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Chromosomal investigations of eight species of Geotrupidae (Coleoptera, Scarabaeoidea)

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Abstract.– The karyotypes of eight species of Geotrupidae are reported and illustrated. *Ceratophyus hoffmannseggi* Fairmaire has seven pairs of autosomes and sex chromosomes which are Xy (♂), XX (♀), while *Anoplotrupes stercorosus* (Scriba), *Geotrupes spiniger* Marsham, *Sericotrupes niger* (Marsham), *Thorectes geminatus* (Gené), *T. intermedius* (Costa), *T. lusitanicus* (Jekel) and *Trypocopris vernalis* (L.) all have 10 pairs of autosomes and sex chromosomes which are Xy (♂), XX (♀). In *A. stercorosus*, *G. spiniger* and *S. niger* the autosomes are mainly acrocentric with variously developed centromeric C-bands which in some cases result in heterochromatic short arms, and in *A. stercorosus* autosome 10 is polymorphic and may have a distinct euchromatic short arm. None of the *A. stercorosus* autosomes shows any sign of median or submedian centromeres, as suggested by COLOMBA *et al.* (2004). *Thorectes geminatus* has autosome 1 metacentric, comparable with that of *T. punctatissimus* (Chevrolat), but in *T. geminatus* autosomes 1 and 2 are about the same length while in *T. punctatissimus* autosome 1 is about 1.5 times the length of autosome 2. Sardinian material of *T. intermedius* shows some chromosomal polymorphism comparable with that reported by COLOMBA *et al*. (1996) from mainly Sicilian material. *T. lusitanus* has six pairs of submetacentric autosomes with heterochromatic short arms while the remaining four pairs of autosomes and the X chromosome are acrocentric. *Trypocopris vernalis* has autosomes 1 – 8 either metacentric or submetacentric, but C-banding shows that in all these chromosomes one arm is entirely heterochromatic.

Résumé.– Les caryotypes de huit espèces de Geotrupidae sont présentés et figurés. *Ceratophyus hoffmannseggi* Fairmaire a sept paires d'autosomes et des chromosomes sexuels Xy (♂) ou XX (♀), alors que *Anoplotrupes stercorosus* (Scriba), *Geotrupes spiniger* Marsham, *Sericotrupes niger* (Marsham), *Thorectes geminatus* (Gené), *T. intermedius* (Costa), *T. lusitanicus* (Jekel) et *Trypocopris vernalis* (L.) ont tous 10 paires d'autosomes et des chromosomes sexuels Xy (♂) ou XX (♀). Les autosomes sont principalement acrocentriques chez *A. stercorosus*, *G. spiniger* et *S. niger,* avec des bandes C centromériques diversement développées qui dans certains cas constituent des bras courts hétérochromatiques, et chez *A. stercorosus* l'autosome 10 est polymorphe et peut avoir un bras court euchromatique distinct. Aucun des autosomes de *A. stercorosus* ne montre de signe de centromère médian ou submédian, contrairement à ce qu'ont suggéré COLOMBA *et al*. (2004). L'autosome 1 de *Thorectes geminatus* est métacentrique, comparable à celui de *T. punctatissimus*

(Chevrolat), mais chez *T. geminatus* les autosomes 1 et 2 sont pratiquement de même longueur alors que chez *T. punctatissimus* l'autosome 1 est d'environ une fois et demi la longueur de l'autosome 2. Les exemplaires sardes de *T. intermedius* montrent un certain polymorphisme chromosomique comparable à celui rapporté par COLOMBA *et al.* (1996) sur du matériel principalement sicilien. *T. lusitanicus* a six paires d'autosomes submétacentriques avec des bras courts hétérochromatiques alors que les quatre paires d'autosomes restants et le chromosome X sont acrocentriques. *Trypocopris vernalis* a des autosomes 1 à 8 soit métacentriques soit submétacentriques, mais le marquage en bandes C montre que chez tous ces chromosomes un bras est entièrement hétérochromatique.

Key Words.– Geotrupidae, chromosomes, polymorphism, karyotypes, C-banding, *Ceratophyus*, *Anoplotrupes*, *Geotrupes*, *Sericotrupes*, *Thorectes*, *Trypocopris*.

Introduction

WILSON and ANGUS (2004) reported chromosomal data on seven species of Geotrupidae, showing among other things that the six Geotrupini involved all had karyotypes comprising 10 pairs of mainly acrocentric autosomes and Xy sex chromosomes – with the parachute association (Xy_p) at first division of meiosis, where these data were available. In contrast, *Typhaeus typhoeus* (L.), the one species of the tribe Chromogeotrupini included in the study had only nine pairs of autosomes, of which one was a long metacentric, plus Xy_p sex chromosomes. Later, ANGUS (2005) reported a typically Geotrupine karyotype of 10 pairs of acrocentric autosomes and Xy sex chromosomes in a second Chromogeotrupine species, *T.* (*Chelotrupes*) *momus* (Olivier), so that the distinctive karyotype of *T. typhoeus* is not a character of the tribe Chromogeotrupini.

In a completely separate development, COLOMBA *et al.* (2004) described the karyotype of *Anoplotrupes stercorosus* (L.) as having five pairs of metacentric/submetacentric autosomes and five pairs of acrocentrics, in contrast to WILSON and ANGUS, who had found all 10 pairs of autosomes in this species to be acrocentric.

The present work reports the results of ongoing investigations of Geotrupid chromosomes and seeks to address the contradictory data on *A. stercorosus*.

Material and methods

The species studied, their localities of origin and the number of specimens from which successful preparations were obtained, are listed in Table 1.

The methods of chromosome preparation and curation of the beetles are as described by WILSON and ANGUS (2004), except that the photographs were scanned into a computer and karyotypes were arranged using Adobe Photoshop.

Chromosomes, and their short arms, were measured on-screen. Two calculations were used. Relative chromosome length (RCL) is the length of each chromosome expressed as a percentage of the total haploid autosome length in the nucleus. This is the procedure adopted for human chromosomes (Paris Conference, 1971). Its main function is to compensate for the different degrees of contraction shown by chromosomes in different preparations. Centromere index (CI) is the length of the short arm of a chromosome expressed as a percentage of the total length of the chromosome. Accurate measurement of CI is difficult because of problems deciding the exact centre of the centromere and the small size of the segments involved. CI may be expressed conveniently using the standard terms for centromere position. Based on SUMNER (2003) the categories are: metacentric – CI 46 – 50; submetacentric – CI 26 – 45; subacrocentric – CI 16 – 25; acrocentric – CI 3 – 15. Both RCL and CI are given as approximate data only as the samples measured were too small to allow statistical analysis.

The specimens studied are now in the Natural History Museum, London.

***Ceratophyus* Fischer**		
C. hoffmannseggi Fairmaire	SPAIN: CADIZ, Tarifa, Playa de los Lances. SALAMANCA, El Cubo de Don Sancho	2 ♂♂ 1 ♀
***Anoplotrupes* Jekel**		
A. stercorosus (Scriba)	MACEDONIA: TETOVO, Šar Planina above Lomnica. ITALY: PARMA, Corniglio. ENGLAND: HAMPSHIRE, New Forest.	1 ♂, 1 ♀ 1 ♂, 1 ♀ 1 ♀
***Geotrupes* Latreille**		
G. spiniger Marsham	ENGLAND: BUCKINGHAMSHIRE, Boveney. ITALY, SICILY: MESSINA, Parco dei Nebrodi, Muto.	3 ♂♂ 1 ♂
***Sericotrupes* Zunino**		
S. niger (Marsham)	ITALY, SARDINIA: SASSARI, Stintino. FRANCE: PAS-DE-CALAIS, Dunes du Mont Saint-Frieux.	1 ♀ 1 ♂
***Thorectes* Mulsant**		
T. (*Silphotrupes* or *Baraudia*) *geminatus* (Gené)	FRANCE, CORSICA: HAUTE-CORSE, Restonica Gorge below Lac de Melo. CORSE-DU-SUD, above Bastelica.	1 ♂ 1 ♀
T. (*Jekelius*) *intermedius* (Costa)	ITALY, SARDINIA: CAGLIARI, Giara di Gesturi. ORISTANO, Sinis. SASSARI, Stintino.	1 ♂, 2 ♀♀ 1 ♂ 1 ♂, 1 ♀
T. (*T.* s. str.) *lusitanicus* (Jekel)	SPAIN: MÀLAGA, La Sauceda.	1 ♂
***Trypocopris* Motschulsky**		
T. vernalis (L.)	MACEDONIA: TETOVO, Šar Planina above Lomnica. CZECH REPUBLIC: MORAVIA, Podyji National Park.	2 ♂♂ 1 ♀

Table 1.– Material analysed.

Results

Ceratophyus hoffmannseggi. Fig. 1 a – c. Published information: none. 2n = 14 + Xy (♂), XX (♀). This karyotype, with only seven pairs of autosomes, is unlike any other so far known from the Geotrupidae. Autosome pair 1 is metacentric, RCL about 24, while all the others are submetacentric (with modified short arms) to acrocentric, with RCLs ranging from about 17 – 9. The X chromosome is acrocentric and is the smallest in the nucleus (RCL about 5.3) apart from the dot-like y chromosome.

Anoplotrupes stercorosus. Fig. 1 d – j. Published information: 2n = 20 + Xy_p (WILSON and ANGUS, 2004), 2n = 20 + XY (COLOMBA *et al*., 2004). WILSON and ANGUS give details of C-banding and COLOMBA *et al.* give C-banding, Ag-banding, fluorochrome staining and FISH hybridisation to reveal nucleolus organisers. WILSON and ANGUS give plain and C-banded preparations from testis of a male from Helvellyn, Cumbria (England) (shown here as Fig. 1 d, e) and a plain preparation from the mid gut of a female from the Forest of Dean (England) (shown here as Fig. 1 f), as well as plain and C-banded first meioses from testis of a Helvellyn male. These preparations show all the autosomes to have one terminal C-band and no obvious indication of centromeres elsewhere on any of the chromosomes. The C-bands are rather stronger on autosomes 1, 2, 5, 8 and 9, and the y chromosome, only slightly smaller than the X, is almost entirely heterochromatic. This interpretation of the sex chromosomes is supported by the meioses shown (as Fig. 2, b, c) by WILSON and ANGUS. The C-banded preparation is repeated here as Fig. 3 b, while an unbanded metaphase I from a Macedonian specimen is shown in Fig. 3 a. The orientation and arrangement of the sex bivalent is very similar in the two preparations, confirming the interpretation of the sex chromosomes by WILSON and ANGUS. COLOMBA *et al*., on the other hand, record autosome pairs 3, 4, 5, 6 and 8 as metacentric to submetacentric, with pairs 1, 2, 7, 9 and 10 acrocentric to subtelocentric. Their C-banded preparation shows four chromosomes with heavy bands at both ends, about six with clear C-bands at one end, one chromosome with a clear submedian band and the rest indistinct. Their silver stained preparation is similar to the C-banding, but clearer, and shows the largely heterochromatic y chromosome.

In an attempt to understand these conflicting data I have investigated *A. stercorosus* from two European localities, one near Corniglio in Apennines of the Provincia di Parma (Italy) and the other near Lomnica in the Šar Planina mountains of northern Macedonia, as well as a further specimen from the New Forest, Hampshire (England), with the objective of obtaining less condensed chromosomes than were figured by WILSON and ANGUS.

Fig. 1 g, h shows a mid gut nucleus from a Corniglio male, plain and C-banded. The chromatids are very clear in most of the chromosomes, and the pattern of terminal C-bands is the same as in the Helvellyn male shown in Fig. 1 e. The chromatids appear to come together in two places in one replicate of autosome 3 (the other replicate is twisted but one of the approaches is clear), but without any clear indication of a centromere. One replicate of autosome 10 has a small short arm, absent from the other one which appears acrocentric. The terminal C-band of the acrocentric replicate is absent from the

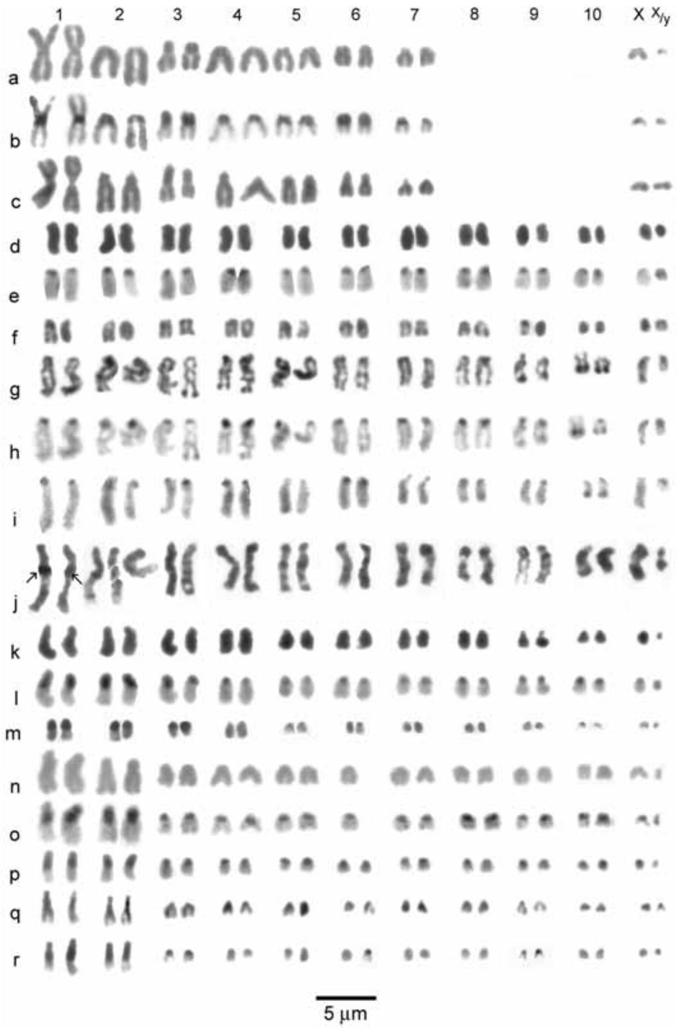

Fig. 1.– Mitotic chromosomes of Geotrupidae, arranged as karyotypes: **a**, **b**, *Ceratophyus hoffmannseggi*, ♂, mid gut, Tarifa, **a** plain, **b** the same nucleus C-banded; **c**, *C. hoffmannseggi*, ♀, mid gut, plain, El Cubo de don Sancho; **d** – **j**, *Anoplotrupes stercorosus*. **d**, **e**, ♂, testis, Helvellyn, **d** plain, **e** C-banded; **f,** ♀, mid gut, Forest of Dean, plain; **g**, **h**, ♂, mid gut, Corniglio, **g** plain, **h** the same nucleus C-banded; **i**, **j**, ♂, testis, Tetovo, **i** C-banded; **j** plain but showing chromomere banding; **d** – **f** from WILSON & ANGUS (2004). **k** – **m**, *Geotrupes spiniger*. **k**, **l**, ♂, testis, Sicily, **k** plain, **l** the same nucleus C-banded; **m** ♂, mid gut, Betteshanger, C-banded, from WILSON & ANGUS (2004). **n** – **r**, *Sericotrupes niger*. **n**, **o**, ♂, mid gut, France, one replicate of autosome 6 missing, **n** plain, **o** the same nucleus C-banded; **p**, ♂, testis, France, complete, C-banded; **q**, **r**, ♀, mid gut, Stintino, **q** plain, **r** the same nucleus C-banded.

one with the short arm, but both replicates have apparent C-bands at the end of the long arm, and in this case the two chromatids do not come together.

Fig. 1 i shows a C-banded preparation from testis of a Macedonian specimen. The C-banding is less pronounced in this specimen, reflecting difficulties with the banding process, but it does hint at the distal C-bands on autosome 10. I often find good C-banding harder to obtain in testis preparations than in those from mid gut.

Fig. 1 j shows a spermatogonial mitosis preparation from a Macedonian male in which the chromosomes are in an early stage of condensation, and show some chromomeric banding. The two replicates of autosome 1 lie across each other in this preparation and the dark section resulting from the crossover points is arrowed – it is artefact! One replicate of autosome 2 is strongly curved and is shown as found (right) and straightened out photographically (in the centre of the triplet). The chromomere banding is in places very clear and where it is present in both replicates of a chromosome the pattern is the same. However, in no case does it appear to show median or submedian centromeres.

I conclude from this work that the centromeres are all either terminal or subterminal, and that most of the C-bands are associated with the centromeres. There is some variation in the strength of the C-bands and it is quite possible that in some cases weak distal C-bands might be demonstrated.

Geotrupes spiniger. Fig. 1 k – m. Published information: 2n = 20 + Xy_p (♂), C-banding (WILSON and ANGUS, 2004). Fig. 1 k, l shows a testis preparation from a very small Sicilian specimen. This specimen has only one subapical ridge on its posterior tibia, suggesting *A. stercorosus*. However, both the chromosomes and the aedeagus confirm that it is *G. spiniger*. The chromosomes are less condensed than in the British specimen shown by WILSON and ANGUS (shown again here as Fig. 1 m), but the arrangement of the karyotype is the same. The X chromosome is clearly very much smaller than in the *G. stercorarius* (L.) shown by WILSON and ANGUS (2004, Fig. 1 k.). C-banded preparations of first metaphase of meiosis (Fig. 3) show three autosomal bivalents, one of which can be a ring, with heavy C-bands, and the other bivalents, including the Xy_p, with scarcely discernible C-bands. C-banded meiotic metaphase I from this Sicilian specimen is shown in Fig. 3 c, d. This confirms the small size of the X chromosome, and shows that one of the larger autosomal bivalents can be either a rod- or a ring bivalent.

Sericotrupes niger. Fig. 1 n – r. Published information: none. 2n = 20 + Xy. Autosomes 1 and 2, RCLs about 19 and 16, are submetacentric to subacrocentric, with heavy C-bands over the centromeres and short arms. Autosomes 3 – 10 are acrocentric with small centromeric C-bands, and their RCLs decrease evenly from about 9 to 7. The X chromosome is acrocentric, similar in size to autosome 10, and with a localised centromeric C-band. The y chromosome is about half this size, without obvious C-banding. There is no difference between the karyotypes of the French and Sardinian material.

Thorectes geminatus. Fig. 2 a – d. Published information: none. 2n = 20 + Xy. The RCLs of the autosomes decrease fairly evenly from about 14 to 7. Autosome 1 is metacentric with a heavy but discrete centromeric C-band. Autosome 2 is submetacentric-subacrocentric with a heavy centromeric C-band and the short arm also largely heterochromatic. Autosome 3 is submetacentric with a heterochromatic long arm. The remaining autosomes are more or less acrocentric with centromeric C-bands, with pairs 5 and 7 more obviously subacrocentric and with heterochromatic short arms. The acrocentric X chromosome is similar in size to autosome 10 and appears extensively heterochromatic. The y chromosome is rather smaller and metacentric with a heavy centromeric C-band.

T. geminatus is interesting in having a largely euchromatic metacentric autosome 1. In this feature it agrees with *T. punctatissimus* (Chevrolat), whose karyotype was reported by WILSON and ANGUS (2004), with the figures repeated here as Fig. 2 e, f. This karyotype is immediately different from that of *T. geminatus* in that autosome 1 is about 1.5 times as long as autosome 2, RCLs about 15 and 11. It is nevertheless worth noting that both species have been placed in the same subgenus of *Thorectes* (*Silphotrupes* Jekel), even though *T. geminatus* is now placed in its own subgenus, *Baraudia* López-Colón. It is also worth noting that some authors place the subgenera of *Thorectes* as separate genera – see BARAUD (1992) and MARTÍN-PIERA and LÓPEZ-COLÓN (2000).

Thorectes intermedius. Fig. 2 g – l. Published information: 2n = 20 +Xy, regional variation (COLOMBA *et al*., 1996), rDNA localisation (VITTURI *et al*., 1999). As reported by COLOMBA *et al*., this species shows a certain amount of chromosome polymorphism. They studied material from four Sicilian localities and one offshore Sardinian one. Some of the polymorphism is shown by the mainland Sardinian material discussed here. Autosomes 1 and 2, RCLs about 14 and 13, are submetacentric, with heterochromatic short arms. Autosome 3 may be similar to autosome 2, but in the Sinis male (Fig. 2 g, h) it is heterozygous for loss of the short arm, the acrocentric variant having a RCL of about 11. Autosome 4, RCL about 11, is subacrocentric, with a distinct heterochromatic short arm. In the Sinis male (Fig. 2 h) the C-banding is distinctly heavier in one replicate than in the other, and this asymmetry is also shown in first metaphase of meiosis (Fig. 3). Autosome 5 is acrocentric, with a strong centromeric C-band, in the Sinis male, but subacrocentric with a distinct short arm in the other material. The Stintino male (Fig. 2 j) has the short arm heterozygous for heterochromatin – uniformly heterochromatic in one replicate, euchromatic in the other one. The remaining subacrocentric material has the short arm heterochromatic. Autosome 6 is slightly shorter than autosome 5, subacrocentric with the short arm euchromatic in the Stintino preparation (Fig. 2 j), heterochromatic in the Giara di Gesturi female (Fig. 2 l), and heterozygous in the Sinis male (Fig. 2 h). Autosomes 7 – 10 are acrocentric, with centromeric C-bands, and their RCLs range from about 8 – 6. The Sinis male (Fig. 2 h) is heterozygous for the strong C-band on autosome 9. The X chromosome is smaller, RCL about 4, acrocentric with a distinct centromeric C-band. The y chromosome, RCL about 3, is the smallest in the nucleus, metacentric in material from Stintino and the Giara di Gesturi, but submetacentric in the Stintino male. Other features noted by COLOMBA *et al*. include additional C-bands

Fig. 2.– Mitotic chromosomes of Geotrupidae, arranged as karyotypes: **a** – **d**, *Thorectes geminatus*. **a**, **b**, ♂, testis, Restonica Gorge, **a** plain, **b** the same nucleus C-banded; **c**, **d**, ♀, mid gut, above Bastelica, **c** plain, **d** the same nucleus C-banded; **e**, **f**, *T. punctatissimus*, ♂, Sanabria, from WILSON & ANGUS (2004), **e** mid gut, plain, **f** testis, C-banded; **g** – **l**, *T. intermedius*. **g**, **h**, ♂, testis, Sinis, **g** plain, **h** the same nucleus C-banded; **i**, **j**, ♂, testis, Stintino, **i** plain, **j** the same nucleus C-banded; **k**, **l**, ♀, mid gut, Giara di Gesturi, **k** plain, **l** the same nucleus C-banded; **m**, **n**, *T. lusitanicus*, ♂, testis, La Sauceda, **m** plain, **n** C-banded; **o** – **r**, *Trypocopris vernalis*. **o**, **p**, ♂, mid gut, Tetovo, **o** plain, **p** the same nucleus C-banded; **q**, **r**, ♀, mid gut, Moravia, **q** plain, **r** the same nucleus C-banded; **s**, *T. pyrenaeus*, ♂, testis, Studland, C-banded, from WILSON & ANGUS (2004).

in all the autosomes. In the present material there is a faint C-band more or less in the middle of the long arm of autosome 1 in all the C-banded material, subterminal C-bands in the long arms of autosomes 2, 3 5 and 6 in the Stintino material, and in autosome 3 of the Giara di Gesturi material. These extra C-bands are rather faint and it is possible that they have not shown in other material. COLOMBA *et al.* also discussed two G-banding differences, which are not included here. G-banding in insects remains controversial and unconvincing (e.g. SUMNER, 1990), though chromomere banding, which in mammals shows the same pattern as G-banding, is known (e.g. ANGUS, 1982). Chromomere banding is shown in the undercondensed mitotic preparation from *A. stercorosus* (Fig. 1 j) but has not been observed in *T. intermedius*. Fig. 3 d shows a C-banded metaphase 1 of the Sinis male. The bivalents showing heterozygosity of the C-bands are labelled and arrowed.

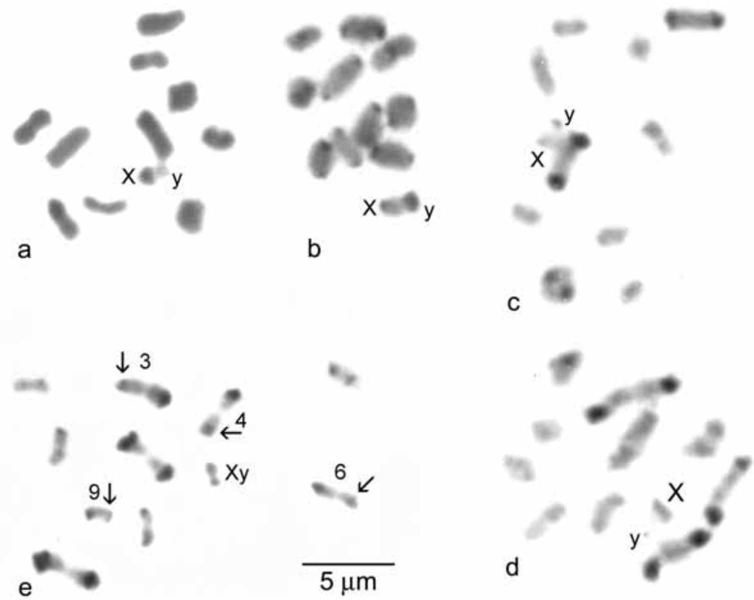

Fig. 3.– First metaphase of meiosis in Geotrupidae: **a**, **b**, *A. stercorosus*. **a**, Macedonia, plain, **b** Helvellyn, C-banded (from WILSON & ANGUS, 2004); **c**, **d**, *G. spiniger*, Sicily, C-banded, **c** showing one ring bivalent, **d** showing only rod bivalents; **e**, *T. intermedius*, Sinis, C-banded, showing the heterozygous C-banding on bivalents 3, 4, 6 and 9, with the smaller C-bands arrowed.

Thorectes lusitanicus. Fig. 2 m, n. Published information: none. 2n = 20 + Xy (♂). Autosomes 1 – 6 are submetacentric with strong C-bands extending on to their short arms. Their RCLs decrease evenly from about 14 – 10. Autosomes 7 – 10 are acrocentric, without obvious C-bands, and their RCLs range from about 8.5 – 6.5. The X chromosome is acrocentric with a distinct centromeric C-band, and RCL about 10. The y chromosome is subacrocentric without a clear centromeric C-band, and RCL about 5.5.

Trypocopris vernalis. Fig. 2 o – r. Published information: none. 2n = 20 + Xy (♂), XX (♀). Autosomes 1 – 8 are metacentric with RCLs steadily decreasing from about 13 – 10, while autosomes 9 and 10 are acrocentric and distinctly smaller, RCLs about 6 – 5. The X chromosome is acrocentric, slightly larger than autosome 10, and the y chromosome, also acrocentric, is slightly smaller than autosome10. This appears a very unusual karyotype for a Geotrupid, with so many metacentric chromosomes. C-banding reveals the true nature of the situation. In all of the metacentric chromosomes one arm is totally heterochromatic. In autosomes 1, 4, 5 and 6 the heterochromatic arm is the (slightly) shorter of the two, while in autosomes 2, 3, 7 and 8 the heterochromatic arm is slightly longer than the euchromatic one. Autosomes 9 and 10, and the X chromosome have strong centromeric C-bands, while the y chromosome appears entirely heterochromatic. A C-banded karyotype of *Trypocopris pyrenaeus* Charpentier, originally figured by WILSON and ANGUS (2004) is shown in Fig. 2 s, for comparison. Autosomes 1 – 3 are submetacentric with heterochromatic short arms which show secondary constrictions. The remaining chromosomes are acrocentric to subacrocentric and all the chromosomes have heavy centromeric C-bands. As in *T. vernalis*, the y chromosome is entirely heterochromatic.

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REFERENCES

ANGUS (R.B.), 1982.– Separation of two species standing as *Helophorus aquaticus* (L.) (Coleoptera, Hydrophilidae) by banded chromosome analysis. *Systematic Entomology*, 7: 265-281.

ANGUS (R.B.), 2005.– The karyotype of *Typhaeus momus* (Olivier, 1789) (Coleoptera, Geotrupidae). *Nouvelle Revue d'Entomologie* (N.S), 22 (2): 115-116.

BARAUD (J.), 1992.– *Coléoptères Scarabaeoidea d'Europe. Faune de France 78*. Fédération française des Sociétés de Sciences naturelles, Paris and Société linnéenne de Lyon, X + 856 pp, 11 plates.

COLOMBA (M.S.), LUZZATO (M.), VITTURI (R.) & ZUNINO (M.), 1996.– Aspetti biogeografici dell'evoluzione del cariotipo: il caso di *Thorectes intermedius* (Costa) (Coleoptera: Geotrupidae). *Biogeographia*,18 (1995): 477-484.

COLOMBA (M.S.), VITTURI (R.), VOLPE (N.), LANNINO (A.) & ZUNINO (M.), 2004.– Karyotype, banding and rDNA FISH in the scarab beetle *Anoplotrupes stercorosus* (Coleoptera Scarabaeoidea: Geotrupidae). Description and comparative analysis. *Micron*, 35 (8): 717-720.

MARTÍN-PIERA (M.) & LÓPEZ-COLÓN (J.I.), 2000.– *Coleoptera Scarabaeoidea 1. Fauna Ibérica. Vol. 14*. Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, 526 pp.

PARIS CONFERENCE, 1971.– Standardization in Human Cytogenetics. Birth Defects: Original Article Series, 8: 7, 1972. The National Foundation, New York (Reprinted in *Cytogenetics*, 11 (1972): 313-362).

SUMNER (A.T.), 1990.– *Chromosome Banding*. Unwin Hyman, London, xiv + 434 pp.

SUMNER (A.T.), 2003.– *Chromosomes: organization and function.* Blackwell Publishing, Oxford, x + 288 pp.

VITTURI (R.), COLOMBA (M.S.), BARBIERI (R.) & ZUNINO (M.), 1999.– Ribosomal DNA location in the scarab beetle *Thorectes intermedius* (Costa) (Coleoptera: Geotrupidae) using banding and fluorescent *in-situ* hybridization. *Chromosome Research*, 7 (4): 255-260.

WILSON (C.J.) & ANGUS (R.B.), 2004.– A chromosomal investigation of seven Geotrupids and two Aegialiines (Coleoptera, Scarabaeoidea). *Nouvelle Revue d'Entomologie* (N.S), 21 (2): 157-170.