

# Revision of the Afrotropical dung beetle genus *Sarophorus* Erichson (Coleoptera: Scarabaeidae)

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The genus *Sarophorus* Erichson is revised. Six new species, *S. bidentatus*, *S. punctatus*, *S. carinatus*, *S. striatus*, *S. latus* and *S. nitidus*, are described. A key to the species is given. Two species-groups are established.

**Key words:** *Sarophorus*, new species, species-groups, key, distribution, southern Africa.

## INTRODUCTION

*Sarophorus* Erichson is a small genus of 'tunneling' dung beetles distributed mainly in southern Africa. It shares a few apparently synapomorphic characters with *Coptorhina* Hope and *Delopeurus* Erichson and is usually placed in the tribe Dichotomiini (Cambeftor, 1991). The validity of this tribe has, however, recently been questioned (Montreuil, 1998).

The genus *Sarophorus* was erected by Erichson (1847) for *Pedaria tuberculata* Castelnau on the grounds of the elytra being sinuate laterally near the base as opposed to being straight in *Pedaria*. Subsequently, three more species originally described in *Pedaria* Castelnau were also placed in this genus: *P. cicatricosa* Péringuey, *P. setulosa* Brancsik (Boucomont 1922) and *P. costata* Fähræus in Boheman (Janssens 1939). Recently we had the opportunity to examine the type of *P. setulosa*, housed in the Field Museum, Chicago. This species was incorrectly transferred to *Sarophorus* and actually belongs to *Pedaria*. Consequently, the genus *Sarophorus* contained three described species up to now.

The genera *Sarophorus* and *Pedaria* are superficially similar and are often confused in collections. Péringuey (1901) commented that the situation of the elytra was variable in the three *Sarophorus* species known to him (*S. tuberculatus*, *S. costatus* and *S. cicatricosus*), hence he considered *Pedaria* and *Sarophorus* to be congeneric. However, the two genera differ strongly in a number of characters apart from the situation of elytra (Table 1).

Large numbers of *Sarophorus* specimens have been collected in the past few decades and are deposited in South African and European museums. During examination of this material new species were found which are described below.

Institutions in which studied material and types are deposited are listed below together with the curators in charge of the collections: AMSA: Albany Museum, Grahamstown, South Africa; F. Gess; BMNH: British Museum (Natural History), London, Great Britain, M. Kerley; MRAC: Musée Royal de l'Afrique Centrale, Tervuren, Belgium, M. De Meyer; SANC: National Collection of Insects, Plant Protection Research Institute, Pretoria, South Africa, R. Stals; SAMC: South African Museum, Cape Town, South Africa, M. Cochrane; TMSA: Transvaal Museum, Pretoria, South Africa: R. Müller, J. Harrison.

## Genus *Sarophorus* Erichson

*Sarophorus* Erichson, 1847: 761. Type species: *S. tuberculatus* (Castelnau 1840: *Pedaria*), by monotypy.

*Pedaria*: Péringuey, 1901: 277.

## Description

Medium-sized beetles (6–10 mm). Colour monotonous black to dark brown without metallic tint; anterior part of clypeus, legs or elytra sometimes slightly paler. Surface of body densely punctate, in some species most of pronotum rugose. Each puncture, except for that of elytral striae, bears a short yellowish seta. Setae sometimes abraded on disc of pronotum and head.

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**Table 1.** Characters to separate *Sarophorus* and *Pedaria* (cf. Figs 1–6).

Character	<i>Sarophorus</i>	<i>Pedaria</i>
Gular plate	With longitudinal groove	Without longitudinal groove
Eyes	Small: distance between eye and gula approximately twice the width of eye in ventral view	Large: distance between eye and gula approximately half the width of eye in ventral view
Genae	More protruding past eyes	Less protruding past eyes
Body shape	Somewhat rectangular	Sub-oval
Abdominal sternites	All sternites visible on disc	Sternite 6 widened and approaching metacoxae
Metacoxae	Separated from epipleura by abdominal sternite 1	Contiguous to epipleura
Lateral margins of elytra	More or less sinuate in basal part	Straight in basal part
Metepisterna	Widened, with convex lateral margin	Slender, with straight or slightly concave lateral margin
Parameres	Symmetrical	Asymmetrical

Clypeus sinuate in middle, rounded to angulate at sides (anterior angles of clypeus strongly protruding and curved upwards in *S. bidentatus* sp. n.). In some species anterior angles of clypeus with short carina directed proximally. Genae obtuse. Frontoclypeal and genal sutures indistinct in most species. Head without horns or tubercles. Eyes small, their dorsal part slit-shaped, ventral part sub-rectangular. Distance between eye and gula approximately twice width of eye in ventral view. Gula with longitudinal groove.

Sides of pronotum more or less parallel, width greater than length. Apical margin not bordered, membranous. Lateral margins with or without border. Base of pronotum not bordered, or only indistinctly bordered with a row of punctures.

Elytra not fused, with humeral umbones, sinuate laterally near base. Elytral intervals flat to convex in apical part, with tubercles in some species. Striae with carinate margins. Scutellum not visible from above. Wings fully developed.

Anterior tibiae with three outer teeth. Anterior tibial spur usually acute and curved downwards. Outer margins of middle and posterior tibiae without transverse keels, serrate in some species. Apices of middle and posterior tibiae densely, regularly or irregularly setose.

Pygidium densely punctate on disc, bordered, with small longitudinal keel in some species.

Parameres symmetrical, their apices strongly to weakly sclerotized, without setae, dorsoventrally depressed in most species. Armature of internal

sac of aedeagus varying among species.

*Sexual dimorphism* apparent in three characters: 1) shape of anterior tibial spur (more strongly curved inwards and downwards in males), 2) setation of apices of middle tibiae (denser in males), and 3) sculpture of clypeus (anterior part more sparsely punctate, usually shiny in females and as coarsely punctate as remaining part of clypeus, usually covered with indument in males). Characters 1 and 2 may occur in the same species.

*Diagnostic characters of Sarophorus.* Shape of the parameres and the armature of the internal sac of the aedeagus are highly specific and should be considered as the most important diagnostic species characters. Other characters include the sculpture of the pronotum and elytra, shape of the clypeus and the anterior tibial spur, as well as the shape and setation of the apices of the middle tibiae.

*Biology.* Although the genus is broadly classed as a tunneling dung beetle, the little information available on its biology rather indicates a feeding preference for very old dung or carrion remains which may imply detritus as a preferred food rather than dung. The largest known series (*S. costatus*, 81 specimens) was collected by J. Harrison in a thin soil layer under an old, dry horse carcass. Beetles can fly but are rarely attracted to light. The preimaginal stages are unknown.

The examined species of *Sarophorus* constitute two distinct species-groups:

1. *tuberculatus* species-group: *S. tuberculatus*, *S. punctatus* sp. n., *S. carinatus* sp. n. and *S. bidentatus*

sp. n. belong to this group. The group is characterized by the following characters: 1) elytral intervals, especially intervals 3, 5 and 7, tuberculate; 2) pygidium with small longitudinal carina; 3) metepisterna relatively narrow with aspect ratio c. 1:2.5 (Fig. 43); 4) internal sac of aedeagus finely granulate, without armature.

*S. bidentatus* sp. n., known from only a single male specimen, is provisionally placed in this species-group on the basis of tuberculate elytral intervals and proportions of metepisterna. However, it differs from other members of the group in a number of characters, especially in the absence of concavities on the base of the propleurae and the internal sac of the aedeagus being armed with asymmetrical sclerites. The shape of the clypeus and apices of the middle tibiae may be characters of sexual dimorphism. Additional material is needed to clarify the position of this species.

2. *costatus* species-group: *S. costatus*, *S. cicatricosus*, *S. striatus* sp. n., *S. latus* sp. n. and *S. nitidus* sp. n. are placed in this group. Species of this group are characterized by the following characters: 1) elytral intervals more or less densely punctate but not tuberculate; 2) pygidium without longitudinal carina; 3) metepisterna relatively wide with an aspect ratio of c. 1:2.0 (Fig. 44); 4) internal sac of aedeagus armed with symmetrically located spinules.

**Key to species of *Sarophorus***

- 1. Elytral intervals with more or less developed tubercles, sometimes carinate, with indistinct punctures (Figs 7, 8, 14, 16) ..... (*tuberculatus* species-group) 2
- Elytral intervals punctate, without tubercles (Figs 15, 19–22) ..... (*costatus* species-group) 5
- 2. Elytral intervals carinate (Fig. 16). Pygidium deeply foveate laterally of medial carina (Fig. 18) ..... *S. carinatus* sp. n. (♀)
- Elytral intervals with oval tubercles (Figs 7, 8, 14). Pygidium less foveate at sides of medial carina (Fig. 17) ..... 3
- 3. Pronotum with smooth, elevated areas (Figs 7, 8) ..... 4
- Pronotum densely punctate to rugose, without smooth areas (Fig. 14) ... *S. punctatus* sp. n.
- 4. Clypeus with protruding anterior angles (Fig. 9). Concavities on base of propleura absent (Fig. 13). Apex of middle tibiae with a bunch of setae (Fig. 26) ... *S. bidentatus* sp. n. (♂)

- Clypeus with angulate, not protruding anterior angles (Fig. 10). Base of propleura with concavities (Fig. 12). Apex of middle tibiae regularly setose (Fig. 11) ..... *S. tuberculatus* (Castelnaud)
- 5. Pronotum coarsely and irregularly punctate, with sub-symmetrically located, more sparsely punctate areas (Fig. 15) ..... *S. cicatricosus* (Péringuey)
- Pronotum more finely, regularly punctate (Fig. 19–22) ..... 6
- 6. Anterior angles of clypeus angulate. Middle tibiae with relatively sparse apical setae in both sexes. Elytra strongly shiny (Fig. 22) ..... *S. nitidus* sp. n.
- Anterior angles of clypeus rounded. Middle tibiae with denser apical setae in males (Fig. 25). Elytra matt in most specimens. .... 7
- 7. Elytral intervals more sparsely punctate on disc (punctures separated by a puncture diameter). Apices of parameres with rounded lateral margins in dorsal view (Fig. 32) ..... *S. striatus* sp. n.
- Elytral intervals more densely punctate on disc (punctures separated by 0.5 puncture diameter). Parameres of different shape (Figs 30, 31) ..... 8
- 8. Body wider (Fig. 20). Apices of parameres wider, weakly sclerotized (Fig. 31) ..... *S. latus* sp. n.
- Body narrower (Fig. 19). Apices of parameres narrower, strongly sclerotized (Fig. 30) ..... *S. costatus* (Fähræus in Boheman)

***tuberculatus* species-group**

***Sarophorus tuberculatus*** (Castelnaud), Figs 7, 10–12, 27, 45  
*Pedaria tuberculata* Castelnaud, 1840: 88.  
*Sarophorus tuberculatus*: Erichson, 1847: 761;  
 Ferreira, 1969: 338.

**Diagnosis**

This species is most similar to *S. punctatus* sp. n. differing from it by the smooth areas on the pronotum and the shape of parameres.

**Description**

Upper side of body black, legs slightly paler. Body length 6.0–8.5 mm.  
*Male* (Fig. 7). *Head*. Anterior margin of clypeus slightly sinuate and flattened medially, anterior

angles angulate, with small keels (Fig. 10). Genae obtuse, separated from clypeal margin by distinct sinuation. Anterior and lateral margins of head with fine border. Frontoclypeal and genal sutures indistinct. Dorsal surface regularly and densely punctate with almost adjoining punctures.

*Pronotum.* Margins not bordered. Surface very densely punctate in posterior part and rugose on disc and in anterior part. Surface usually with 16 irregular, smooth areas distributed sub-symmetrically.

*Elytra.* Sutural intervals 3, 5 and 7 with small rounded tubercles on disc and each with elongated tubercle at base. Intervals 6 and 8 with elongated tubercles at apex. Interval 9 with a row of partly fused tubercles. Intervals indistinctly punctate. Striae with carinate margins, indistinctly punctate.

*Venter.* Base of propleura with small concavities for apices of retracted middle femora (Fig. 12). Disc of pygidium densely punctate and pubescent, with small longitudinal carina from middle of basal margin to middle of disc. Abdominal and prothoracic sternites regularly, coarsely punctate. Disc of metasternum concave. Mesosternum with two small convex areas.

*Legs.* Spur of anterior tibia curved downwards. Apices of middle and posterior tibiae with relatively sparse, unequal setae (Fig. 11).

*Aedeagus.* Apices of parameres rounded in lateral aspect (Fig. 27). Internal sac finely granulate, without armature (Fig. 35).

*Female* differs from male in having anterior part of clypeus smooth and shiny.

*Material examined.* 99 specimens. SOUTH AFRICA: *Eastern Cape Province:* Algoa Bay, Brauns., 1 spm. (SAMC), 2 spm. (TMSA); Hogsback, 1978, 1 spm., C. Scholtz (UPSA). *Western Cape Province:* Ysterfontein, 16 spm. (SAMC); 8 km W of Ysterfontein, 33°15'S 18°11'E, 28.viii.1983, groundtraps, 70 days, 1 spm., Endrödy-Younga and Penrith (TMSA); Saldanha, ix.1912, 37 spm. (SAMC); 8 km NW of Ysterfontein, Farm Blombos, 5.ix.1978, 7 spm., Aschenborn (SANC); Geelbek, 4.ix.1979, 3 spm., Davis (SANC); Velddrif, 17.x.1971, 2 spm., Bornemissza, Kirk (SANC); 33 km NW Port Alfred, 30.viii.1977, 1 spm., Davis (SANC); 23 km S of Avontuur, 4.v.1976, 1 spm., Davis, Aschenborn leg. (SANC); 12 km SE of Langebaan, Farm Geelbek, 7.IX.1979, 5 spm., Davis (SANC); Rust en Vrede, Oudtshoorn Distr., x.1951, 14 spm. (SAMC); Bo Kouga, Uniondale Distr., iii.1954, 1 spm. (SAMC); Darling, 1905, 2 spm., L. Péringuey (SAMC);

Swartberge Hagas Farm, 33°24'S 22°46'E, 2.iii.1979, sandy valley, 1 spm., S. Endrödy-Younga (TMSA); Somerset, i.1884, 3 spm. (SAMC); Little Karoo, Raubenheimer Dam, 33°25'S 22°19'E, 21.x.1993, donkey dung, 2 spm., S. Endrödy-Younga (TMSA).

***Sarophorus punctatus* sp. n.**, Figs 14, 17, 29, 36, 45

#### *Diagnosis*

This species is most similar to *S. tuberculatus* but differs from it in having the pronotum without smooth areas and in the widened and depressed apices of parameres.

#### *Description*

*Male holotype* (Fig. 14). Upper side of body black, legs and lateral parts of head slightly paler. Body length 7.2 mm.

*Head.* Anterior margin of clypeus sinuate medially, anterior angles obtuse. Genae obtuse, separated from clypeal margin by weak sinuation. Anterior and lateral margins of head with very fine border. Frontoclypeal and genal sutures indistinct. Dorsal surface regularly, coarsely punctate with adjoining punctures.

*Pronotum.* Lateral margins with fine border in posterior part. Surface mostly rugose, coarsely punctate near base, with sub-symmetrically located tubercles; some lateral tubercles cariniform.

*Elytra.* Sutural intervals convex. Intervals 3, 5, 7 and 9 with elongated tubercles. Intervals 6 and 8 with elongated tubercles at base and apex. Intervals indistinctly punctate. Striae 1–3 more or less distinctly punctate in posterior half, with carinate margins. Punctuation of other striae indistinct.

*Venter.* Base of propleura with concavities for apices of retracted middle femora. Disc of pygidium densely, regularly punctate and pubescent, with short carina near middle of basal margin (Fig. 17). Abdominal and prothoracic sternites coarsely and almost regularly punctate. Disc of metasternum concave. Mesosternum with two small convex areas.

*Legs.* Spurs of anterior tibiae very short, with rounded apex. Apices of middle and posterior tibiae with relatively sparse, unequal setae.

*Aedeagus.* Parameres with strongly sclerotized, widened and flattened apices (Fig. 29). Internal sac granulate, without armature (Fig. 36).

*Female* differs from male in having anterior part of clypeus smooth and shiny.

*Paratypes*. Body length 7.0–7.5 mm.

*Type material*. 8 specimens. Holotype ♂: SOUTH AFRICA, *Western Cape Province*, Keurboomstrand, 34°00'S 23°27'E, 8.xii.1976, groundtraps, 8 days, S. Endrödy-Younga. 7 paratypes (1♂, 6 ♀) with the same data. Type material is deposited in TMSA.

***Sarophorus bidentatus* sp. n.**, Figs 8, 9, 13, 26, 28, 37, 45

#### *Diagnosis*

This species can be separated from other *Sarophorus* species by the protruding anterior angles of the clypeus with relatively long setae on the dorsal surface, the absence of the concavities on the base of the propleura, the bunch of apical setae on the ventral side of the middle tibia, and the internal sac of the aedeagus being armed with asymmetrical sclerites.

#### *Description*

*Male holotype* (Fig. 8). Upper side of body dark brown, pubescent with short, yellowish setae. Body length 7.5 mm.

*Head*. Anterior angles of clypeus strongly protruding and curved upwards (Fig. 9), with long setae on dorsal side. Genae auriculate, separated from clypeal margin by sinuation. Frontoclypeal suture absent. Dorsal surface regularly and densely punctate with almost adjoining punctures.

*Pronotum*. Margins not bordered. Surface very densely punctate (punctures longitudinally elongated on anterior part), with 14 small, elevated, smooth areas located sub-symmetrically.

*Elytra*. Sutural intervals convex. Intervals 3, 5 and 7 with small, elongated tubercles on disc and base. Intervals 6 and 8 with elongated tubercles at base and apex. Interval 9 with a row of partly fused tubercles. Striae with carinate margins, punctate.

*Venter*. Base of propleura without concavities for apices of retracted middle femora (Fig. 13). Disc of pygidium densely punctate and pubescent. Abdominal and prothoracic sternites almost regularly, coarsely punctate. Disc of metasternum concave.

*Legs*. Spur of anterior tibia short and slightly curved downwards. Apices of middle tibiae irregularly setose, with bunch of setae in the middle of ventral side (Fig. 26).

*Aedeagus*. Apices of parameres rounded in lateral aspect. Base of parameres with distinct angle in

lateral aspect (Fig. 28). Internal sac armed with asymmetrical sclerites (Fig. 37).

*Type material*. Holotype ♂: SOUTH AFRICA, *Northern Cape Province*, Namaqualand, Kamieskroon, 30°12'S 17°56'E, ix.1930 (SAMC).

***Sarophorus carinatus* sp. n.**, Figs 16, 18, 45

#### *Diagnosis*

This species is similar to *S. tuberculatus* and *S. punctatus* sp. n. but differs from them by having the elytra with cariniform tubercles, and a pygidium that is deeply foveate on each side of the middle carina.

#### *Description*

*Female holotype* (Fig. 16). Upper side of body dark brown, elytra and legs slightly paler. Body length 6.2 mm.

*Head*. Anterior margin of clypeus sinuate medially and angulate laterally. Genae rounded, separated from clypeal margin by distinct sinuation. Anterior and lateral margins of head with very fine border. Frontoclypeal suture absent. Anterior part of clypeus smooth, remaining part of head regularly punctate with adjoining punctures.

*Pronotum*. Lateral margins with fine border, anterior margin and base not bordered. Surface irregularly and coarsely punctate with punctures becoming larger towards base of pronotum. Punctures on disc more or less round, elongated on sides. Pronotum with 17 elevated, irregular, smooth areas sub-symmetrically located, including one near anterior margin.

*Elytra*. Sutural intervals convex. Intervals 3, 5, 7 and 9 with long, cariniform tubercles on disc. Intervals 6 and 8 with shorter tubercles at base and apex. Intervals indistinctly punctate. Striae with carinate margins, punctate in apical part.

*Venter*. Base of propleura with feebly visible concavities for apices of retracted middle femora. Disc of pygidium coarsely punctate, with strong carina almost reaching apical border, deeply foveate on each side of the carina (Fig. 18). Abdominal and prothoracic sternites with almost regular, coarse punctation.

*Legs*. Spur of anterior tibia short and slightly curved downwards. Apices of middle and posterior tibiae with relatively sparse, unequal setae.

*Type material*. Holotype ♀: SOUTH AFRICA, *Mpumalanga*, Lydenburg Distr., Ohrigstad, 24°45'S 30°34'E, iii.1962, humus, N. Leleup (TMSA).

**costatus species-group*****Sarophorus costatus*** (Fähræus in Boheman),  
Figs 19, 30, 38, 45*Pedaria costata* Fähræus in Boheman, 1857: 204.*Sarophorus costatus*: Janssens, 1939: 11, 12;  
Ferreira, 1969: 338.**Diagnosis**

This species is most similar to *S. striatus* sp. n. and *S. latus* sp. n. but differs from the first in having more coarsely punctate elytral intervals and striae, the presence of a keel at the apex of the elytra and parameres with angulate lateral margins. It differs from the second species in its narrower body, the lateral margins of the pronotum being not bordered, and the presence of narrower, strongly sclerotized apices of the parameres.

**Description**

Upper side of body black, legs slightly paler. Body length 7.0–10.0 mm.

*Male* (Fig. 19). *Head*. Anterior margin of clypeus sinuate medially, anterior angles rounded. Genae obtuse. Anterior and lateral margins of clypeus with very fine border. Frontoclypeal and genal sutures indistinct. Dorsal surface regularly and densely punctate (punctures separated by 0.5–0.3 puncture diameter).

*Pronotum*. Anterior angles with fine border, other margins not bordered. Surface densely punctate with almost adjoining punctures.

*Elytra*. Intervals flat on disc, becoming slightly convex toward apex, coarsely punctate with almost adjoining punctures. Striae shiny, with carinate margins (each stria appears as three fine lines), punctate (punctures separated by 2–3 puncture diameters). Intervals 5–7 fused at apex, forming a distinct keel.

*Venter*. Base of propleura with concavities for apices of retracted middle femora. Disc of pygidium densely punctate. Sixth abdominal sternite sparsely punctate on disc and more densely at sides. Sternites 2–5 punctate, with a row of punctures along anterior margin on disc and regularly punctate with almost adjoining punctures at sides. Disc of metasternum concave and coarsely punctate (punctures separated by 0.5 puncture diameter).

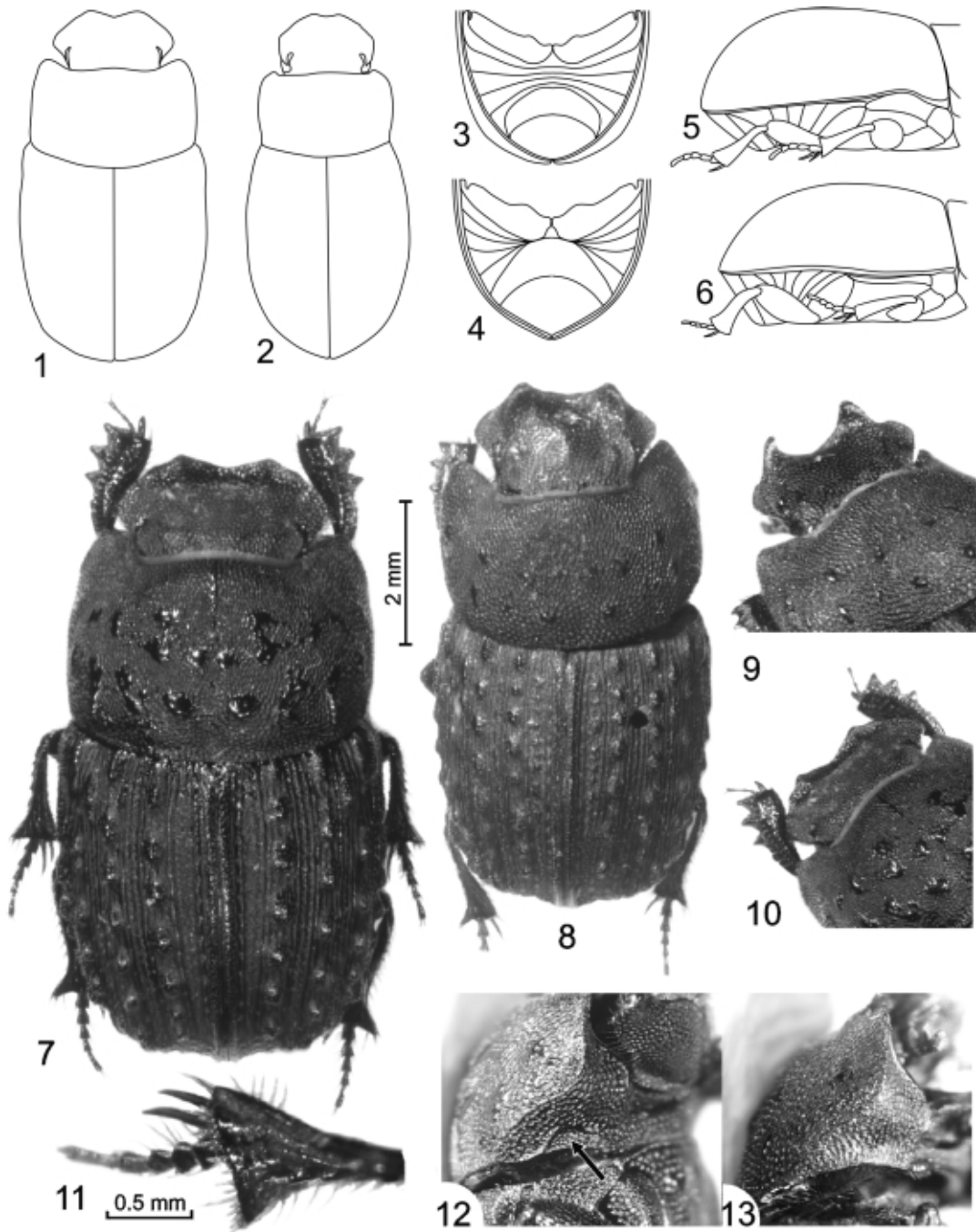
*Legs*. Spur of anterior tibia strongly curved downwards and inwards. Apices of middle and posterior tibiae with dense, unequal setae.

*Aedeagus*. Apices of parameres flattened and widened, their lateral margins angulate in dorsal view (Fig. 30). Internal sac of aedeagus armed with symmetrically located spinules (Fig. 38).

*Female* can be separated from male by anterior tibial spur not curved inwards and by sparsely setose apices of middle and posterior tibiae.

*Material examined*. 283 specimens. SOUTH AFRICA: Limpopo Province: 15 km E Louis Trichardt, Farm Welgevonden, 15–17.i.1995, horse carcass, 81 spm., J. Harrison (TMSA); Amatola, Scott farm, 22°56'S 29°23'E, 26.i.1998, dung, 1 spm., R. Müller (TMSA); Blouberg, 3–5.i.1955, 5 spm. (TMSA); Blyderiver Canyon, 24°35'S 30°49'E, 5.v.1981, groundtrap with faeces, 1 spm., sifted gallery forest litter, 1 spm., S. Endrödy-Younga (TMSA); Guernsey, 24°29'S 31°06'E, 12–26.xii.1985, 3 spm., C. Scholtz (UPSA); Happy Rest Nature Reserve, 23°02'S 29°40'E, 1–5.iv.1976, from under stones, 1 spm., Proz.-Schulze (TMSA); Klaserie, x.1981, 1 spm., E. Holm (UPSA); Kruger NP, Nwash-tsumbe, 22°47'S 31°17'E, 5.ii.1994, buffalo dung, 2 spm., S. Endrödy-Younga (TMSA); Kruger NP, Punda Maria sands, 22°38'S 30°59'E, 11.ii.1994, elephant dung, 3 spm., S. Endrödy-Younga (TMSA); Letaba, 1978, 1 spm., C. Scholtz (UPSA); Messina, Hart's farm, 21.x.1978, 4 spm., C.R. Owen (TMSA); Mmafete, 24°11'S 30°06'E, 28.xi.1985, 6 spm., A. Evans and C. Bellamy (UPSA); Sand River Mt, 24°32'S 27°39'E, 18–19.xii.1985, 1 spm., C. Bellamy and D. d'Hotman (UPSA); Zoutpansberg Distr., Thabina, 13.xi.1905, 1 spm., C. Swierstra (TMSA); Waterberg, 1898–99, 1 spm., V. Jutrzencka (TMSA); Waterberg, Farm 223, 24°11'S 27°50'E, 11.ii.1976, groundtraps, 3 spm., UV light, 7 spm., A. Strydom (TMSA); Wildtuin, 22°55'S 31°26'E, 25.iv.1989, 1 spm., L. Le Roux (UPSA); 10 km W of Magoebas-kloof, 23°46'S 29°57'E, 10.ii.1971, 1 spm., Bornemissza, Ascherborn (SANC); 15 km SW of Kuruman, 27°30'S 23°17'E, 19.xii.1975, 5 spm., Ascherborn (SANC); 30 km SE of Phalaborwa, 24°04'S 30°55'E, 17.i.1973, 2 spm., Davis (SANC); 4 km NW of Mandadzidzi, Kruger National Park, 22°41'S 31°09'E, 25.iii.1977, 1 spm., Cambefort, Davis (SANC); Mkluhlu, Kruger National Park, 24°59'S 31°46'E, 8.iii.1972, 1 spm., Kirk (SANC); Numbi Gate, Kruger National Park, 25°08'S 31°19'E, 4.ii.1971, 3 spm., Bornemissza (SANC); 42 km E of Pietersburg, 23°56'S 29°53'E, 18.i.1973, 2 spm., Davis (SANC); 6 km W of Wylies Poort, 22°53'S 29°52'E, 18.iii.1972, 1 spm., Kirk (SANC); Ben Alberts Nature Reserve, Thabazimbi, 24°37'S

- 27°23'E, 24–28.xi.1980, 3 spm., van Tonder (SANC); Mogol Nature Reserve, Ellisras Distr., 23°58'S 27°45'E, 19–23.xi.1979, 10 spm., van Tonder (SANC). *Nort West Province*: 30 km SE of Zeerust, ii.1970, 7 spm., L. Schulze and R. Jones (TMSA); 9 km NE of Zeerust, 25°31'S 26°09'E, 27.ii.1973, 1 spm., Bornemissza, Temby (SANC); Harte, 25°45'S 27°55'E, 11.iii.1995, 1 spm., D. de Beer (UPSA); Potchefstroom, iv.1903, 2 spm. (TMSA); Rustenburg, 12.iv.1936, 1 spm.; 27.ii.1999, 1 spm., A. Wagemaker (UPSA); 22 km W of Rustenburg, 25°38'S 27°02'E, 9.i.1973, 1 spm., Davis (SANC); Saartjiesnek, 25°46'S 27°54'E, xii.1985, 2 spm., E. Holm (UPSA); Schoemansville, xii.1932, 1 spm., G. Kobrow (TMSA); Kalkheuveld, x.1908, 2 spm., C. Swierstra (TMSA); Castle Gorge, 66 km W of Pretoria, 25°45'S 27°33'E, 02.i.1970, 4 spm., Bornemissza (SANC). *Gauteng*: Boekenhoutskloof, 25°33'S 28°29'E, 25.iii.1994, blesbok skin, 11 spm., J. Harrison (TMSA); Boekenhoutskloof, 30 km NE of Pretoria, 5.xi.1976, 10 spm., Stickler (SANC); 15 km W of Rust de Winter, 25°19'S 28°28'E, 10.ii.1973, 1 spm., Bornemissza (SANC); Hartebeespoort Dam, 25°44'S 27°51'E, 25.i.1971, 1 spm., Bornemissza (SANC); Ditholo, 25°29'S 28°16'E, 2.iii.1996, 1 spm., A. Schoeman (UPSA); Mdala, 25°14'S 28°52'E, 14.xii.1997, 1 spm., C. Sole (UPSA); Meyerton, 1–7.xii.1957, 1 spm., J. Heyns (TMSA); Pretoria, x.1949, 1 spm., G. van Son (TMSA); Soutpan, Pretoria, 25°25'S 28°05'E, 8.ii.1973, cow dung, 1 spm., S. Endrödy-Younga (TMSA); Vereniging, 26°43'S 28°67'E, 1.iii.1997, 1 spm., I. Russo (UPSA); Wagendrift, 25°31'S 28°32'E, 26.ii.1990, 1 spm., J. Warrens (UPSA); 5 km S of Soutpan, Pretoria, 3.ii.1968, 2 spm., L. and R. Jones (TMSA); Johannesburg, x.1934, 1 spm., G. Kobrow (TMSA). *Mpumalanga*: 18 km S of Nelspruit, 25°37'S 30°58'E, 30.xi.1986, groundtrap with faeces, 53 days, 1 spm., S. Endrödy-Younga (TMSA); 20 km W of Nelspruit, 25°25'S 30°47'E, 31.x.1972, 1 spm., Davis (SANC); De Kuilen, Lydenburg Distr., 25°10'S 30°32'E, 12.ii.1981, 5 spm., Moolman, Harrop (SANC); Mahushe Shongwe Nature Reserve, near Mzinti, 25°45'S 31°44'E, 4–5.ii.1995, 41 spm., Chown, Stals, Browne (SANC); 20 km NE of Skukuza, 24°53'S 31°45'E, 3.xi.1984, 2 spm., C. Scholtz (UPSA); Kaapmuiden, 5.iv.1983, 1 spm., S. Chown (UPSA); Kruger NP, 1 km NW of Skukuza, 24°59'S 31°37'E, 22.i.1995, groundtraps with faeces, 1 spm., S. Endrödy-Younga and Ch. Bellamy (TMSA); Kruger NP, Pumbe sands, 24°13'S 31°56'E, 24.i.1995, groundtraps with faeces, 1 spm., S. Endrödy-Younga and Ch. Bellamy (TMSA); Loskop Nature Reserve, 4.iii.1995, 1 spm., E. Westhuizen (UPSA); Loskopdam, 25°25'S 29°20'E, 3.iii.1995, 2 spm., A. Nel (UPSA); Lydenburg, 1896, 1 spm., P. A. Krantz (TMSA); Nascott Game Reserve, 25°54'S 29°40'E, 3.iii.1986, groundtrap with faeces, 45 days, 1 spm., G. du Plessis (TMSA); Nelspruit Distr., Farm de Hoop, 20–21.xi.1972, 1 spm., A. Strydom (TMSA); Nelspruit Nature Reserve, Koppie, 25°29'S 30°55'E, 29.xi.1986, groundtraps with meat and faeces, 13 spm., S. Endrödy-Younga (TMSA); Pretoriuskop, 25°10'S 31°16'E, 3.xii.1984, 1 spm., C. Scholtz (UPSA); Watervalriverpass, 24°54'S 30°21'E, 5–6.xi.1980, cattle dung, 4 spm., S. Endrödy-Younga (TMSA); Waterval-Onder, 22.xi.1910, 1 spm., A. Janse (TMSA). *Free State*: Cornelia, 28°47'S 27°16'E, 17.iii.1987, 2 spm., S. Gothe (UPSA). *KwaZulu-Natal*: Gwaliweni, Ingwavuma Distr., 7–14.iv.1961, 1 spm., D.W. Rorke (TMSA); Hluhluwe, xii.1960, 12 spm., G. van Son (TMSA); Hluhluwe Game Reserve, 28°05'S 32°05'E, 19–28.xi.1992, buffalo dung, 46 spm., S. Endrödy-Younga (TMSA); Hluhluwe, 28°01'S 32°17'E, 1–7.x.1970, 1 spm., Bornemissza, Ascherborn (SANC); Mkuzi, iv.1950, 2 spm., Koch (TMSA); Mkuze Game Reserve, Msinga Hide, 27°39'S 32°14'E, 27.iii.1972, 1 spm., Olsen (SANC); Ndumu, 7.i.1971, 16 spm., de Moor (TMSA); Ndumu Game Reserve, 26°54'S 32°17'E, 1.xii.1992, white rhino dung, 1 spm., S. Endrödy-Younga (TMSA); Ndumu, xii.1960, 2 spm., G. van Son (TMSA); Ndumu Game Reserve, 26°53'S 32°16'E, 9.x.1972, 2 spm., Olsen (SANC); New Hanover, xii.1954, 1 spm., M. B. Bayer (TMSA); Pietermaritzburg, x.1956, 1 spm., M. C. Rees (TMSA); Umfolozi Game Reserve, 28°03'S 31°32'E, 6.iv.1974, cattle dung, 8 spm., S. Endrödy-Younga (TMSA); Umfolozi, 28°29'S 32°10'E, 1–7.x.1970, 10 spm., Bornemissza, Ascherborn (SANC); Umgeni Valley, 27.IV.1959, 1 spm., C. Dickson (TMSA); 1 km E of Jozini, 27°25'S 32°05'E, 15.x.1978, 2 spm., Bornemissza, Ascherborn (SANC); 5 km SE of Kokstad, 30°34'S 29°27'E, 18.i.1976, 1 spm., Dewhurst (SANC). *Northern Cape Province*: Smythe Farm, near Olifantshoek, 27°53'S 22°55'E, x.1992, 8 spm., Steenkamp (SANC). *Eastern Cape Province*: Dwesa, settlement, 32°15'S 28°49'E, 25.ii.1985, horse dung, 1 spm., S. Endrödy-Younga (TMSA); Ntsubane Forest Station, 31°27'S 29°44'E, 25.xi.1987, cattle dung, forest, 1 spm., S. Endrödy-Younga (TMSA); Port St John's, Silaka Bay, 31°33'S 29°30'E, 2.xii.1987, UV light, 7 spm., S. Endrödy-



**Figs 1–13.** 1, 3, 5, *Sarophorus* sp.; 2, 4, 6, *Pedaria* sp.; 7, 10–12, *S. tuberculatus*, male; 8, 9, 13, *S. bidentatus*, holotype male. 1, 2, body shape; 3, 4, abdomen in ventral view; 5, 6, pterothorax and abdomen in lateral view; 7, 8, general view; 9, 10, head and pronotum; 11, apex of middle tibia; 12, 13, prothorax in lateral view (concavity for apices of retracted middle tibia in 12 indicated by an arrow).



Younga (TMSA); 16 km E of Mount Frere, 30°51'S 29°06'E, 9.xi.1974, 1 spm., Temby (SANC). ZIMBABWE: Bulawayo, 30.i.1928, 1 spm., R. Stevenson (TMSA); 40 mi W of Birchenough Bridge, 19°58'S 32°20'E, 4.i.1972, 1 spm., Bornemissza, Kirk (SANC); Kyle Game Reserve, 20°11'S 31°01'E, 2.i.1972, 2 spm., Bornemissza, Kirk (SANC). BOTSWANA: 4 km N of Lobatsi, 14.iv.1973, 2 spm., Davis (SANC).

***Sarophorus cicatricosus* (Péringuey), Figs 15, 34, 41, 45**

*Pedaria cicatricosa* Péringuey, 1901: 280, 281.

*Sarophorus cicatricosus*: Boucomont, 1922: 490. Ferreira, 1969: 338.

**Diagnosis**

This species can be separated from similar species (*S. costatus*, *S. striatus* sp. n., *S. latus* sp. n. and *S. nitidus* sp. n.) by the irregularly punctate pronotum with sparsely punctate, slightly elevated areas and by the apices of the parameres being rounded in lateral aspect.

**Description**

Upper side of body black, legs slightly paler. Body length 7.5–8.0 mm.

*Male* (Fig. 15). *Head*. Anterior margin of clypeus deeply and triangularly sinuate, anterior angles angulate. Genae obtuse. Anterior and lateral margins of clypeus with very fine border. Frontoclypeal and genal sutures indistinct. Dorsal surface regularly and densely punctate with adjacent punctures.

*Pronotum*. Anterior angles with fine border, other margins not bordered. Surface densely and irregularly punctate, with a few feebly elevated sparsely punctate areas.

*Elytra*. Intervals almost flat on disc becoming slightly convex toward apex, coarsely punctate with almost adjoining punctures. Striae with carinate margins, punctate (punctures separated by 2–4 puncture diameters). Intervals 5–7 fused at apex, forming a keel.

*Venter*. Base of propleura with concavities for apices of retracted middle femora. Disc of pygidium densely punctate. Abdominal sternites densely and regularly punctate. Disc of metasternum concave and coarsely punctate with adjoining punctures.

*Legs*. Spur of anterior tibia short and strongly curved downwards. Apices of middle and poste-

rior tibiae with relatively sparse, unequal setae. The holotype has the right anterior tibia with bifurcated spur. Although indicated as diagnostic for this species in the original description, this character is abnormal; spur of left tibia is not bifurcated, of typical shape for the genus.

*Aedeagus*. Apices of parameres weakly sclerotized, rounded in lateral aspect (Fig. 34). Internal sac with fine, sub-symmetrically distributed spinules (Fig. 41).

*Female* unknown.

*Type material examined*. We could not find an exemplar labelled as the type of the *P. cicatricosa* in SAMC, where it was deposited according to Péringuey (1901), but we found two specimens labelled 'Mashunaland, Salisbury [Harare: ZIMBABWE], G.A. Marshall, 1894' [printed], 'Pedaria vulnerata typ, 1897[?]' [Péringuey's handwriting]. The name 'vulnerata' has never been published in combination with either *Pedaria* or *Sarophorus*. Because the two specimens agree very well with the description and originate from the type locality of *S. cicatricosus* we suspect that these two specimens are the only available types of this species. The holotype was not properly designated in the publication, but it can be inferred from the text that the description was largely based on the specimen with an abnormally bifurcated spur of the anterior tibia. This specimen should be considered as the holotype. The paratype comprises anterior (head and pronotum) and posterior parts from two individuals that differ considerably in size.

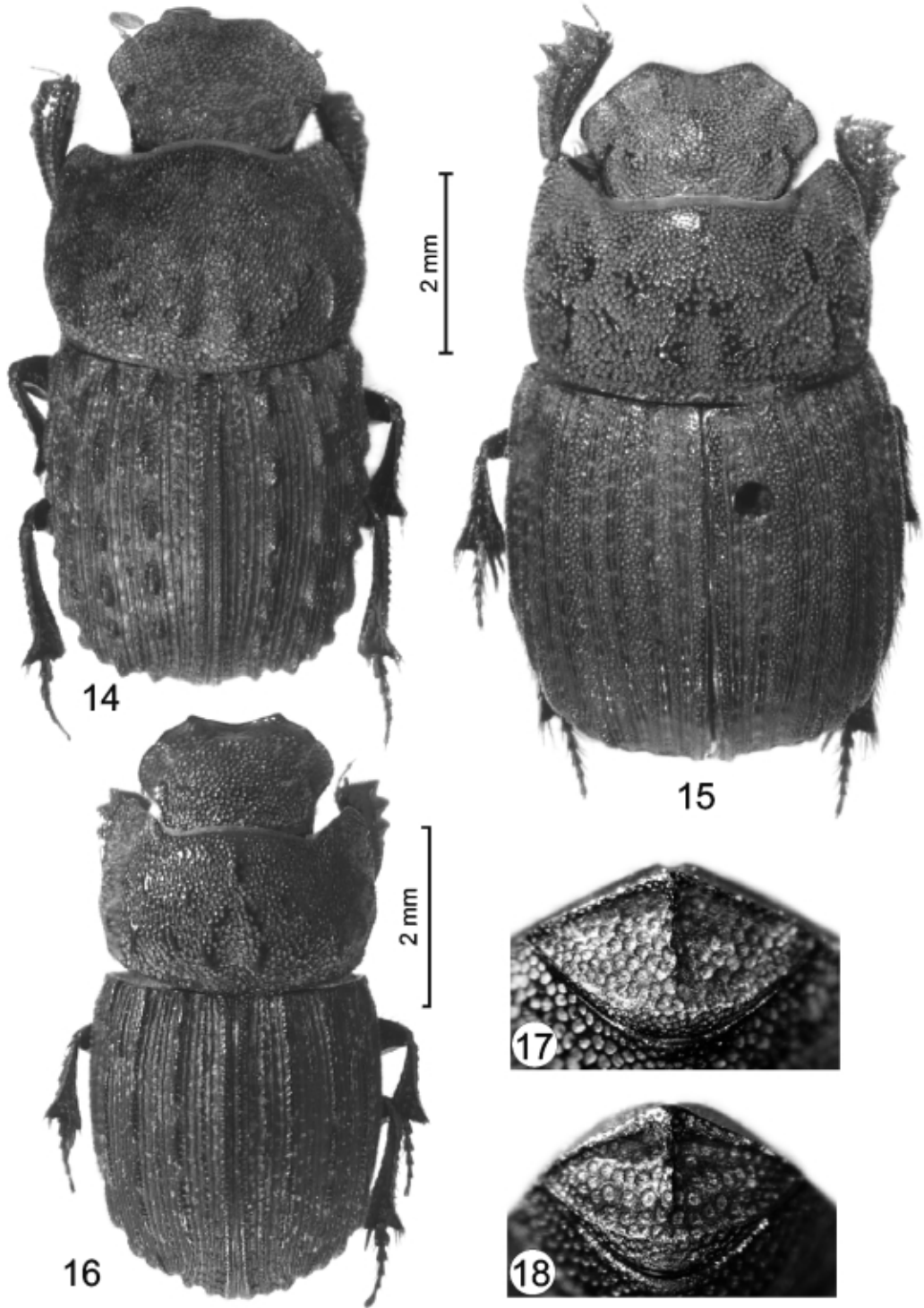
*Additional material examined*. 12 specimens. ZIMBABWE: Harare, xi.1897, 2 spm., i.1091, 7 spm., Marshall (BMNH); Matopo Mountains, i.1903, 1 spm. (BMNH). ZAMBIA: Serenje District, 12.xii.1907, 1 spm. (BMNH). DEMOCRATIC REPUBLIC OF CONGO: Kundelungus [mountains?], 10°0'S 28°0'E, Mme Tinant, 1 spm. (MRAC).

***Sarophorus nitidus* sp. n., Figs 22, 33, 39, 45**

*Sarophorus cicatricosus*: Balthasar 1960: 61, 62 (misidentification).

**Diagnosis**

This species is most similar to *S. costatus* but differs from it in its strongly shiny dorsal surface, the absence of a distinct keel on the apices of the elytra, sparsely setose apices of middle and posterior tibiae in both sexes, and the shape of the apices of the parameres.



**Figs 14–18.** 14, 17, *Sarophorus punctatus*, holotype male; 15, *S. cicatricosus*, holotype male; 16, 18, *S. carinatus*, holotype male. 14–16, general view; 17, 18, pygidium.

**Description**

*Male holotype* (Fig. 22). Upper side of body black, strongly shiny. Body length 7.6 mm.

*Head.* Anterior margin of clypeus sinuate medially and angulate laterally. Genae obtuse. Anterior and lateral margins of clypeus with very fine border. Frontoclypeal and genal sutures indistinct. Dorsal surface regularly and densely punctate with almost adjoining punctures.

*Pronotum.* Anterior angles with fine border, other margins not bordered. Surface densely, regularly punctate.

*Elytra.* Intervals almost flat on disc, becoming slightly convex toward apex, densely punctate. Striae shiny, with slightly carinate margins, punctate (punctures separated by 2–3 puncture diameters). Apices of elytra without keel.

*Venter.* Base of propleura with concavities for apices of retracted middle femora. Disc of pygidium densely punctate. Abdominal sternite 6 sparsely punctate on disc and more densely so at sides. Sternites 2–5 punctate with a row of punctures along anterior margin on disc and regularly punctate with almost adjoining punctures at sides. Disc of metasternum concave and coarsely punctate (punctures separated by 0.5 puncture diameter).

*Legs.* Spur of anterior tibia curved strongly downwards and slightly inwards. Apices of middle and posterior tibiae sparsely setose.

*Aedeagus.* Apices of parameres acute in lateral view, their lateral margins angulate in dorsal view (Fig. 33). Internal sac with sub-symmetrically located spinules (Fig. 39).

*Female* differs from male in the more sparsely punctate anterior part of clypeus and the more slender and less inwardly curved spur of anterior tibiae. Body length 7.4 mm.

*Type material.* Holotype ♂: TANZANIA, Tanganyika Terr., Longido, Masai Distr., 1500 m., 17–20.iv. 1957, Basilewsky and Leleup. Paratype ♀ with the same data. Type material is deposited in MRAC.

***Sarophorus striatus* sp. n.**, Figs 21, 23, 24, 32, 40, 45

**Diagnosis**

This species is most similar to *S. costatus* and *S. latus* sp. n. and differs from them in its more finely punctate elytral intervals, the absence of a distinct keel at apex of elytra, the apices of the parameres being rounded lateral margins, and the

paler, brown colour of the body.

**Description**

*Male holotype* (Fig. 21). Upper side of body brown, disc of head and pronotum slightly darker. Body length 8.5 mm.

*Head.* Anterior margin of clypeus slightly sinuate medially, rounded at sides of sinuation. Genae obtuse. Anterior and lateral margins of clypeus with very fine border. Frontoclypeal and genal sutures absent. Dorsal surface regularly, densely punctate. Punctures separated by 0.3–0.5 puncture diameter.

*Pronotum.* Anterior angles with fine border, other margins not bordered. Surface densely punctate with two sub-symmetrically located, small, smooth areas.

*Elytra.* Intervals almost flat on disc becoming slightly convex toward apex, shagreened, punctate (punctures separated by a puncture diameter on disc becoming indistinct at apex). Striae fine, shiny, with slightly carinate margins, punctate. Punctures separated by 2–3 puncture diameters on first stria and about five puncture diameters on other striae.

*Venter.* Base of propleura with concavities for apices of retracted middle femora. Disc of pygidium densely punctate. Sixth abdominal sternite sparsely punctate on disc and more densely so at sides. Sternites 2–5 with a row of punctures along anterior margin on disc and regularly punctate with almost adjoining punctures at sides. Disc of metasternum concave and coarsely punctate. Punctures separated by 0.5 puncture diameter.

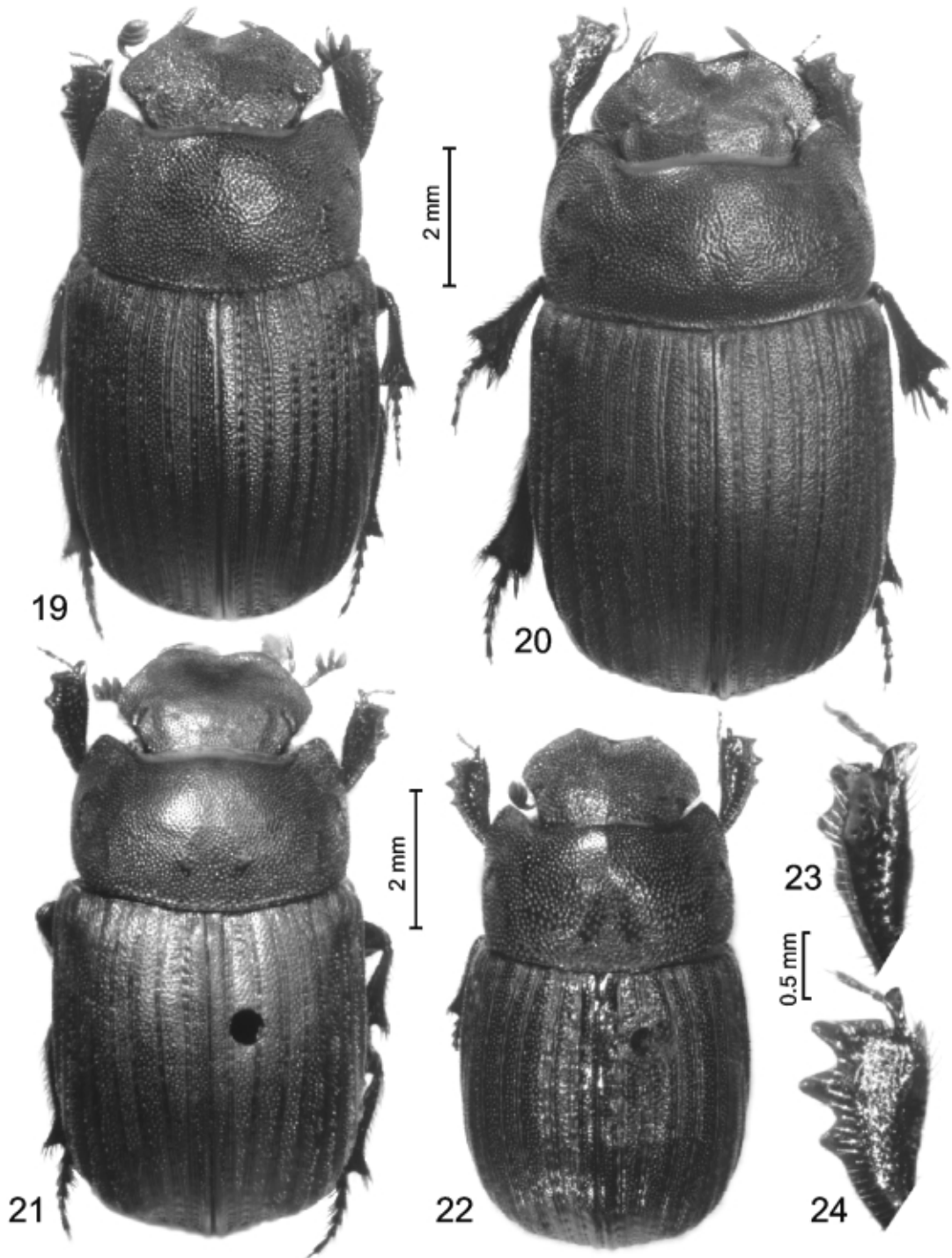
*Legs.* Spur of anterior tibia strongly curved downwards and inwards (Fig. 23). Apices of middle and posterior tibiae with dense, unequal setae.

*Aedeagus.* Apices of parameres flattened, their lateral margins rounded in dorsal aspect (Fig. 32). Internal sac with sub-symmetrically located spinules (Fig. 40).

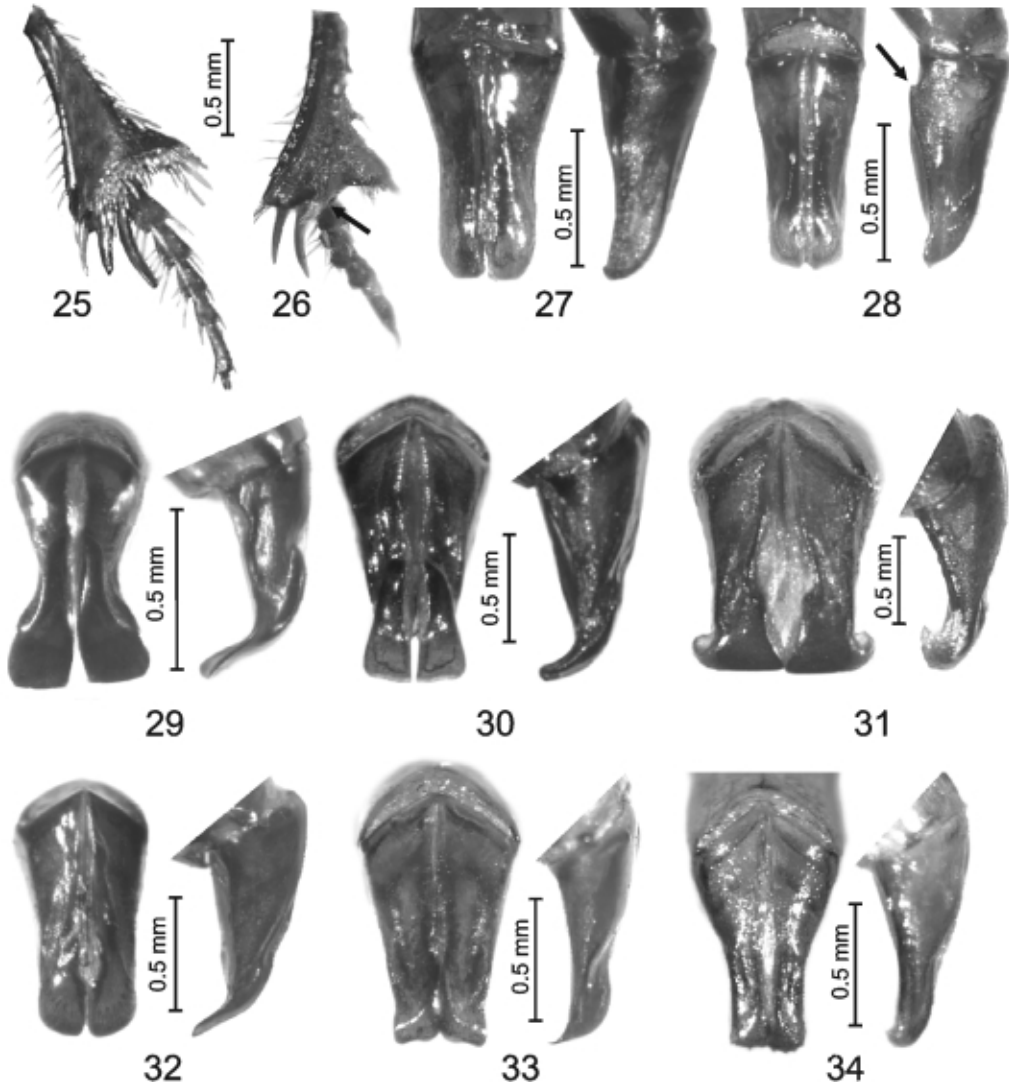
*Female.* Separated from male by the anterior tibial spur that is not curved inwards (Fig. 24) and by the sparsely setose apices of middle and posterior tibiae.

*Paratypes.* Body length 8.0–9.0 mm.

*Type material.* 33 specimens. SOUTH AFRICA, Holotype ♂: *Western Cape Province*, 23 km S of Avontuur, 4.v.1976, Davis and Aschenborn (SANC). Paratypes: *Eastern Cape Province*, 11 mi S of Grahamstown, 17.v.1971, 1♂, 1♀, Aschenborn



**Figs 19–24.** 19, *Sarophorus costatus*; 20, *S. latus*, holotype; 21, 23, 24, *S. striatus* (21, 23, holotype, 24, paratype); 22, *S. nitidus*, holotype. 19–22, general view of male; 23, 24, anterior tibia (23, male; 24, female).



**Figs 25–34.** 25, 31, *Sarophorus latus*, holotype; 26, 28, *S. bidentatus*, holotype; 27, *S. tuberculatus*; 29, *S. punctatus*, holotype; 30, *S. costatus*; 32, *S. striatus*, holotype; 33, *S. nitidus*, holotype; 34, *S. cicatricosus*, holotype. 25, 26, middle tibiae of male; 27–34, parameres in dorsal and lateral views.

(SANC); Grahamstown, Strowan, 25.i.1969, 2♂, 1♀; 18.ii.1969, 1♂; 22.x.1968, 1♂; 11.xii.1968, 1♂; Burntkraal, 13.iii.1969, 1♀; 13.iii.1969, 1♀; 1.x.1969 1♀, Gess (AMSA); 7 mi W of Paterson, 6.iii.1971, 1♀, Aschenborn (SANC); 7 km N of Paterson, 6.iv.1974, 1♂, Temby (SANC); Demiskraal, 28.i.1977, 1♀, Bornemissza (SANC); Addo Park, 16–20.xii.1996, 3♂, Wolmarans (TMSA); 9 km E of Hankey, 28.i.1977, 1♀, Bornemissza (SANC); *Western Cape Province*, Uniondale Distr., Bo Kouga, iii.1954, 5♂, 9♀ (SAMC).

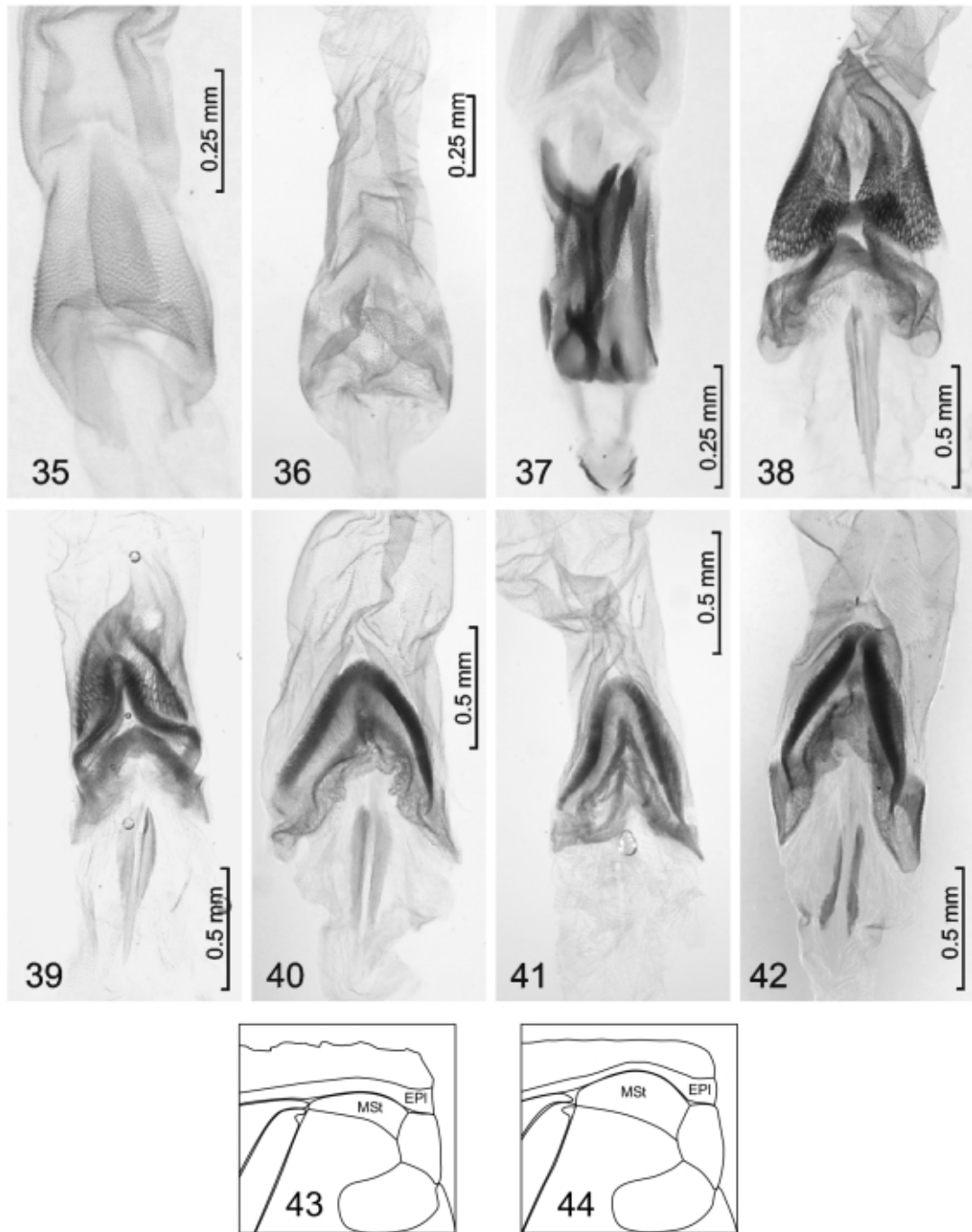
***Sarophorus latus* sp. n.**, Figs 20, 25, 31, 42, 45

**Diagnosis**

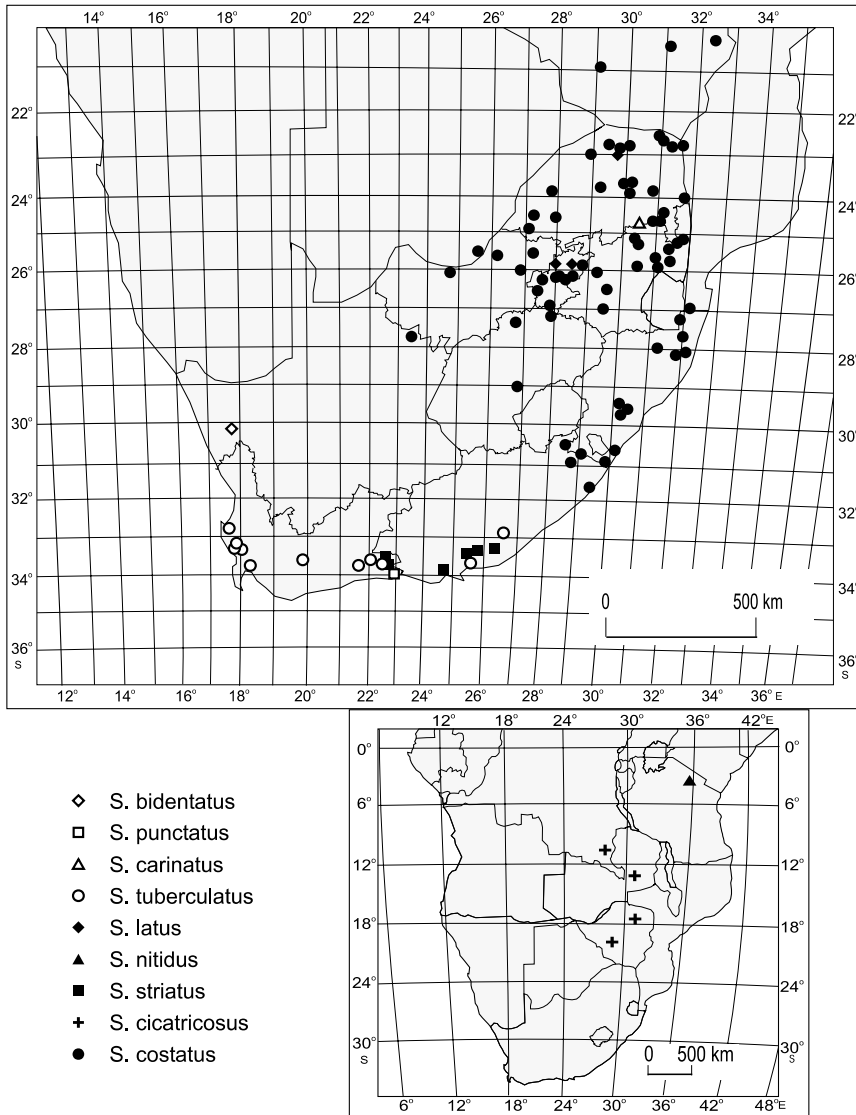
This species is most similar to *S. striatus* and *S. costatus* and differs from them in its wider body, the distinctly bordered lateral margins of the pronotum and the weakly sclerotized, widened and downwardly curved apices of the parameres.

**Description**

*Male holotype* (Fig. 20). Body relatively wide.



**Figs 35–44.** 35, *Sarophorus tuberculatus*; 36, *S. punctatus*, holotype; 37, *S. bidentatus*, holotype; 38, *S. costatus*; 39, *S. nitidus*, holotype; 40, *S. striatus*, holotype; 41, *S. cicatricosus*; 42, *S. latus*, holotype; 43, *tuberculatus* species-group sp.; 44, *costatus* species-group sp. 35–42, internal sacs of aedeagi; 43, 44, shape of metepisternum (MSt metepisternum, EPI elytral epipleuron).



**Fig. 45.** Distribution maps of *Sarophorus* species.

Upper side of body black to dark brown, legs slightly paler. Body length 8.5 mm.

*Head.* Anterior margin of clypeus slightly sinuate medially, anterior angles rounded. Genae obtuse. Anterior and lateral margins of clypeus with very fine border. Frontoclypeal and genal sutures absent. Dorsal surface regularly and densely punctate. Punctures separated by 0.5–0.3 puncture diameter.

*Pronotum.* Anterior angles and lateral margins bordered, other margins not bordered. Surface densely and regularly punctate with almost

adjoining punctures.

*Elytra.* Intervals flat on disc becoming slightly convex toward apex, coarsely punctate with almost adjoining punctures. Striae shiny, with carinate margins, punctate. Punctures separated by 2–3 puncture diameters. Intervals 5–7 fused at apex of elytron, forming a distinct keel.

*Venter.* Base of propleura with concavities for apices of retracted middle femora. Disc of pygidium densely punctate. Sixth abdominal sternite sparsely punctate medially and more densely laterally. Sternites 2–5 punctate with a row of

punctures along anterior margin on disc and regularly punctate laterally. Disc of metasternum concave and coarsely punctate. Punctures separated by 0.5 puncture diameter.

*Legs.* Spur of anterior tibia strongly curved downwards and inwards. Apices of middle and posterior tibiae with dense, unequal setae (Fig. 25).

*Aedeagus.* Apices of parameres widened and curved downwards (Fig. 31). Internal sac with sub-symmetrically located spinules (Fig. 42).

*Female.* Separated from male by the anterior tibial spur, which is not curved inwards, and by the sparsely setose apices of middle and posterior tibiae.

*Paratypes.* Body length 8.0–9.0 mm.

*Type material.* 20 specimens. SOUTH AFRICA. Holotype ♂: Gauteng, Farm Rhenosterpoort, 25°43'S 28°56'E, 27.xii.1975, bird carcass, L. Schulze. Paratypes: 3♂, 4♀ with the same data; 4 spm. with

the same data but collected in horse dung (♂) and baboon faeces (2♂, 1♀); 3♂, 1♀ with the same data but collected 3.xii.1975 in horse dung; 2♂ with the same data but collected 6.i.1979 and 17.xii.1980; 1♂, Pretoria, Waterkloof [other data lacking]; 1♂, Limpopo Province, Happy Rest NR, 23.02'S 29.40'E, 1–5.iv.1976, from under stones, Prozesky-Schulze. Type material is deposited in TMSA.

#### ACKNOWLEDGEMENTS

We thank the curators of collections for providing material for this study and the two anonymous reviewers for valuable comments on the manuscript. Staff at the Laboratory of Microscopy and Microanalysis, University of Pretoria, are acknowledged for providing access to digital photography facilities and technical support. This work has been supported by a University of Pretoria Postdoctoral Fellowship to A.E.

#### REFERENCES

- BALTHASAR, V. 1960. Coleoptera, Scarabaeidae. *Annales du Musée Royal du Congo Belge, Série 8°*, **88**: 55–66.
- BOHEMAN, C.H. 1857. *Insecta Caffrariae annis 1838–1845 a J.A. Wahlberg collecta amici auxilium sussultus descripsit. Coleoptera.* (Officina Norstedtiana), Holmiae, **2**: 1–395.
- BOUCOMONT, A. 1922. Les Coléoptères coprophages du genre *Pedaria* Castelnau. *Bulletin du Museum National d'Histoire Naturelle* **7**: 490–495.
- CAMBEFORT, Y. 1991. Biogeography and evolution. In: Hanski, I. & Cambefort, Y (Ed.). *Dung Beetle Ecology*. 51–67. Princeton University Press, Princeton.
- ERICHSOHN, W.F. 1847. *Naturgeschichte der Insecten Deutschlands*. I. *Coleoptera* **3/5**: 641–800.
- FERREIRA, M. 1969. Os escarabádeos de Africa (Sul do Sáara). I. *Revista de Entomologia de Moçambique* **11**: 5–1088.
- JANSSENS, A. 1939. Coprini. *Exploration du Parc National Albert. Mission G.F. de Witte* **29**: 1–104.
- MONTREUIL, O. 1998. Analyse phylogénétique et paraphylie des Coprini et Dichotomiini (Coleoptera, Scarabaeidae). Scenario biogéographique. *Annales de la Société Entomologique de France (N.S.)* **34(2)**: 135–148.
- PÉRINGUEY, L. 1901. Descriptive catalogue of the Coleoptera of South Africa (Lucanidae and Scarabaeidae). *Transactions of the South African Philosophical Society* **12**: 1–563.

Accepted 7 March 2003