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APHODIUS PEDELLUS (DEGEER), A SPECIES DISTINCT FROM *A. FIMETARIUS* (LINNAEUS) (COLEOPTERA: APHODIIDAE)

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Aphodius pedellus (DeGeer), currently listed as the oldest synonym of *A. fimetarius* (Linnaeus), is shown to have a karyotype consistently different from that of *A. fimetarius* and it is therefore regarded as a separate species. No examples of hybrid karyotypes have been observed even though the two species frequently occur together. Morphological analysis of specimens with known karyotypes has shown that the two species can be separated by details of the endophallus and head shape of males, and the pronotal punctation of females. The type series of *Scarabaeus fimetarius* Linnaeus and *S. pedellus* DeGeer have been studied and identified on the basis of the morphological features associated with the two karyotypes. Lectotypes have been designated, confirming the usage of *Aphodius fimetarius* (L.) and *A. pedellus* (DeGeer) adopted in this paper.

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In the course of a survey of the chromosomes of scarabaeoid dung beetles at present being carried out as a research programme for a Ph.D. degree, two completely different karyotypes were discovered in English material clearly referable to *Aphodius fimetarius* (Linnaeus) on current taxonomic treatments (e.g. Baraud 1992). Study of material with known karyotypes has revealed small morphological differences between beetles with the two karyotypes. Study of the type series of *Scarabaeus fimetarius* in Linnaeus's collection, and of DeGeer's types of *Scarabaeus pedellus*, borrowed from the Riksmuseum, Stockholm, has shown that the two karyotypes refer to these two species. *Scarabaeus pedellus* DeGeer is the oldest synonym of *A. fimetarius* listed by Dellacasa (1988) and is therefore the valid name for the second species.

Material and methods

The material used for chromosome analysis is shown in table 1. It comprised 62 *A. fimetarius* (35 males and 27 females) and 34 *A. pedellus* (16 males and 18 females). English localities are listed by Vice-County (Dandy 1969), while French localities are listed by Département and the Dutch and Cyprus localities are listed by Province and District. Additional dead material in the collections of the Natural History Museum, London and R. B. Angus (Egham) has been examined to gain some idea of the distributions of the two species.

Chromosome preparations were obtained from mid-gut and testis cells of living adults, following the methods described by Angus (1982) and Shaarawi & Angus (1991). Treatment in both colchicine and hypotonic potassium chloride was for 12.5 min. C-banding was performed on 2-day old slides, using a 7-minute treatment with saturated barium hydroxide at room temperature (ca 23°C) followed by 1 hour in salt-sodium citrate (2x SSC) at 60°C.

Endophalli of males were inflated using the technique described by Angus et al. (2000). With *Aphodius* species this technique is only possible if the endophallus is partly everted as a result of colchicine injection of the beetles. All the beetles were card mounted and kept as entomological specimens.

Results

Chromosomes

Karyotypes of the two species are shown in figs. 1-9. In both species there are nine pairs of autosomes and

Table 1. Material used for chromosomal analysis.

Locality	Species
England	
V.C. 9 Dorset: Purbeck	*A. fimetarius*
	A. pedellus
V.C. 9 Dorset: Arne	*A. pedellus*
V.C.11 South Hants: New Forest, Bolderwood Hill	*A. fimetarius*
	A. pedellus
V.C.11 South Hants: Romsey	*A. fimetarius*
V.C. 13 West Sussex: Singleton	*A. fimetarius*
	A. pedellus
V.C. 14 East Sussex: Rye	*A. fimetarius*
V.C. 16 East Kent: Betteshanger	*A. fimetarius*
V.C. 16 East Kent: Deal	*A. fimetarius*
V.C. 17 Surrey: Runnymede	*A. pedellus*
V.C. 19 Middlesex: Staines Moor	*A. pedellus*
V.C. 22 Berks: Old Windsor	*A. fimetarius*
	A. pedellus
V.C. 24 Bucks: Boveney	*A. fimetarius*
V.C. 37 Worcester: Wyre Forest	*A. pedellus*
France	
Indre: La Brenne	*A. fimetarius*
	A. pedellus
Indre et Loire: Souvigné	*A. fimetarius*
Loire et Maine: Le Lion d'Angers	*A. pedellus*
Netherlands	
Zuid-Holland: Leidschendam, Vlietland	*A. fimetarius*
Cyprus	
Paphos District: Kholetria	*A. fimetarius*

the sex chromosomes are Xy (male), XX (female). The karyotype of *A. fimetarius* is characterised by the long heterochromatic regions in autosome 2 and the X chromosome following C-banding treatment (fig. 3), and by the absence of any almost acrocentric chromosomes. In unbanded preparations (figs 1, 2) the heterochromatic parts of the chromosome arms lie closely applied to one another. The X chromosome, with a relative length of about 15, is as long as the longest autosome pair. No chromosomal variation has been detected in *A. fimetarius*. The karyotype of *A. pedellus* (figs. 4-9) is characterised by a complete absence of long heterochromatic regions as well as the presence of three pairs of small chromosomes (autosome pairs 8 and 9, and the X chromosome), which appear almost acrocentric. There are two chromosome polymorphisms in this species. Chromosome 5 may have a pericentric inversion polymorphism. In one form the centromere index (the length of the short chromosome arm as a percentage of the total length of the chromosome) is about 30, while in the other it is about 20. The difference is clearly visible in heterozygotes (figs. 6, 7). Heterozygotes have been found at Purbeck and in the Wyre Forest, but all other material has been homozygous for the form with the longer short arms. The other polymorphism involves the occurrence of a B chromosome (figs. 8, 9). This has been found in material from Purbeck and Arne, and up to two B chromosomes have been found. The B chromosomes are clearly different from all the normal chromosomes present in the *A. pedellus* karyotype, and are also unlike any *A. fimetarius* chromosome.

The two karyotypes are very distinctive and hence easily recognised, even if only partial karyotypes are present. The number of distinctive chromosomes present in both species means that any hybrid karyotypes would be easy to detect. In fact, none has been found, even in samples where the two species were collected together.

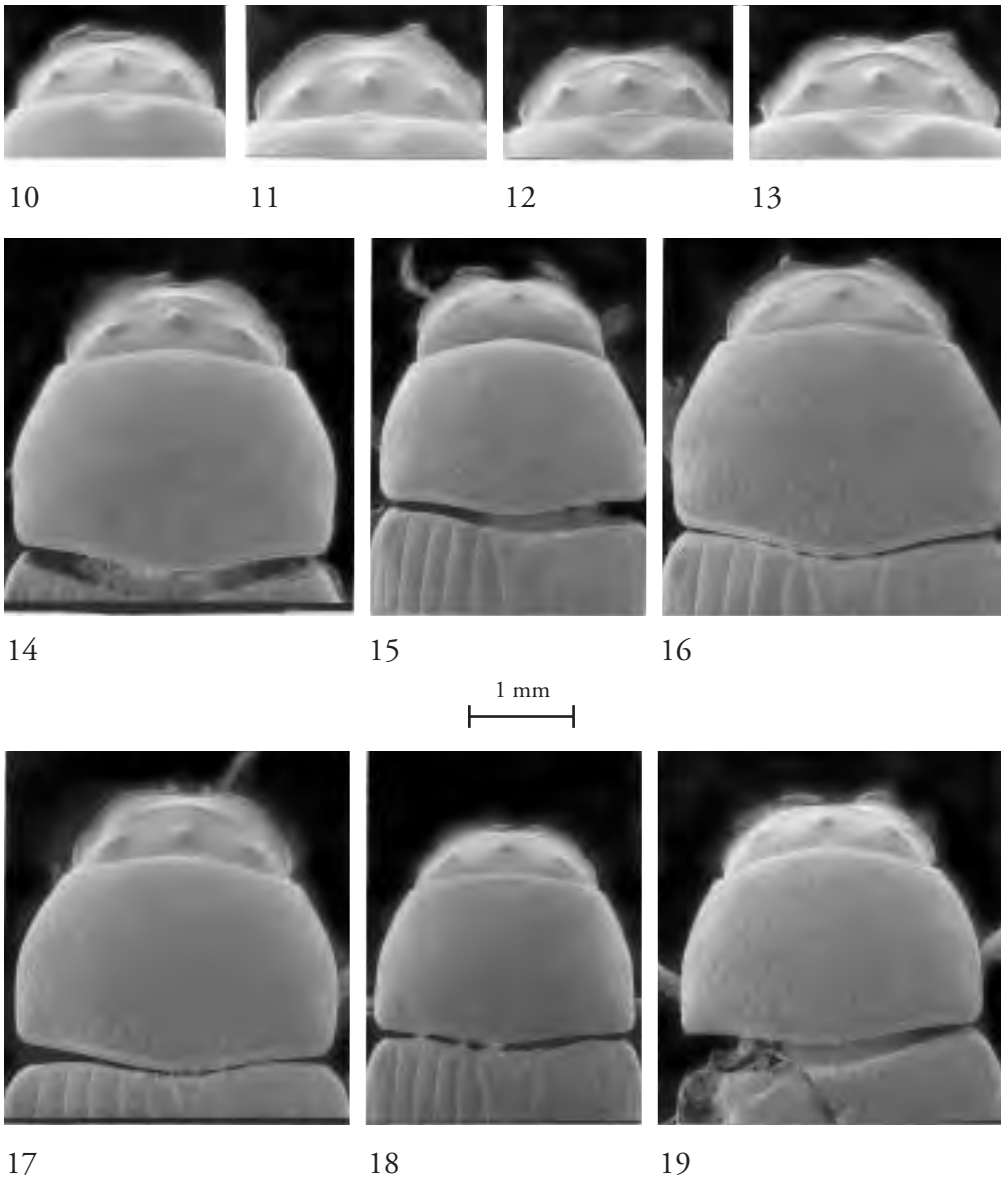
Morphology

Study of specimens with known karyotypes has revealed characters enabling most material to be identified. The shape of the head in males and the pronotal punctation in females allow identification of most specimens. Details of the inflated endophallus of males appear to give a completely reliable separation of the two species.

Figs. 10-13 show the heads of males of the two species. Fig. 10 shows an *A. fimetarius* with the minimum development of the lateral lobes of the clypeus, while fig. 11 shows the maximum development. Figs. 12 and 13 show the range of development of the lobes found in *A. pedellus*. In practice there is very little overlap in the development of the lobes in the two species. Male *A. fimetarius* generally have the lobes feebly developed and very seldom have the posterior part of the lobes divergent – normally they are parallel to one another. In *A. pedellus* the lobes are more pronounced with the posterior part always clearly divergent. The lateral lobes of females are more variable so that although there is a tendency for them to be more pronounced in *A. pedellus*, there is significant overlap in their form in the two species.

Figs. 14-16 show the range of development of the pronotal punctation in female *A. fimetarius*, while figs. 17-19 show the range in *A. pedellus*. Most *A. fimetarius* have the punctation sparser than in *A. pedellus*, the arrangement in most specimens being between the conditions shown in figs. 14 and 16, with the clear areas either side of the disc generally larger than in fig. 16. There is often a somewhat irregular double row of punctures on the disc. Although there is some variation in the extent of the pronotal punctation in *A. pedellus*, this is generally dense and does not normally involve clear areas either side of the disc (compare figs. 16 and 17). However, there are occasional specimens which cannot be iden-

Figs. 1-9. Mitotic chromosomes from mid-gut cells of *Aphodius*. – 1-3, *A. fimetarius:* 1, male from Purbeck, unbanded; 2, female from Rye, unbanded; 3, male from Deal, C-banded. – 4-9, *A. pedellus:* 4, male from Purbeck, unbanded; 5, male from the New Forest, C-banded; 6, female from the Wyre Forest, unbanded and with chromosome 5 heterozygous for a pericentric inversion; 7, C-banded preparation from the same specimen as fig. 6; 8, female from Purbeck, unbanded and with 1 B chromosome; 9, C-banded preparation from the same specimen as fig. 8.



Figs. 10-19. *Aphodius fimetarius* and *A. pedellus*. – 10-13, heads of males: 10, 11, *A. fimetarius* from Deal, showing minimum and maximum development of the lateral lobes; 12, *A. pedellus* from Arne, with minimum development of the lateral lobes; 13, *A. pedellus* from the New Forest, with maximum development of the lateral lobes. 14-19, heads and pronota of females. 14-16, *A. fimetarius*: 14, from the Brenne, with minimal punctation; 15 from Singleton &16 from the New Forest, with maximum punctation. 17-19, *A. pedellus:* 17 from the New Forest & 18 from the Brenne, with minimal punctation; 19, from Staines Moor, with maximum punctation.

tified on this character (figs. 15 and 18). The pronotal punctation in males of both species is variable and does not help in identification.

Aedeagophores with inflated endophalli of both species are shown in figs. 20-23. Inflation is difficult and this means that any possible differences in the apical section of the endophallus cannot be assessed reliably. In some specimens, especially of *A. fimetarius*, the inflated endophallus bends back below the aedeagophore, but this may be the result of disruption of the internal duct caused by insertion of the glass microelectrode. Such bending of the endophallus has not been observed in other *Aphodius* species. The endophallus of *A. fimetarius* appears consistently wider than that of *A. pedellus*, and this is associated with a difference in the basal part of the darkened sclerotised strut which lies on the dorsal surface of the proximal part of the endophallus. In *A. fimetarius* the morphologically left side of the strut becomes separated from the main (right hand) part and stops at the level of the paramere tips, while the main part continues basally between the parameres. The photograph (fig. 21) shows this clearly, while the scanning electron micrograph (fig. 20) shows the general shape. In *A. pedellus*, although the micrograph shows the left side of the strut becoming separated basally, it extends between the parameres, like the main section. The photograph (fig. 23) shows that the basal portion of the strut becomes paler medially, with both sides darker. This is easily seen and appears to be a reliable character for separating the species, when the endophallus can be inflated.

The characters used in separation of the species may be summarised as follows:

1. **Males**. Endophallus of aedeagus with right hand part of dorsal strut of basal section extending basally between the parameres (fig. 21). Head with lateral lobes of the clypeus generally less pronounced, their outer margins parallel basally (figs. 10, 11). **Females**. Coarse punctation of pronotum less well developed, often almost absent over most of the disc (fig. 14), or with distinct impunctate areas either side of mid line on disc (fig. 16) .....*A. fimetarius*
– **Males**. Endophallus with both sides of dorsal strut of basal section becoming less distinct at level of paramere tips (fig. 23), and a distinct pale area medially at this level. Head with lateral lobes of clypeus generally more pronounced, their outer margins divergent basally (figs 12, 13). **Females**. Coarse punctation of pronotum more strongly developed, with at most some thinning of the punctation over disc, and without distinct impunctate areas (figs 17, 19) .....*A. pedellus*

Types and Taxonomy

Aphodius fimetarius is among the insects which Linnaeus (1758) included in the 10th edition of his Systema Naturae, and thus dates from the start of binominal nomenclature. Linnaeus described the species as *Scarabaeus fimetarius*, and stated that it has red elytra ('elytris rubris'). He described it as inhabiting the dungheaps of Europe. He also referred to an earlier, prebinominal, description in his Fauna Suecica, so presumably some at least of his material must have come from Sweden. After his description of *S. fimetarius* he added a description of a variety β with grey elytra ('elytris griseis'). This form was considered by DeGeer (1774) and Fourcroy (1785) to be the true *S. fimetarius*, and both authors described the species with red elytra under new names.

Scarabaeus fimetarius Linnaeus

Linnaeus's collection, held by the Linnean Society in Burlington House, London, contains six specimens, all with red elytra, arranged in two rows, standing as *Scarabaeus fimetarius*. There is no material with pale fawn ('griseus') elytra, nor any labelled as form β. The top row consists of three females, all on identical pins, pinned through an unnumbered hand-written name label '*fimetarius*', written with a fairly broad nib. A printed label with the number 32 (the number given to *S. fimetarius* in the 12th edition of Systema Naturae) has been placed under the name label. The second row consists of two unlabelled males and one female with a hand-written label 'Angl. Jones', in a different handwriting from the name label. This is not a Linnaean specimen and was presumably added by Smith after he brought Linnaeus's collection to London. Of the unlabelled males, one is on a similar pin to the females in the top row, while the other is on a finer pin. The present arrangement of the Linnaean beetles dates from 1979 (M. Fitton, pers. comm.). It replaces the arrangement done by A. G. Gabriel in 1929, an arrangement which carefully preserved the arrangement done by J. E. Smith after he purchased Linnaeus's collection (Day and Fitton 1978). Photographs of the collection taken by Dr W. H. T. Tams (a previous curator) in the early 1940's show the same three females pinned through the *fimetarius* name label, and the two males standing immediately to the right of it, with the one on the finer pin next to the label. The British specimen stands, pinned through its own label, immediately to the left of the *fimetarius* name label. According to Lindroth (1957) Linnaeus arranged his collection according to the 10th edition of the Systema Naturae, and wrote the numbers used in that edition on the name labels. This would give *S. fimetarius* the number 22. Angus (1970) showed that in at least some cases (*Silpha aquatica* L.) unnumbered labels in broad handwriting were older

20 21 22 23

Figs. 20-23. Aedeagi with inflated endophalli. – 20, scanning electron micrograph & 21, photograph of the same *A. fimetarius* from Deal; 22, scanning electron micrograph & 23, photograph of the same *A. pedellus* from the New Forest. Scale 1 mm.

than the numbered ones in fine handwriting, and in any event, the majority of the name labels with the Linnaean beetles lack these numbers. Mikkola and Honey (1993) discussed various pins in the Linnaean collection, and described the original Linnaean pins in some detail. These are long pins used for larger insects, and not found through most of the smaller beetles. Mikkola and Honey refer to these pins as probably being associated with the more than 400 specimens Linnaeus had accumulated by the autumn of 1730. They then refer to 'pins of variable appearance but belonging to the original Linnaean collection' associated with later material. The pins through the five specimens lacking locality data are not of the British pattern and all seem likely to be genuinely Linnaean. Mikkola and Honey (1993) concluded from their study of the collection that the material added by Smith was carefully labelled, and that the authenticity of the apparent Linnean specimens was more reliable than Lindroth (1957) had supposed. M. Honey (pers. comm.) has examined the material standing as *Scarabaeus fimetarius*, and noted that one female and the two males are pinned obliquely, with the pin inserted through the right elytron, while the other two females have the pin inserted vertically through the left elytron. He commented that oblique pinning was very frequent, though not universal, in the Linnaean Noctuidae (Lepidoptera). The five specimens mentioned include both the species discussed in this paper. The female at the right hand end of the top row has the pronotal punctation very reduced, as in the female shown in fig. 14. It is the most distinctive specimen in the series and is here designated Lectotype. It is 7.8 mm long, and is the specimen pinned obliquely. It has been labelled as the lectotype of *Scarabaeus fimetarius* L. and as *Aphodius fimetarius* (L.). This lectotype designation fixes the identity of *Aphodius fimetarius* as the species whose karyotype is shown in figs 1-3. The other two females, paralectotypes, include one with the pronotum rather more punctate, as fig. 16, conspecific with the lectotype, and one with the punctation more as in fig. 17. This may be *A. pedellus* DeGeer. All three females have the lateral lobes of the clypeus weak. The male on the same type of pin as the females has the clypeal lobes strong, intermediate between the males shown in figs 12 and 13. It is *A. pedellus*. The male on the finer pin has weak clypeal lobes and is *A. fimetarius*.

Scarabaeus pedellus DeGeer

DeGeer's material of *S. pedellus* consists of three specimens, mounted on identical short pins. Two, a male and a female are pinned through the pronotum, while the third, a female, is pinned through the left elytron. All have the clypeal lobes well developed, and both females have extensive pronotal punctation. All are conspecific and are not the same species as the lectotype of *S. fimetarius* L. The female pinned through the left elytron is here designated Lectotype as it is the most distinctive specimen. The pronotal punctation is similar to that of the specimen shown in fig. 17, and there are no areas clear of punctation. The specimen is 6.5 mm long. It has been labelled as the lectotype of *Scarabaeus pedellus* DeGeer, and as *Aphodius pedellus* (DeGeer). The other two specimens are paralectotypes. The lectotype fixes the identity of *Aphodius pedellus* DeGeer as the species whose karyotype is shown in figs. 4-9.

Distribution and Ecology

The detailed distributions of the two species remain to be worked out and are not part of the present research. The British material so far studied suggests that *A. fimetarius* is the principal species (possibly the only species) present in extreme south-east England. As yet no differences in the ecologies of the two species have been detected, and they occurred together at Singleton (West Sussex), on the Isle of Purbeck (Dorset) and in the Brenne region of France. The only published figures of the chromosomes of either species are by Virkki (1951), who worked on Finnish material. Virkki's drawing of spermatogonial metaphase is hard to interpret, but his statement that the X chromosome is one of the smaller ones suggests that his material was *A. pedellus*. It seems likely that *A. pedellus* is the more widely distributed species. Thus a single male from the Irkutsk district of eastern Siberia (coll. R. B. Angus) has very strongly developed clypeal lobes and appears to be good *A. pedellus*, and a preliminary check of North American material in the Natural History Museum, London, suggests that it is all *A. pedellus*. According to Baraud (1992) the species is introduced in North America and Australia. Identification of the Australian species must await study of suitable material.

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