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A chromosomal analysis of four European species of Aphodius ILLIGER, subgenera Colobopterus MULSANT, Coprimorphus MULSANT, Otophorus MULSANT and Teuchestes MULSANT (Coleoptera: Aphodiidae)

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Abstract

The karyotypes of *Aphodius (Colobopterus) erraticus* (L.), *A. (Coprimorphus) scrutator* (HERBST), *A. (Otophorus) haemorrhoidalis* (L.) and *A. (Teuchestes) fossor* (L.) are described and illustrated. All four species have nine pairs of autosomes and sex chromosomes which are Xy (male) and XX (female). The karyotypes of all four species are distinctive, but the sequence of relative chromosome lengths is strikingly similar in *A. erraticus* and *A. scrutator*.

Key words: Coleoptera, Scarabaeoidea, Aphodiidae, Aphodius, chromosomes, karyotypes, C-bands.

Introduction

The species included in the present study all belong to subgenera with conspicuously long scutella. At one stage (e.g. JESSOP 1986) these species were grouped together in the single subgenus (or genus) *Colobopterus* MULSANT, but nowadays they are regarded as not particularly closely related to one another. Thus DELLACASA et al. (2000) raise all the subgenera to generic rank and make no reference to relationships between particular "genera", and MATÉ (2003) places them in different parts of *Aphodius* in his DNA-based phylogeny. All four species have published information on their chromosomes, but in no case has a clear karyotype been illustrated, nor has C-banding been attempted.

Material and methods

The material used in the present study is listed in Table 1. English localities are referred to their Vice-Counties, as listed by DANDY (1969). French localities are listed by Département, using the abbreviations given by FULLARD & DARBY (1969). The British Vice-Counties from which material has been obtained are as follows: 14, East Sussex; 15, East Kent; 17, Surrey; 24, Bucks; 37, Worcester; The French Départements are: I, Indre; ML, Maine et Loire.

Species	Localities
Aphodius (Colobopterus) erraticus (L.)	England. 14: Rye; 17: Box Hill; 24: Chalfont St Giles. France. I: La Brenne; ML: Le Lion d'Angers
Aphodius (Coprimorphus) scrutator (HERBST)	France. I: La Brenne.
Aphodius (Otophorus) haemorrhoidalis (L.)	England. 17: Box Hill.
Aphodius (Teuchestes) fossor (L.)	England. 17: Runnymede, Cooper's Hill France. I: La Brenne.

Results

Subgenus Colobopterus MULSANT

Aphodius erraticus. Fig. 1a, b. Material analysed: 5 specimens. Published information: 2N = 20 (σ), 9 bivalents + Xy_p (VIRKKI 1951). $2N = 18 + Xy_p$. A very distinctive karyotype, with all the autosomes and the X chromosome more or less acrocentric, and the y chromosome small, dot-like. The RCLs of the autosomes range from about 17–5, with a sharp decrease in size between autosomes 5 and 6 (RCLs about 13 and 8). The X chromosome is about the same size as autosome 9. C-banding (Fig. 1b) shows all the autosomes and the X chromosome with heavy centromeric C-bands, and autosomes 1–8 with very short heterochromatic short arms. Autosomes 1–6 show secondary constrictions in these short arms (Fig. 1a), while autosomes 7 and 8, and the X chromosome have terminal secondary constrictions at the tips of their short arms.

Subgenus Coprimorphus MULSANT

Aphodius scrutator. Fig. 1c, d. Material analysed: 1 specimen. Published information: 2N = 20 (σ), 9 bivalents + Xy (VIRKKI 1954). 2N = 20 (φ). The sex chromosomes cannot be identified as only one female was available for analysis. However, Virkki's figure of a spermatogonial metaphase (VIRKKI 1954: Fig. 1) shows a dot-like y chromosome and one rod-like chromosome rather smaller than all the others, suggesting that the X chromosome may be smaller than the autosomes. It therefore seems possible that the chromosome placed as pair 10 in Fig. 1c, d is the X chromosome range from about 17 to 5, with a sharp decrease between autosome 5 (RCL about 12) and autosome 6 (RCL about 9). Chromosomes 1–5 are metacentric or submetacentric, pairs 6, 7, 9, and 10 are subacrocentric to almost acrocentric, and pair 8 is acrocentric. C-banding (Fig. 1d) shows distinct centromeric C-bands on all the chromosomes.

Subgenus Otophorus MULSANT

Aphodius haemorrhoidalis. Fig. 1e–g. Material analysed: 7 specimens; Published information: 9 bivalents + Xy (σ), (VIRKKI 1951). 2N = 18 + Xy. The RCLs of the autosomes range from about 15–7, and the X chromosome (RCL about 12) is similar in size to autosomes 2 and 3. The y chromosome is a small acrocentric, RCL about 3. Autosomes 1 and 3–9 are more or less metacentric, while autosome 2 and the X chromosome are submetacentric, with the long arm about twice the length of the short arm. C-banding (Fig. 1f) shows autosomes 1, 2 and 8, and the X chromosome to have long heterochromatic arms, while autosomes 3 and 5 have secondary constrictions in their long arms, which may also appear somewhat darker. Autosomes 3, 4, 6 and 7, and the y chromosome, have distinct localised centromeric C-bands.

Subgenus Teuchestes MULSANT

Aphodius fossor. Fig. 1h–j. Material analysed: 3 specimens. Published information: 2N = 20 (σ), 9 + Xy (VIRKKI 1951). 2N = 18 + Xy. The RCLs of the autosomes range from about 18–7, and the X chromosome (RCL about 6.5) is slightly smaller than autosome 9. The y chromosome is very small, dot-like. Autosomes 1–4 are more or less metacentric, 6 and 7 are submetacentric, and the remaining autosomes and the X chromosome are more or less subacrocentric. C-banding (Fig. 1i, j) shows all the autosomes with strong but localised centromeric C-bands. The centromeric C-band of the X chromosome is more diffuse and the y chromosome appears to be at least mainly heterochromatic.

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Fig. 1: Mitotic chromosomes of subgenera *Colobopterus*, *Coprimorphus*, *Otophorus* and *Teuchestes*; a) *Aphodius* (*Colobopterus*) erraticus, φ , mid-gut, Staines Moor; b) *A. erraticus*, ϑ , mid-gut, La Brenne, Cbanded; c, d) *A.*(*Coprimorphus*) scrutator, φ , mid-gut, La Brenne, c: plain, d: C-banded, from the same specimen; e) *A.* (*Otophorus*) haemorrhoidalis, ϑ , mid-gut, Box Hill; f) *A. haemorrhoidalis*, ϑ , mid-gut, Box hill, C-banded; g) *A. haemorrhoidalis*, φ , mid-gut, Box Hill; h, i) *A. (Teuchestes) fossor*, ϑ , mid-gut, Cooper's Hill, a: plain, b: C-banded, from the same specimen; j) *A. fossor*, φ , mid-gut, La Brenne, Cbanded.

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Discussion

Aphodius (Colobopterus) erraticus has a very distinctive karyotype. Not only is it the only *Aphodius* included in the present study in which all the chromosomes (except the dot-like y chromosome) are more or less acrocentric, but it is the only one of the 44 species whose karyotypes were illustrated by WILSON (2002) with this arrangement. The other striking feature of the karyotype is the rather abrupt decrease in size between autosomes 5 and 6. *Aphodius (Coprimorphus) scrutator* has a karyotype showing both obvious differences from that of *A. erraticus* (autosomes 1–5 are metacentric or submetacentric), and also a strange similarity in the abrupt decrease in size between autosomes 5 and 6, and the sequence of RCLs along the karyotype. In both species the C-bands are moderate and localised near the centromere.

Species of the subgenera *Colobopterus* and *Coprimorphus* have not only the long scutellum, but also a rather flattened, almost *Onthophagus*-like body form. Whether or not this body form and the similarities of the karyotypes of the species studied here have phylogenetic significance must remain a question.

Aphodius (Teuchestes) fossor and A. (Otophorus) haemorrhoidalis, while agreeing with the previous species in having a long scutellum, are very different in body form, being cylindrical. Their karyotypes are also quite unlike those of A. erraticus and A. scrutator, and also clearly different from one another, especially as regards the C-banding, which is confined to the centromere regions in A. fossor, but extends along the long arms of four pairs of autosomes and the X chromosome in A. haemorrhoidalis. There is at present no suggestion that either of these subgenera is particularly closely related to Colobopterus and Coprimorphus, or that they are closely related to one another.

The DNA phylogeny of MATÉ (2003) does not place any of these subgenera as a closely knit unit, but tends to place *Coprimorphus* and *Teuchestes* along with *Aphodius* s.str., in one section of *Aphodius*, *Otophorus* in a different one, and *Colobopterus* in an even more different area of the genus. The DNA phylogeny of Iberian Aphodiini by CABRERO-SAÑUDO & ZARDOYA (2004) is based on a far smaller number of species and includes only *A*. (*Colobopterus*) erraticus of the species studied here, so is of limited use. However, it places *A. erraticus* near *A*. (*Calamosternus*) granarius (L.) and far from subgenus *Aphodius* s.str., and in both these placements it agrees with the Maté's work. It does seem, from these studies that the similarity of the karyotypes of *A. erraticus* and *A. scrutator* probably does not have phylogenetic significance. This is in line with the general pattern of chromosome data revealed by WILSON'S (2002) studies: karyotype information often reveals clear differences between species, including sibling species (WILSON 2001), but without obvious karyotype-groups associated with subgenera (WILSON & ANGUS 2003, 2004a, b; ANGUS et al. 2004).

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