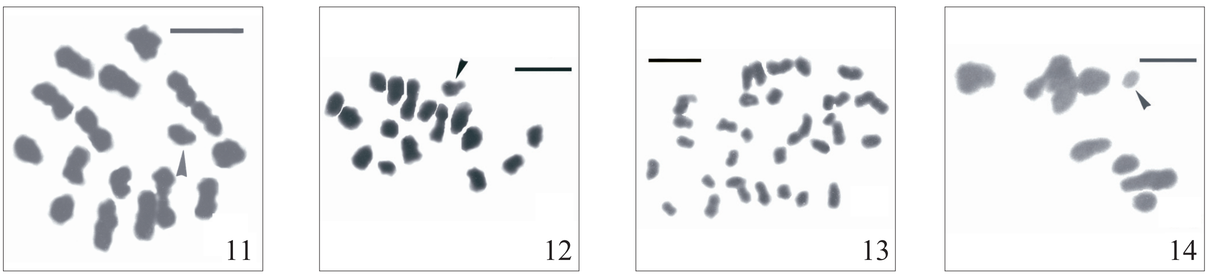
Meiotic metaphases I showing a $13 + Xy_p$ meioformula (2n = 28) with similar small bivalents including the "parachute" Xy_p sex-chromosomes have been found in this species (Fig. 8).



Figs 1-4. Fig. 1. Metaphase I of *Ambrostoma superbum* with 19 + Xy_p, the Xy_p is arrowheaded. Scale = 5 μm. Fig. 2. Spermatogonial mitotic prometaphase of *A. superbum* with 2n = 40 chromosomes, the pair of largest autosomes are arrowheaded.. Scale = 5 μm. Figs 3 and 4. Spermatogonial mitotic metaphase (3) and karyogram (4) of *Chrysolina marginata* showing 2n = 40 chromosomes, the X- and y-chromosomes are at the lower right hand of the karyogram. Scale = 5 μm.



Figs 5-10. Fig. 5. Metaphase I of *Chrysolina gebleri* with 12 + XY_p, the symmetric XY_p is arrowheaded. Scale = 5 μm. Fig. 6. Metaphase I of *Chrysolina colasi* with 11 + Xy_p, the lumen of distended Xy_p is arrowheaded. Note also the four large bichiasmate autosome bivalents. Scale = 5 μm. Fig. 7. Metaphase I of *Oreina fairmairiana* with 11 + Xy_p, the Xy_p is arrowheaded. Scale = 5 μm. Fig. 8. Metaphase I of *Colaspidema barbarum* with 13 + Xy_p, the Xy_p is arrowheaded. Scale = 5 μm. Fig. 9. Metaphase I of *Crosita altaica* with 14 + Xy_p, the Xy_p is arrowheaded. Scale = 5 μm. Figs. 10. Interpretative drawing from a metaphase I of *Crosita rugulosa* with 14 + Xy_p, the Xy_p is arrowheaded. Scale = 5 μm.



Figs. 11-14. Figs. 11 and 12. Metaphases I of *Phratora polaris* (11) and *Ph. vitellinae* (12) with 16 + Xy_p, the Xy_p are arrowheaded. Scale = 5 μm. Fig. 13. Spermatogonial mitotic metaphase of *Phratora vulgatissima* showing 2n = 34 chromosomes. Scale = 5 μm. Fig. 14. Metaphase I of *Platyphora spectabilis* with 11 + Xy_p, the Xy_p is arrowheaded. Note that six autosome pairs are overlapped in three pair groups. Scale = 5 μm.

Crosita altaica

A meiotic formula of 14 + Xy_p (2n = 30) comprised of large autosomal bivalents and the small Xy_p sex-chromosome system characterizes the metaphases I of *C. altaica* (Fig. 9).

Crosita rugulosa

The same karyotype meioformula of 14 + Xy_p (2n = 30), with similar large autosomal bivalents as in the former and a small Xy_p, have also been found in metaphases I of this congeneric species (Fig. 10).

Subtribe Chrysomelina

Phratora polaris

Metaphases I include sixteen medium sized and small unichiasmate autosomal bivalents and a "parachute" male sex-chromosome, thus a meioformula of 16 + Xy_p, 2n = 34 chromosomes (Fig. 11).

Phratora vitellinae

This species has the same meioformula as the previous one, 16 + Xy_p, (2n = 34), from which it differs by having a lower number of medium sized autosomal bivalents, since most of them are small (Fig. 12).

Phratora vulgatissima

The spermatogonial mitotic metaphases display 2n = 34 chromosomes, mostly of small size, but whose shapes are not easily identified (Fig. 13). A meioformula of 16 + Xy_p has also been observed in this species (not shown).

Subtribe Doryphorina

Platyphora spectabilis

One individual from this species exhibited a meioformula of 11 + Xy_p, (2n = 24), made of eight medium and three small autosomal bivalents, plus the "parachute" sex-chromosome pair (Fig. 14).

Discussion and Conclusions

The chromosomal results obtained in these twelve species of Chrysomelinae leaf beetles are in a close agreement with those reported before and recently reviewed elsewhere, based on nearly 260 taxa (PETITPIERRE 2011). First, the wide range of diploid numbers from 2n = 24 to 2n = 40 chromosomes fits well within the even wider range from 2n = 12 to 2n = 50 currently known for the whole subfamily. Second, the modal chromosome number for Chrysomelinae, 2n = 24, displayed in nearly one third of the total checked species (PETITPIERRE & SEGARRA 1985; PETITPIERRE 2011), is here represented by three among the twelve sampled taxa. And third, all of our sampled species show the "parachute-like", Xy_p or XY_p, sex-chromosome systems, matching well with the 79% figure so far found for all chrysomelines (PETITPIERRE 2011).

The 2n = 40 (Xy_p) observed in *Ambrostoma superbum* is the first cytogenetic finding for the genus *Ambrostoma*, constituted by 13 species from East Asia (KIPPENBERG 2010). Since this genus seems to be taxonomically related to *Chrysolina* (DACCORDI 1994), it is not surprising that nearly 20% of the 70 examined species in the latter have 2n = 40 chromosomes. In addition, the meta- or submetacentric chromosome shape of its karyotype agrees with the prevalent chromosome structure found in chrysomelines (PETITPIERRE 2011), and also in the remaining beetles (SMITH & VIRKKI 1978; VIRKKI 1984).

The genus *Crosita* was also unworked to date from chromosomal grounds. As in *Ambrostoma, Crosita* with ten described species (KIPPENBERG 2010), is also taxonomically related to *Chrysolina* (DACCORDI 1994). However, contrary to the former genus, the 2n = 30 (Xy_p) karyotype observed in the two examined species of *Crosita* is only found in one taxon of *Chrysolina, Ch. lucidicollis grossepunctata* (quoted as *Ch. gypsophilae* in PETITPIERRE 1982), a species which is not morphologically close to *Crosita*. Therefore assuming 2n = 30 (Xy_p) is the putative modal number and sex-chromosome system for *Crosita*, the data do not indicate any relationship with the species of *Chrysolina* studied to date sharing these karyotypic characteristics.

We have analyzed three species in the genus *Chrysolina,* one of them *Ch. marginata* was previously cytogenetically studied, 19 + Xy_p (PETITPIERRE 1981), though not in its karyotypic architecture as reported herein. The karyotype of *Ch. marginata* is composed of 40 chromosomes of gradually decreasing size, most of them biarmed, so its fundamental arm number is FN = 74. Conversely, other species belonging to the same subgenus *Chalcoidea*, such as *Ch. carnifex* and *Ch. interstincta*, also share with *Ch. marginata* 2n = 40 (Xy_p) chromosomes, but all are acrocentrics and are similar in size except for the tiny y-chromosome (PETITPIERRE 1981; PETITPIERRE *et al.* 2004), and a much lower fundamental number of FN = 40. These differences in their karyotype architecture are also congruent with molecular phylogenetics based on two mitochondrial gene markers. *Ch. marginata* is more distantly related within the same clade, in respect to *Ch. carnifex* and another species of the subgenus *Chalcoidea*, than the latter are to each other (GARIN *et al.* 1999).

The meioformula of *Chrysolina gebleri*, 12 + XY_p (2n = 26) is coincident both in diploid number and symmetric "parachute" sex-chromosome system with those of *Ch. lagunovi* (in the same subgenus *Pleurosticha*) and those of *Ch. poretzkyi* and *Ch. tundralis,* in the closely related subgenus *Arctolina*. Morphological similarity of the two subgenera *Pleurosticha* and *Arctolina* and problems with their recognition have been previously discussed (MIKHAILOV 2007a, 2008). The cytogenetic resemblance provides further support for their close interrelationship. While *Ch. lagunovi, Ch. poretzkyi* and *Ch. tundralis* are all from the Ural mountain range, *Ch. gebleri* is from the Altai mountains and presumably represents a relict species of the subgenus *Pleurosticha* (MIKHAILOV 2007b), although it shares the same meioformula. This XY_p sex-chromosome "parachute" system, with both elements of similar size, may be a synapomorphic character for the two subgenera, but it has also been detected in *Ch. umbratilis* (PETITPIERRE *et al*. 2004), which belongs to the subgenus *Sphaerochrysolina* (KIPPENBERG 2010), therefore a distinct and presumably distantly related taxon. *Chrysolina colasi* has a meioformula of 11 + Xy_p which agrees with the karyotype of 2n = 24 chromosomes reported and illustrated by PETITPIERRE (1981, as *Oreina colasi*). The four large autosomal bivalents observed correspond to the four large autosomal pairs we found in spermatogonial metaphases. Moreover, the karyotype of *Ch. colasi* is clearly asymmetric with two striking groups differing in chromosome size: one group of large elements and another of small elements, a common characteristic shared with the other seven surveyed species in the subgenus *Stichoptera*. This remarkable feature is conserved in spite of the high variation in diploid numbers, from 2n = 22 to 2n = 34 in the eight examined species of *Stichoptera* (PETITPIERRE 1999, 2000; PETITPIERRE *et al.* 2004).

The meioformula of *Oreina fairmairiana*, 11 + Xy_p (2n = 24), is also found in all but one of the twelve studied species of *Oreina* (PETITPIERRE 1981, 1999). Since these sampled species represent five of the six established subgenera (KIPPENBERG 2010), the 11 + Xy_p meioformula could be taken not only as modal but also as the most plesiomorphous for the genus *Oreina.* In this sense, we emphasize again that this formula is modal and maybe ancestral for the closely related genus *Chrysolina,* although it is much more heterogeneous cytogenetically than *Oreina* (PETITPIERRE 1981, 1999; PETITPIERRE *et al.* 2004; PETITPIERRE & MIKHAILOV 2009).

Colaspidema barbarum displays a meioformula of 13 + Xy_p (2n = 28), constituted by small autosomal bivalents and the Xy_p. A related species, *Colaphus sophiae*, has a similar formula in males with 13 + X (2n = 27) (LACHOWSKA *et al.* 1996) but differs in the sex-chromosome system, XO instead of Xy_p. Although KIPPENBERG (2010) includes both genera in his tribe Entomoscelini, an opinion which is not shared by other authors (DACCORDI 1994; PETITPIERRE 2011), the only examined Palaearctic genus in this group, *Entomoscelis,* with two studied species, has a different diploid number of 2n = 26 (Xy_p) (PETITPIERRE *et al.* 1988).

The three studied species of the genus *Phratora*: *Ph. polaris, Ph. vitellinae* and *Ph. vulgatissima,* share the same meioformula of 16 + Xy_p (2n = 34) in agreement with two previously analyzed congeneric species, *Ph. tibialis* and *Ph. laticollis* (PETITPIERRE 1982; PETITPIERRE & SEGARRA 1985). These species seem to differ only in the number of medium and small chromosomes, thereby in their chromosomal architecture, a feature that should be more accurately investigated. As stated before (PETITPIERRE & SEGARRA 1985; PETITPIERRE 2011), the subtribe Chrysomelina to which *Phratora, Chrysomela, Phaedon, Prasocuris, Hydrothassa* and *Plagiosterna* belong to along with some other genera, show the 2n = 34 (Xy_p) karyotype as the modal and presumably the ancestral state for this higher taxon.

The Neotropical *Platyphora spectabilis* has a diploid chromosome number of 2n = 24 (Xy_p), which was also reported in the congeneric *P. aulica* (PETITPIERRE *et al.* 1988), and in three additional genera of Doryphorina, the subtribe in which they are placed, but it is not yet clear whether this value can be considered as the most plesiomorphous for this group (PETITPIERRE 2011).

Acknowledgements

We are greatly indebted to J. A. JURADO-RIVERA (Esporles, Mallorca) for collecting the specimen of *Platyphora spectabilis* and to Dr. Nathan RANK (Sonoma State Univ., California) for specimens of the three examined species of *Phratora.* Drs. M. A. CONESA and A. MOLINS (Palma de Mallorca) are also acknowledged for their valuable help in the process of scanning and improving our micrographs.

References

DACCORDI M. 1982. Chrysomelinae. (In: Leaf Beetle Genera (Coleoptera: Chrysomelidae). T.N. Seeno and J. A. Wilcox eds). Entomography **1**: 75-95.

DACCORDI M. 1994. Notes for phylogenetic study of Chrysomelinae, with descriptions of new taxa and a list of all the known genera (Coleoptera: Chrysomelidae: Chrysomelinae). Proc. Third Int. Sympos. Chrysomelidae, Beijing 1992, Backhuys Publ., Leiden, The Netherlands. Pp. 60-84.

GARIN C.F., JUAN C., PETITPIERRE E. 1999. Mitochondrial DNA phylogeny and the evolution of host-plant use in palearctic *Chrysolina* (Coleoptera, Chrysomelidae). J. Mol. Evol. **48**: 435-444.

KIPPENBERG H. 2010. Chrysomelidae, (In: Catalogue of Palaearctic Coleoptera vol. 6 Chrysomeloidea, I. Löbl & A. Smetana eds. Apollo Books, Stenstrup, Denmark): 390-443.

LACHOWSKA D., ROŻEK M., HOLECOVÁ M. 1996. A cytogenetic study of eight beetle species (Coleoptera: Carabidae, Scarabaeidae, Cerambycidae, Chrysomelidae) from Central Europe. Folia Biol. (Kraków) **44**: 99-103.

MIKHAILOV Yu.E. 2007a. A new species of the genus *Chrysolina* Motsch. (Coleoptera, Chrysomelidae) from the mountains of Tuva and Buryatia. Entomol. Review **87**: 1038-1040.

MIKHAILOV Yu.E. 2007b. Contribution to our knowledge of the subgenus *Pleurosticha* Motschulsky, 1860 (Coleoptera, Chrysomelidae, *Chrysolina*). 2. Species from the southern edge of their distribution. Euroasian Entomol. J. **6**: 255-264. (In Russian).

MIKHAILOV Yu.E. 2008. A contribution to the knowledge of leaf beetles of the subgenus *Arctolina*, genus *Chrysolina* (Coleoptera, Chrysomelidae). Entomol. Review **88**: 1132-1140.

PETITPIERRE E. 1981. New data on the cytology of *Chrysolina* Mots. and *Oreina* Chevr. (Coleoptera, Chrysomelidae). Genetica **54**: 265-272.

PETITPIERRE E. 1982. Chromosomal findings on 22 species of Chryomelinae (Chrysomelidae: Coleoptera). Chromosome Inform. Serv. **32**: 22-23.

PETITPIERRE E. 1999. The cytogenetics and cytotaxonomy of *Chrysolina* Mots. and *Oreina* Chevr. (Coleoptera, Chrysomelidae, Chrysomelinae). Hereditas **131**: 55-62.

PETITPIERRE E. 2000. The cytogenetics and cytotaxonomy of the subgenus *Stichoptera* of *Chrysolina* (Coleoptera, Chrysomelidae). (In: Some Aspects on the Insight of Insect Biology, R. C. Sobti & J.S. Yadav eds. Narendra Publ. House, Delhi, 1999): 181-188.

PETITPIERRE E. 2011. Cytogenetics, cytotaxonomy and chromosomal evolution of Chrysomelinae revisited (Coleoptera, Chrysomelidae). ZooKeys **157**: 47-79.

PETITPIERRE E., MIKHAILOV Yu.E. 2009. Chromosomal evolution and trophic affiliation in the genus *Chrysolina* (Coleoptera: Chrysomelidae). (In: Research on Chrysomelidae vol. 2. P. Jolivet, J. Santiago-Blay & M. Schmitt. eds. Brill, Leiden-Boston): 225-234.

PETITPIERRE E., SEGARRA C. 1985. Chromosomal variability and evolution in Chrysomelidae (Coleoptera), particularly that of Chrysomelinae and Palearctic Alticinae. Entomography **3**: 403-426.

PETITPIERRE E., SEGARRA C., YADAV J.S., VIRKKI N. 1988. Chromosome numbers and meioformulae of Chrysomelidae. (In: Biology of Chrysomelidae. P. Jolivet,. E. Petitpierre. & T. H. Hsiao eds. Kluwer Academic Publishers, Dordrecht, The Netherlands): 161-186.

PETITPIERRE E., KIPPENBERG H., MIKHAILOV Yu., BOURDONNÉ J.C. 2004. Karyology and cytotaxonomy of the genus *Chrysolina* Motschulsky (Coleoptera, Chrysomelidae). Zool. Anz. **242**: 347-352.

REID C.A.M. 2002. A new genus of Chrysomelinae from Australia (Coleoptera: Chrysomelidae). Coleopts. Bull. **56**: 589-596.

REID C.A.M., JURADO-RIVERA J.A., BEATSON M. 2009. A new genus of Chrysomelinae from Australia (Coleoptera: Chrysomelidae). Zootaxa **2207**: 53-66.

RILEY E.G., CLARK S.M., FLOWERS R.W., GILBERT A.J. 2002. Family 124. Chrysomelidae Latreille (1802) (Chrysomelidae). (In: Chrysomelinae: in American Beetles vol. 2. Polyphaga: Scarabaeoidea through Curculionoidea, R.H. Arnett, M.C. Thomas, P.E. Skelley & J.H. Frank eds. CRC Press, Boca Raton): 648-653.

SMITH S.G., VIRKKI N. 1978. Coleoptera. (In: Animal Cytogenetics, vol. 3: Insecta. 5. B. John ed. Gebrüder Borntraeger, Berlin-Stuttgart.

VIRKKI N. 1994. Chromosomes in Evolution of Coleoptera. (In: Chromosomes in Evolution of Eukaryotic groups, vol. 2. A.K. Sharma. & A. Sharma. eds. CRC Press, Boca Raton, Florida): 41-76.