Zootaxa 2344: 17–28 (2010)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Two new species of *Onthophagus* (Coleoptera: Scarabaeidae) from Indochina, with a discussion of some problems with the classification of *Serrophorus* and similar subgenera

SERGEY I. TARASOV[1,2] & OLEG N. KABAKOV[3]

[1]*Department of Entomology, Natural History Museum of Denmark/University of Copenhagen, Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen, Denmark. E-mail: sergxf@yandex.ru*
[2]*Institute of Natural Science, Kaluga State Pedagogical University, Stepana Razina str. 26, Kaluga 248023, Russia*
[3]*(Deceased) Bassejnaja str. 53-94, St.-Petersburg, 196135, Russia*

Abstract

Two new species of *Onthophagus* Latreille, 1802 are described from Indochina: *O.* (*Sunenaga*) *streltsovi* **sp. n.** and *O.* (*Sinonthophagus*) *nampatensis* **sp. n.** Some problems with the current systematics of *Onthophagus*, especially with respect to the subgenera *Serrophorus*, *Sunenaga* and *Macronthophagus* are discussed.

Key words: *Onthophagus*, Indochina, new species, *Sunenaga*, *Sinonthophagus*, systematics

Introduction

The globally distributed genus *Onthophagus* Latreille, 1802, which includes about 2000 species, is a mega-diverse group of scarab beetles. The diversity of this genus in the Oriental biogeographic region is very rich, second only to the diversity of the Afrotropical region. Despite the increasing number of described species during recent years, the Oriental *Onthophagus* are still poorly studied. In this paper, two new species of *Onthophagus* are described. One of the new species, *O. streltsovi*, has a combination of morphological characters that indicates its position in either the subgenus *Serrophorus* Balthasar, 1963 or *Sunenaga* Ochi, 2003 but cannot be unequivocally placed in either based on the currently accepted taxonomic definitions of these subgenera. Tentatively, this species is placed in the subgenus *Sunenaga*, but the problems associated with this decision are discussed at length. These problems stem from the fact that the current subgeneric classification of the genus seems to be poorly developed and sometimes artificial, not monophyly based. The majority of specimens used for the descriptions of the new species were collected by one of us (S.T.) in Laos in 2007–2008.

Materials and methods

Specimens and collections

The material examined in the present study is kept in the following institutions:

BMNH British Museum (Natural History), London, UK (M. Barclay)
FMNH Field Museum of Natural History, Chicago, USA (A. Newton, M. Thayer, J. Boone)
ZISP Zoological Institute, St.-Petersburg, Russia (A. Frolov)
ZMUC Zoological Museum (Natural History Museum of Denmark), University of Copenhagen, Denmark (A. Solodovnikov, O. Martin)

Accepted by A. Smith: 19 Dec. 2009; published: 26 Jan. 2010

Microscopy and illustrations

All photos were made with a digital camera attached to a dissecting microscope (Leica MZ16A ®). Aedeagi and their internal structures were photographed in glycerin. First, the dissected aedeagi were macerated in 10% solution of KOH for several hours then they were rinsed with distilled water, after which the internal sac was separated from the aedeagus. Finally, both the internal sac and the aedeagus were placed in glycerin for storage.

All photos with the lamella copulatrix (Figs. 2 a, c, b, d; 3a, b) represent the inner side of the lamella when the internal sac is not everted, the top of each figure corresponds to the margin nearest to the parameres.

Abbreviations for lamella copulatrix parts

The lamella copulatrix is one of the complexes of sclerites of the aedeagus internal sac of *Onthophagus.* These characters were often used for classification purposes of this genus (see for example, Zunino 1979; Palestrini 1980, 1982, 1992; Zunino & Halffter 1988). However, the comparative morphology of this structure, especially the homology of some of its sclerites among various species of the genus, is still not completely understood. We cannot resolve all these issues in our rather limited study here, so we provide a tentative morphological plan for the lamella copulatrix for descriptive purposes and use rather neutral terminology for various sclerites. However, we also tried to make this terminology compatible as possible with the earlier studies (for example, Zunino & Halffter 1988, Palestrini 1992).

The parts of lamella copulatrix in the text and in Figs. 2–3 are abbreviated as follows:

AIS	additional internal sclerite
ALS	additional lateral sclerite
AMS	additional median sclerite
IL	inferior left part
IR	inferior right part
SL	superior left part
SP	superior part
SR	superior right part

***Onthophagus* (*Sunenaga*) *streltsovi* Tarasov & Kabakov, sp. n.**
(Figs. 1a, b; 2c, e, f)

Material examined. *Holotype* (ZMUC), male bearing the following labels:

1. White, printed: S LAOS, Bolaven plateau B.Thongvai, N15°14.741' E106°31.916' h=1150–1300m dung trap, primary montane forest, 8–16.06.2008, leg. S. Tarasov

2. Orange, printed: HOLOTYPUS *Onthophagus streltsovi* S. Tarasov & O. Kabakov det. 2009

Paratypes. 147 specimens, South Laos, Bolaven Plateau, B.Thongvai, N15°14.741' E106°31.916', h 1150–1300m, dung trap (human), primary montane forest, 8–16.06.2008 leg. S. Tarasov (ZMUC); 1 specimen, South Laos, Bolaven Plateau, B.Thongvai, N15°14.741' E106°31.916', h 1300m, carrion trap, primary montane forest, 12–16.06.2008, leg. S. Tarasov (ZMUC); 1 specimen, South Laos, Bolaven Plateau, B.Thongvai, N15°14.741' E106°31.916', h 1150m, carrion trap, disturb montane forest, 10–16.06.2008, leg. S. Tarasov (ZMUC); 81 specimens, Laos: Champasak province: Bolaven Plateau, Ban Thongvai, old logging road N of the village, 1095m, 15°14.288'N, 106°31.891'E, selectively logged forest, 8–16.06.2008; FMHD#2008-039, dung trap (human), A. Solodovnikov, M. Thayer & A. Newton (FMNH); 134 specimens, Laos: Champasak province: Bolaven Plateau, Ban Thongvai, old logging road N of the village, 1170m, 15°14.494'N, 106°31.807'E, selectively logged forest, 8–16.06.2008; FMHD#2008-042, dung trap (human), A. Solodovnikov, M. Thayer & A. Newton (FMNH); 23 specimens, Laos: Champasak province: Bolaven Plateau, Ban Thongvai, old logging road N of the village, 1035m, 15°13.96'N, 106°31.731'E, selectively logged forest, 8–16.06.2008; FMHD#2008-036, dung trap (human), A. Solodovnikov, M. Thayer & A.

Newton (FMNH); 6 specimens, Laos: Champasak province: Bolaven Plateau, Ban Thongvai, old logging road N of the village, 995m, 15°13.761'N, 106°31.749'E, selectively logged forest, 8–16.06.2008; FMHD#2008-033, dung trap (human), A. Solodovnikov, M. Thayer & A. Newton (FMNH).

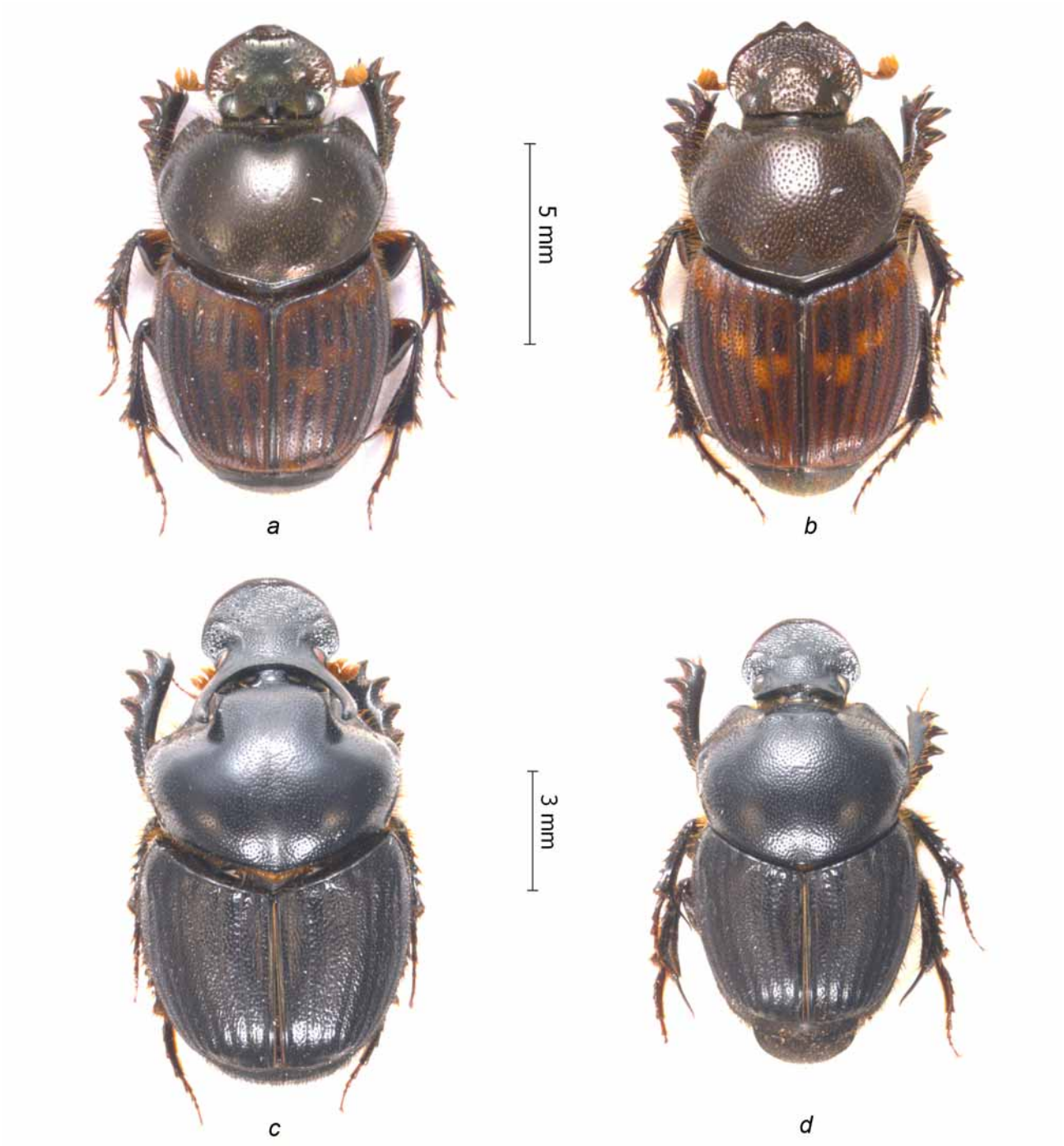

FIGURE 1. Habitus of *Onthophagus*. a, b—*O. streltsovi*; c, d—*O. nampatensis*; a, c—males, holotypes; b—female, paratype; d—small male paratype.

Description. Head and pronotum black with slight green luster, rarely slightly red; elytra yellow-brown, intervals with black, interrupted stripes; rarely stripe pattern weakly expressed; pygidium, metasternum laterally, femur yellow or yellow-black; abdominal sternites yellow usually with black stripes basally; antennal club yellow; elytra with short, black setae turning yellow depending on light angle; pronotum, head, pygidium, abdominal side with longer yellow setae. Length 10–12 mm.

Male major (Fig. 1a). Head rounded; apex of clypeal margin anteriorly reflexed upwards; frontoclypeal ridge absent in larger males and present with slightly raised strip in smaller males; vertex with small hook-shaped horn broadened basally and bent backwards; eyes completely divided with genal appendage; clypeus sparsely punctate; antennal scapus anteriorly with slight ridge, not serrate.

Pronotum convex; anterior, lateral and basal sides marginate, postlateral section strongly sinuate; anterolateral angles rounded, anterior part slightly concave in middle behind cephalic horn; disc sparsely covered with fine punctures (separated by 1–2 puncture diameters) becoming denser and larger laterally; anterior part of propleura with ridge almost reaching propleural lateral margin.

Elytra densely covered with scattered punctures becoming denser on 7th and 8th intervals. Pygidium covered with scattered large punctures separated by 1–2 diameters of a puncture, with longitudinal black strip medially; basal edge marginate.

Protibia with four outer teeth, internal apical angle with large tooth about two times smaller than apical spur; apical spur modified in males: small, acuminate, slightly bent outward; mesotibial and metatibial apex produced into three distinct lobes bearing short and long setae.

Aedeagus as in Figs. 2e, f. Lamella copulatrix as in Fig. 2c.

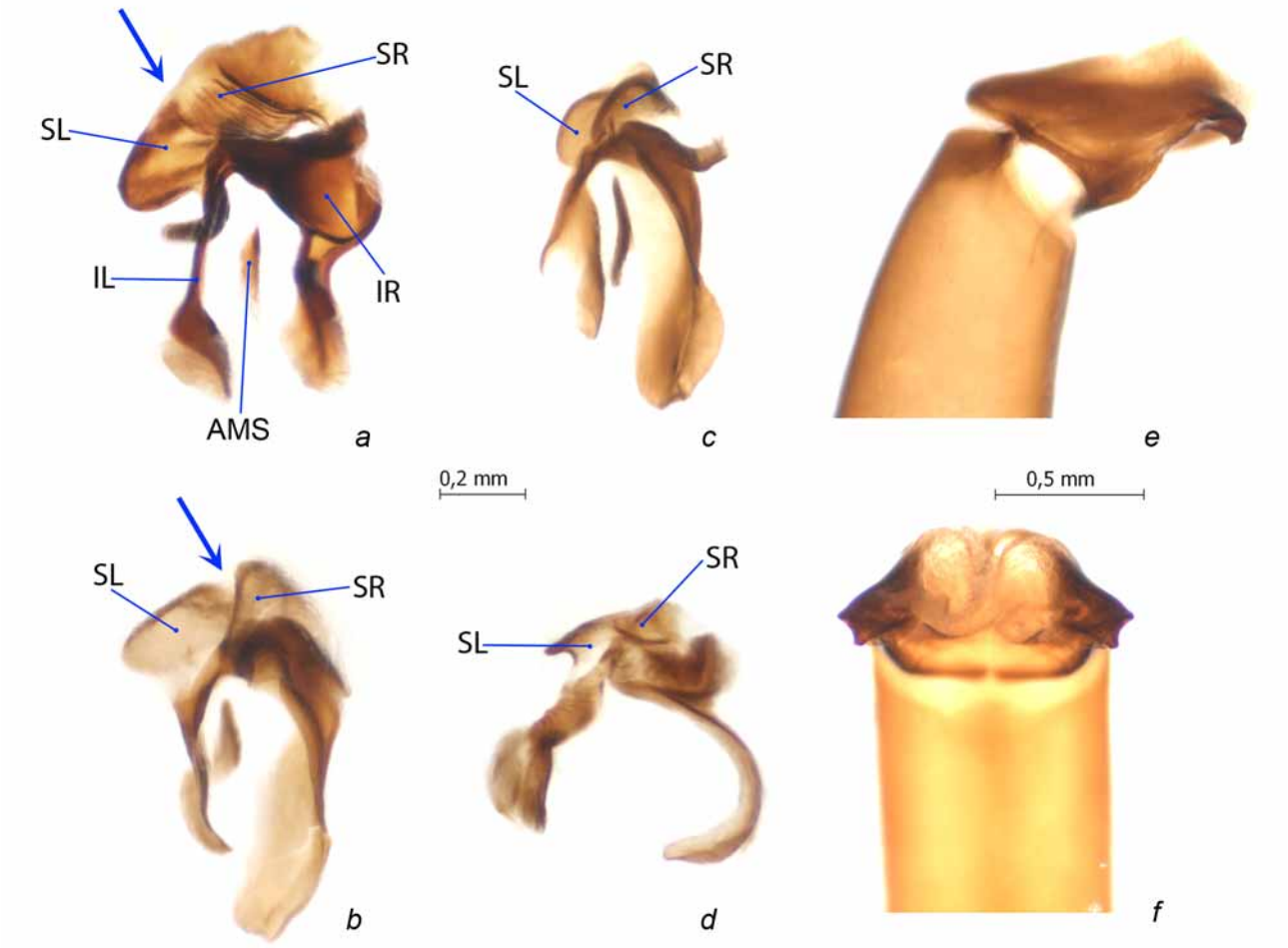

FIGURE 2. Elements of genitalia of *Onthophagus*. a—*O. seniculus* (fused area of SL and SR indicated by arrow); b—*O. anguliceps* (separation of SL and SR indicated by arrow); c, e, f—*O. streltsovi*; d—*O. manipurensis*; a–d—lamella copulatrix; e—aedeagus, lateral view; f—aedeagus, apical view.

Female (Fig. 1b). Female differs from male by clypeus slightly reflexed along anterior margin and incised medially, with each side of the incision lobed; frontoclypeal ridge present; vertex without horn; head and pronotum sparsely covered with large, dense punctures separated by a diameter or less; pronotum less convex; internal apical angle of protibia with small indistinctive tooth; apical spur of protibia larger, more acuminate and slightly bent inward.

Variation. Males vary allometrically in the degree of expression of some features of the clypeus, horn, pronotum and punctation. Small males usually have less anteriorly reflexed clypeus; vertex not armed with horn, or, sometimes, only with small tubercle; pronotum more flat, not concave, disc more densely punctured.

Holotype (Fig. 1a). Major male, length 11.4 mm. Head and pronotum black with slight green luster; elytra yellow-brown, intervals with black, interrupted stripes; pygidium yellow-black; metasternum laterally and femur yellow; abdominal sternites yellow with black stripes basally, antennal club yellow; apex of clypeal margin anteriorly reflexed upwards; vertex with small hook-shaped horn broadened basally and bent backwards; Pronotum convex, slightly concave in middle behind cephalic horn; disc sparsely covered with fine punctures (separated by 1–2 puncture diameters) becoming denser and larger laterally.

Differential diagnosis. This species is similar to *O. digitatus* Arrow, 1931 from Sikkim, India (we have examined the male lectotype of *O. digitatus*, which is deposited at the BMNH). Both species posses similar body shape, especially of the head and pronotum; vertex in males armed with small horn bent backwards; internal apical angle of protibia with large tooth in males; protibial apical spur small, acuminate, slightly bent outward; mesotibial and metatibial apex produced into three distinct lobes; aedeagus and lamella copulatrix similarly shaped. The characters separating two these species are summarized in Table 1. Both species are probably also similar to *O. kaengkrachangus* Masumoto, Ochi & Hanboonsong, 2008 from Thailand. Unfortunately the types of the latter have not been examined, but as we can see from its original description, *O. kaengkrachangus* shares almost the same combination of characters with *O. streltsovi* and *O. digitatus*: head and the rest of body specifically shaped; "protibiae with inner side of terminal edge bluntly projected; terminal spur rather bold". Also, all three species have similar shape of aedeagus. Only one remarkable character, the male vertex with small horn bent backwards, is not reported for *O. kaengkrachangus*. This is likely due to the lack of major males in the type series.

TABLE 1. Diagnostic characters separating the new species *O. streltsovi* from *O. digitatus*.

Characters	*O. streltsovi*	*O. digitatus*
Matasternal posterior depression	Absent	Present
Coloration	Head and pronotum black; elytra yellow-brown, intervals with black interrupted stripes; pygidium, metasternum laterally, abdomen,	Black
Punctation of pronotum	Disc sparsely covered with fine punctures becoming denser and larger laterally	Disc not punctate, smooth; pronotum covered with large punctures laterally
Aedeagus	Parameral preapical section distinctly excavated	Parameral preapical section without excavation

These three species probably represent a monophyletic group. Reasons for its current taxonomic position are provided in the "Discussion" section below.

Etymology. The new species is named after Dr. Alexey Streltsov, Professor of Kaluga University in Russia, to whom we are much obliged for personal help and support during research as well as in everyday life. In particular, it was thanks to Alexey Streltsov that the long field trip to Laos by S.T. was possible.

Distribution and Ecology. The species is known from many specimens, but only from the type locality in Bolaven Plateau, South Laos (Fig. 4). Almost all specimens were collected in montane forest by means of pifall traps baited with human dung.

Onthophagus (Sinonthophagus) nampatensis Tarasov & Kabakov sp.n.

(Figs. 1c, d; 3a–d)

Material examined. *Holotype* (ZMUC), male bearing the following labels:

1. White, printed: LAOS, Khammouane prov. 10km W of Ban Khun Kham (Nahin) N18°8.922' E104°28.629', h280m, limestone tropical forest, dung trap (human). 4–18.06.2008 leg. S. Tarasov

2. Orange, printed: HOLOTYPUS *Onthophagus (Sinonthophagus) nampatensis* S. Tarasov & O. Kabakov det. 2009

Paratypes: 1 ♂, Laos, Khammouane province 10km W of Ban Khun Kham (Nahin) N18°8.922' E104°28.629', h280m, limestone tropical forest, dung trap 4–18.06.2008 leg. S. Tarasov; 1 ♂, North Thailand, Doi Suthep, 19.6.1958, h1100m, leg. B. Degerbøl (ZMUC).

Description. Body black, slightly lustrous, elytra with stronger luster; antennae and mouthparts orange; elytra and abdomen with short black setae turning white depending on light angle; rest of abdominal side and pygidium with long, orange hairs. Length 10.0–12.8 mm.

Male major (Fig. 1c). Head rounded; frontoclypeal ridge slightly expressed, in smaller males more distinct; vertex with a pair of long, tapering and inwardly-rounded horns connected by ridge; eyes completely divided by genal appendage; clypeus densely, transversely rugulose.

Pronotum with distinct excavations near anterior angles, anterior part protruding forward between cephalic horns; postlateral section strongly sinuate; anterior and lateral edges marginate, basal edge shortly marginate only near median basal depression; anterior angles slightly protruded forward, widely rounded; pronotal disc covered with simple, sparse punctures (separated by 1–2 puncture diameters) becoming denser and rasplike anteriorly; anterior part of propleura with ridge almost reaching propleural lateral margin.

Elytra shagreened, sparsely and densely punctured.

Protibia with four outer teeth, median part of anterior edge slightly produced into triangle tooth, internal apical angle with small tooth; apical spur short, acuminate; metatibiae strongly triangularly broadened toward apex; mesotibial and metatibial apex with short and long setae.

Aedeagus as in Figs. 3c, d. Lamella copulatrix with additional internal sclerite (AIS) and small additional lateral sclerite (ALS) (Fig. 3a); superior part simple (Fig. 3b).

Female. Unknown.

Variation. Males vary allometrically in the degree of expression of such body parts as horns, pronotum and punctation. Small males (Fig. 1d) usually have small horns; anterior part of pronotum with two tubercles medially; pronotum flatter, not concave; disc more densely punctured.

Holotype (Fig. 1c). Major male, Length 12.8 mm. Body black, slightly lustrous, elytra with stronger luster; antennae and mouthparts orange. Head rounded; frontoclypeal ridge weakly expressed (more distinct in smaller males); vertex with a pair of long, tapering and inwardly-rounded horns connected by ridge. Pronotum with distinct excavations near anterior angles, anterior part protruding forward between cephalic horns; disc covered with simple, sparse punctures (separated by 1–2 puncture diameters) becoming denser and rasplike anteriorly.

Differential diagnosis. The new species is most similar to *Onthophagus (Sinonthophagus) productus* Arrow, 1907 but differs by slightly sparser punctation of the pronotum and distinctly different shape of parameres. It can be also separated from all other species of the subgenus *Sinonthophagus* Kabakov, 2006 by the unique shape of parameres with protruding lateral lobes (Figs. 3c, d).

Taxonomic notes. This species has been already cited in two papers as *nomen novum in litteris* (Kabakov & Napolov 1999, Kabakov 2006) but has not been described. Moreover, the specimen previously indicated as the holotype (Kabakov 1999) is not included in the type series in this paper because its aedeagus was lost. Though we are certain that the specimen previously chosen as the holotype is conspecific with the current type specimens (also it was collected in the same area with the holotype), we deliberately excluded it from the type series because the new species can be reliably separated from the close *O. productus* only by the characters of structure of parameres. For practical reasons we use the same species name as the *nomen nudum* in Kabakov & Napolov (1999) and Kabakov (2006).

Distribution and Ecology. The new species is known only from north Thailand and central Laos (Fig. 4). In Laos, this species was collected by pitfall traps baited with human dung installed in limestone forest.

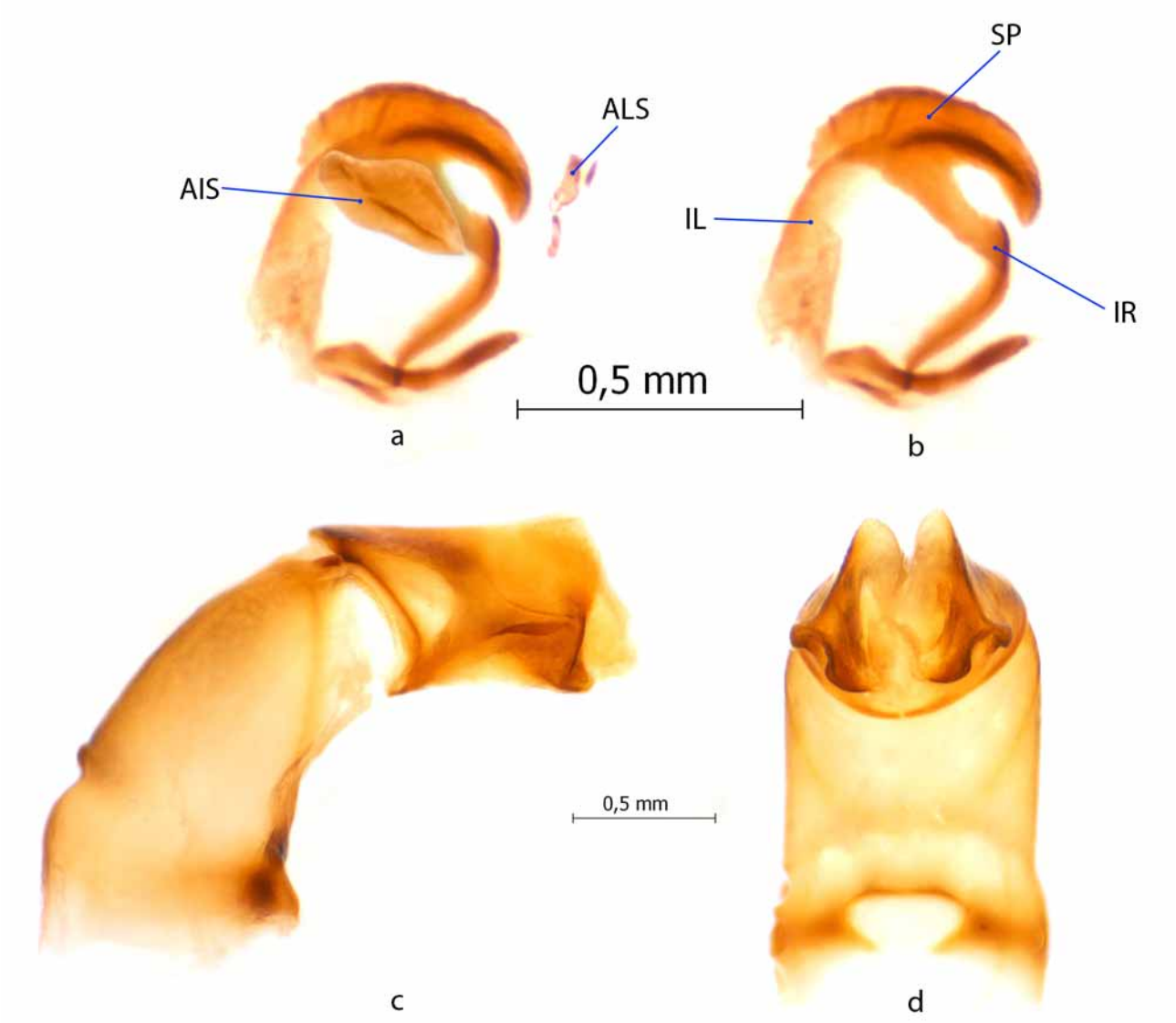

FIGURE 3. Elements of genitalia of *Onthophagus nampatensis*. a—lamella copulatrix; b—lamella copulatrix, AIS and ALS removed; c—aedeagus, lateral view; d—aedeagus, apical view.

Discussion

Although finding the taxonomic placement of *Onthophagus nampatensis* was straightforward, classifying *O. streltsovi* within the current system of the genus turned out to be a problem. Morphologically, *Onthophagus streltsovi* is very similar to a group of species now shared between the subgenera *Serophorus* and *Sunenaga* (see the last column in Table 2). But, through the modern history of systematics of the genus *Onthophagus*, these species were in constant flux among subgeneric groups proposed by various authors. This can be easily seen in the Table 2 by tracking the position of the species from its last column ("Present Paper") through all other columns representing alternative classifications. These alternative classifications, in addition, are in considerable conflict with each other, and obviously vary in the nature and quality of the respective supporting arguments as well as the accuracy of the taxonomic procedures. Because of all these complications, we also provide a detailed review and discussion of the classification of the relevant portion of the genus (see Table 2) in order to justify our proposed taxonomic placement for *O. streltsovi*.

Arrow (1931) did not use formal subgenera within *Onthophagus*, he used only species groups. In his classification, the species reviewed here were shared between two of his groups, Group 4 and Group 12.

Group 4 was defined by mesotibial and metatibial apex produced into three distinct lobes. This group included three species that are currently assigned to the subgenus *Sunenaga*, in addition to the species from the present genus *Proagoderus* Lansberge, 1883. Group 12 was not precisely defined by presence of any unique character(s) and, with the exception for *O. atropolitus* d'Orbigny, 1902, consisted of the species placed in the subgenus *Serrophorus* (Balthasar, 1963), the species currently in the subgenus *Macronthophagus* Ochi, 2003 and some other species.

Balthasar (1935) described the subgenus *Serrophorus* for the following species: *O. senex* Boucomont, 1914, *O. seniculus* (Fabricius, 1781), *O. diabolicus* Harold, 1887, *O. rubricollis* Hope, 1831, *O. nilgirensis* Gillet, 1921, and *O. manipurensis* Arrow, 1907. However, that time he did not designate the type species for the subgenus. Therefore, according to the Article 13 ICZN (1999) this name with the publishing date in 1935 is unavailable. Afterwards, Balthasar (1963) used this subgenus again but with a somewhat different species composition: *O. seniculus*, *O. senex*, *O. atropolitus*, *O. rectecornutus* Lansberge, 1883, and *O. sagittarius* (Fabricius, 1775) (with only *O. seniculus* and *O. senex* consistent with the initial concept of the subgenus in 1935). It is noteworthy that Balthasar (1963) designated the type species, *O. seniculus* (Fabricius, 1781), for this subgenus. Therefore, it is the author and date "*Serrophorus* Balthasar, 1963", which is considered as available and used in this paper. The subgenus *Serrophorus* Balthasar, 1963 (also in Balthasar 1935) was described based on the anteriorly serrate antennal scapus. According to Balthasar (1963), another subgenus bearing serrate scapus was *Digithonthophagus* Balthasar, 1959, but the latter could be distinguished from the former by having protibia extremely elongate.

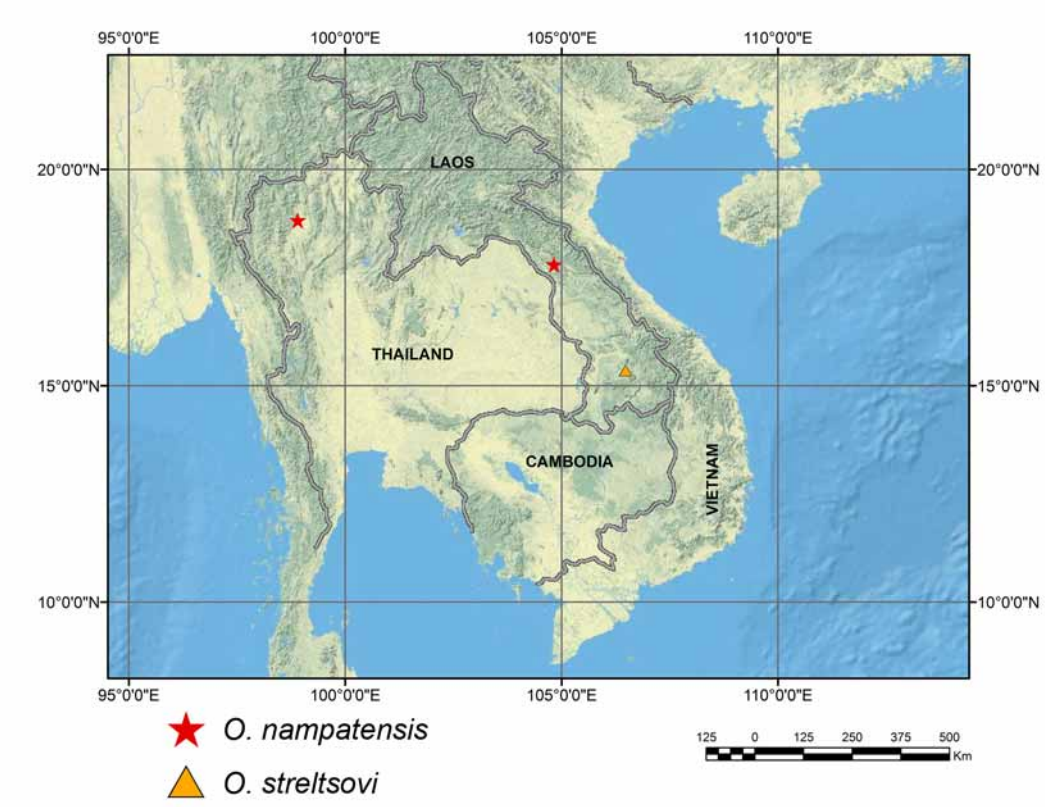

FIGURE 4. Distribution map of *O. streltsovi* and *O. nanpatensis.*

Subsequently, *Serrophorus* was reinvestigated by Palestrini (1980). Based on the study of the structure of the aedeagus, including shape of its lamella copulatrix, she considered this subgenus to be an artificial group. As a result, two species, *O. rectecornutus* and *O. sagittarius*, were moved to *Onthophagus sensu stricto*, and *Serrophorus* was synonymised with the subgenus *Parascatonomus* Paulian, 1932. The three species remaining in *Serrophorus* after the mentioned taxonomic changes by Palestrini (1980) naturally became the members of the genus *Parascatonomus.*

TABLE 2. The species composition of *Serrophorus* and similar taxa according to different authors

Arrow (1931)	Balthasar (1935)	Balthasar (1963)	Palestrini (1980)	Kabakov & Yanushev (1983)	Kabakov & Napolov (1999)	Ochi (2003a)	Present paper
Group 4	**subgenus**	**subgenus**	**subgenus**	**subgenus**	**genus *Serrophorus***	**subgenus**	**subgenus**
O. anguliceps[1]	***Serrophorus***	***Serrophorus***	***Parascatonomus***	***Serrophorus***	**Balthasar, 1963**	***Serrophorus***	***Serrophorus***
O. aviculus[2]	**Balthasar, 1935**	**Balthasar, 1963**	**Paulian, 1932**	**Balthasar, 1963**	*S. anguliceps*	**Balthasar, 1963**	**Balthasar, 1963**
O. badeni	*O. diabolicus*	*O. atropolitus*	*O. senex*	*O. anguliceps*	*S. atropolitus*	*O. atropolitus*	*O. atropolitus*
O. digitatus	*O. manipurensis*	*O. rectecornutus*	*O. seniculus*	*O. avocettoides*	*S. avocettoides*	*O. laevis*	*O. laevis*
O. gladiator	*O. nilgirensis*	*O. sagittarius*	.....	*O. diabolicus*	*S. diabolicus*	*O. muelleri*[5]	*O. senex*
O. imperator	*O. rubricollis*	*O. senex*	***Onthophagus***	*O. laevis*	*S. manipurensis*	*O. rectecornutus*	*O. seniculus**
Group 12	*O. senex*	*O. seniculus**	***sensu stricto***	*O. manipurensis*	*S. senex*	*O. sagittarius*	**subgenus**
O. bonasus	*O. seniculus*	**subgenus**	*O. rectecornutus*	*O. rectecornutus*	*S. seniculus**	*O. senex*	***Sunenaga* Ochi,**
O. catta3		***Digitonthophagus***	*O. sagittarius*	*O. sagittarius*	***Onthophagus***	*O. seniculus**	**2003**
O. manipurensis		**Balthasar, 1959**	.....	*O. seniculus**	***incertae sedis***	**subgenus**	*O. anguliceps**
O. nilgirensis		*O. anguliceps*			*O. laevis*	***Macronthophagus***	*O. avocetta*
O. rectecornutus		*O. avocetta*			.....	**Ochi, 2003**	*O. avocettoides*
O. rubricollis		*O. blumei*			**subgenus**	*O. cludtsi*	*O. blumei*
.....		*O. bonasus**			***Gibbonthophagus***	*O. curvicarinatus*	*O. digitatus*
		O. cameloides			**Balthasar, 1963**	*O. diabolicus*	*O. streltsovi*
		O. diabolicus			*O. rectecornutus*	*O. manipurensis*	
		O. digitatus			.....	*O. menieri*	
		O. gazella				*O. nilgirensis*	
		O. manipurensis				*O. rubricollis*	
		O. nilgirensis[4]				*O. uenoi**	
		O. ribbei				**subgenus *Sune-***	
		O. rubricollis				***naga* Ochi, 2003**	
		O. wallacei				*O. anguliceps**	
		.....				*O. avocetta*	
						O. avocettoides	
						O. blumei	
						O. cameloides	
						O. digitatus	
						O. mindanaensis	
						O. ribbei	
						O. wallacei	

[1] *O. anguliceps* Boucomont, 1914. sensu Arrow (1931) = *O. avocetta* Arrow, 1933
[2] *O. aviculus* Arrow, 1931 = *O. anguliceps* Boucoumont, 1914
[3] *O. catta* (Fabricius, 1787) = *O. gazella* (Fabricius, 1787)
[4] as synonym of *O. diabolicus* Harold, 1887
[5] transferred to *Serrophorus* by Ochi and Kon, 1994
*indicates the type species of subgenus
..... indicates that some other species were included in the subgenus

However, the subgenus *Serrophorus* was still used in the checklist of species of *Onthophagus* from southern China and Vietnam (Kabakov & Yanushev 1983) with the following species included: *O. seniculus, O. rectecornutus, O. sagittarius, O. laevis* Harold, 1880, *O. diabolicus, O. manipurensis, O. anguliceps* Boucomount, 1914 and *O. avocettoides* Kabakov, 1994. Later, however, the same author (Kabakov 1992) suggested that subgenera *Serrophorus, Parascatonomus, Pseudonthophagus* Balthasar, 1959 and the genus *Proagoderus* Lansberge, 1883 are closely related and probably the first three could be just the subgenera of the genus *Proagoderus.* Also, *Parascatonomus* was raised to generic rank and separated from the subgenus *Serrophorus* by having an anteriorly raised, prow-shaped metasternum. Thereafter (Kabakov 1994), *Serrophorus* was raised to genus rank as well. In the next checklist of Indochinese Scarabaeinae (Kabakov & Napolov 1999), two species, *S. senex* and *S. atropolitus,* were recorded for the region and added to the list. It is noteworthy that Kabakov & Napolov (1999) moved *S. laevis* to the genus *Onthophagus incertae sedis* (*sensu lato* in the sense of Kabakov 1994) and *S. rectecornutus* also placed within *Onthophagus,* but in the subgenus *Gibbonthophagus* Balthasar, 1963.

The next step was the paper of Ochi (2003a) where he tried to reclassify those species of *Onthophagus* which possess a serrate antennal scapus. He considered *Serrophorus* as a subgenus of *Onthophagus* but indicated that the serrate scapus is shared between different species group of this genus. So, two new subgenera, *Macronthophagus* and *Sunenaga,* which include species before placed in *Serrophorus,* were described, and status of other Asian subgenera with serrate scapus was again redefined.

In our opinion all above discussed changes do not solve the taxonomic problems of the groups now considered in *Serrophorus* and related taxa. In this paper we also do not attempt to resolve these problems and fix anything formally, but we attempt to define the right way for further research of this complex. First and foremost, we must clearly state that none of previous studies were consistent with the principle of monophyly, and none of them included any phylogenetic analysis of the whole problematic complex of species. Therefore, it was not demonstrated which characters are synapomorphies of certain groups and which are not. We agree with Ochi (2003a) that serrate scapus occurs in different *Onthophagus* lineages. Also, as our unpublished phylogenetic analysis shows, two other characters, which hitherto were considered significant and widely utilized in the systematics of *Onthophagus,* are homoplastic: the extremely elongated protibiae in males, and mesotibial and metatibial apex produced into three distinct lobes. At the same time, the set of characters that are phylogenetically informative seem to be the structure of aedeagus including the internal sac, in particular sclerites of the lamella copulatrix. With such re-evaluation of characters, we again would like to review the species composition and status of *Serrophorus*, *Macronthophagus* and *Sunenaga* and justify our proposed taxonomic placement for the problematic new species *O. streltsovi*.

According to Ochi (2003a), *Serrophorus* contained all species originally placed in the subgenus by Balthasar (1963), plus *O. muelleri* Lansberge, 1883 (transferred by Ochi and Kon (1994) from *Parascatonomus*) and *O. laevis*. But considering the structure of the aedeagus and lamellae copulatrix, the following species have to be undoubtedly excluded from *Serrophorus*: *O. rectecornutus, O. sagittarius* and *O. muelleri*. These three species were placed in *Serrophorus* based on highly homoplastic characters such as serrate scapus, extremely elongated protibiae in males, and mesotibial and metatibial apex produced into three distinct lobes. So, tentatively we place only four species in *Serrophorus*: *O. seniculus, O. senex, O. atropolitus* and *O. laevis*.

The subgenus *Macronthophagus,* with the type species *O. uenoi* Ochi, 1995 (for a review see Ochi 2003b), is likely monophyletic group of seven closely related species (probably *O. curvicarinatus* Boucomont, 1914 should be excluded) distributed in southeast Asia. Four species of this subgenus: *O. diabolicus* Harold, 1887, *O. manipurensis, O. nilgirensis* Gillet, 1921 and *O. rubricollis* Hope, 1831 were initially placed in *Serrophorus* Balthasar, 1935. The remaining three species were not in that subgenus because they were described after Balthasar conducted his work. All species of *Macronthophagus* posses similarly shaped aedeagus and lamellae copulatrix (U-shaped with very thin inferior left and right parts, for example see Fig. 2d) along with the complex of the following external characters: antennal scapus serrate; mesotibial and metatibial apex produced into three distinct lobes, mesotarsal and metatarsal first tarsomere broadened, especially in females; internal apical angle of protibia with small spine in males and very small

tooth in females; body large; vertex with lamina-shaped horn. Therefore, the validity of this subgenus seems to be well supported.

The subgenus *Sunenaga* was comprised of nine species in its original taxonomic limits: *O. anguliceps* (the type species), *O. avocetta* Arrow, 1933, *O. avocettoides*, *O. blumei* Lansberge, 1883, *O. digitatus*, *O. cameloides* d'Orbigny, 1900, *O. mindanaensis* Boucomont, 1914, *O. ribbei* Boucomont, 1914, and *O. wallacei* Harold, 1871. This subgenus was distinguished mainly on the basis of following characters: mesotibial and metatibial apex produced into three distinct lobes; antennal scapus serrate; male clypeal margin reflexed, male head shape sometimes modified. It has to be noted that no significant genital similarities were found among the included species. Having re-examined all species (except *O. cameloides*), and taking into account external characters along with the structure of aedeagus and lamella copulatrix, we can state that *Sunenaga* in that sense represents an artificial, non-monophyletic group. The last five from the above listed species have to be excluded from this subgenus, but their position within the genus *Onthophagus* is unclear and awaits further research. The type species of this subgenus, *O. anguliceps*, together with *O. avocetta*, *O. avocettoides* and *O. blumei* represent a monophyletic group (hereafter called *anguliceps*-group) sharing a similarly shaped aedeagus (and almost identical lamella copulatrix, for example see Fig. 2b) and unique structure of head in major males: clypeal margin reflexed into long finger-like process; lateral margins strongly produced outwards into upward process; vertex with horn. Based on similarly shaped lamella copulatrix (for example see Fig. 2c), structure of aedeagus, and habitus, *O. streltsovi* together with *O. digitatus* and probably *O. kaengkrachangus* form a monophyletic group (hereafter called *digitatus*-group), closely related to *anguliceps*-group, but distinguished from the latter by the lack of specifically modified head and protibia in major males. The structure of the lamella copulatrix in *O. seniculus* (the type species of *Serrophorus*) is also close to that in the *anguliceps*-group and *digitatus*-group but differs from both of them more strongly than those two groups differ from one another. All three groups (*anguliceps*-group, *digitatus*-group and *Serrophorus* in our sense) share a probable synapomorphy: presence of the additional median sclerite (AMS) between the inferior parts of lamella copulatrix (Figs. 2a–c). But representatives of *Serrophorus* (in the sense of this paper) seem to be a sister group to the lineage formed by the *digitatus*-group and *anguliceps*-group, because the former possess aedeagi with lobed and medially notched bases and the superior left and right parts of the lamella copulatrix fused together (Fig. 2a, indicated with arrow). In the *anguliceps*-group and *digittaus*-group the superior left and right parts are almost completely divided (Fig. 2b, c, indicated by arrow). The shape of the lamella copulatrix of *Macronthophagus* seems to be even more different from the lineage (*Serrophorus* (*anguliceps* + *digitatus* groups)). First, it lacks the additional median lamella; second, the shape of the inferior parts is strongly modified (Fig. 2d). Although this subgenus has fused superior left and right parts, which probably indicates its closer relation to *Serrophorus* then to the lineage formed by the *digitatus*-group and *anguliceps*-group, all four groups (*Macronthophagus*, *Serrophorus*, *anguliceps*-group and *digitatus*-group) have a U-shaped lamella copulatrix that might also indicate their sister relationships at a higher phylogenetic level. However, this character is present in some other, probably related onthophagine lineages (for example *Parascatonomus*). So, whether it is a synapomorphy of the above mentioned group is not yet resolved.

The here hypothesized close relationships of *Serrophorus*, the *anguliceps*-group and the *digitatus*-group support the opinions of some authors (Kabakov & Yanushev 1983, Kabakov 1994) that these groups be combined into the single taxon *Serrophorus*. However, this would be a premature taxonomic action because no shared external morphological characters have been found to support the combination of these three groups. Only the specific shape of the lamella copulatrix is indicative, but this is not a practical character since it is difficult to observe. As a result, we recognize two subgenera, *Serrophorus* and *Sunenaga*, and consider that the latter comprises two species goups: the *anguliceps*-group and the *digitatus*-group. The placement of *digitatus*-group in *Sunenaga* makes the diagnosis of this subgenus using external characters difficult. We include the following species in the subgenus *Sunenaga*: *O. anguliceps*, *O. avocetta*, *O. avocettoides*, *O. blumei*, *O. digitatus*, *O. kaengkrachangus* and *O. streltsovi*.

The question about the subgeneric/generic status of *Serrophorus* and related taxa discussed here remains still open and awaits future phylogenetic research on the tribe Onthophagini.

Acknowledgements

We are very grateful to Alexey Streltsov (Kaluga University, Russia) for his valuable help at various stages leading to this paper. We are also very thankful to Alexey Solodovnikov (ZMUC) for his suggestions, advice, support and the review of the manuscript. Our thanks are due to: Margaret Thayer and Alfred Newton (FMNH), Maxwell Barclay (BMNH) and Andrey Frolov (ZISP) for making material under their care available for this study. We are very grateful to Dr. Robert Angus (University of London) and Dr. Andrew Smith (Canadian Museum of Nature) for the linguistic review of the manuscript. This paper is completed during the stay of one of us (S.T.) as a visiting intern student at the Department of Entomology of the Natural History Museum of Denmark (ZMUC, Copenhagen), under financial support from the grants US NSF DEB-0715705 awarded to A. Solodovnikov (ZMUC) and A. Newton (FMNH), and from the frame grant 27989 of the Department of Entomology at ZMUC awarded to Thomas Pape. Overall support of that Entomology Department at Copenhagen is appreciated.

References cited

Arrow, G.J. (1931) *The Fauna of British India III, Coprinae*. Taylor & Francis, London, 428 pp.

Balthasar, V. (1935) *Onthophagus*-arten Chinas, Japans und der angrenzenden Ländern. *Folia Zoologica et Hydrobiologica*, 8, 303–353.

Balthasar, V. (1963) *Monographie der Scarabaeidae und Aphodidae der palaearktischen und orientalischen Region. Band 2 Coprinae (Onitini Oniticellini Onthophagini).* Tschechoslowakische Akademie der Wissenschaften Prague, 627 pp.

ICZN, (1999) *International Code of Zoological nomenclature (4th Ed)*. International Trust for Zoological Nomenclature, London, 306 pp.

Kabakov, O.N. (1992) Taxonomic position of *Parascatonomus* (Onthophagini, Scarabaeidae) with the description of new species from Southeast Asia. *Systematics and Ecology of Insects from Vietnam*, 196–209. (in Russian)

Kabakov, O.N. (1994) New species of the lamellicorn beetles subfamily Scarabaeinae (Coleoptera: Scarabaeidae) from Vietnam and neighbouring countries. *Entomological Review*, 73 (2), 300–317.

Kabakov, O.N. (2006) *Beetles of the subfamily Scarabaeinae (Insecta: Coleoptera: Scarabaeidae) of the fauna of Russia and adjacent countries.* Scientific Publications KMK, Moscow, 374 pp. (in Russian)

Kabakov, O.N. & Napolov, A. (1999) Fauna and ecology of Lamellicornia of subfamily Scarabaeinae of Vietnam and some parts of adjacent countries: South China, Laos, and Thailand. *Latvijas Entomologs*, 37, 58–96.

Kabakov, O.N. & Yanushev, B.B. (1983) Material on the fauna and ecology of the genus *Onthophagus* (Scarabaeidae) from Southeastern Asia. *In: Fauna and ecology of the animals of Vietnam*. Nauka, Moscow, pp. 156–165. (in Russian)

Ochi, T. (2003a) Studies on the Coprophagous Scarab beetles from East Asia. VII. Descriptions of two new subgenera of the genus *Onthophagus. Giornale Italiano di Entomologia*, 10(51), 259–274.

Ochi, T. (2003b) Studies on the Coprophagous Scarab beetles from East Asia. VIII. Revision of the subgenus *Macronthophagus* of *Onthophagus*. *Giornale Italiano di Entomologia*, 10(51), 275–300.

Ochi, T. & Kon, M. (1994) Dung beetles collected from Sabah, Borneo. *Elytra*, 22(2), 281–298.

Palestrini, C. (1980) Il sottogenere *Serrophorus. Bollettino del Museo di Zoologia dell'Universita di Torino*, 3, 13–20.

Palestrini, C. (1982) Il sottogenere *Pseudonthophagus*. *Bollettino della Societa Entomologica Italiana*, 114 (4–7), 97–102.

Palestrini, C. (1992) Sistematica e zoogeografia del genere *Onthophagus* sottogen. *Proagoderus* Lansberge (Coleoptera Scarabaeoidea). *Memorie della Società Entomologica Italiana. Genova*, 71(1), 1–358.

Zunino, M. (1979) Gruppi artificiali e gruppi naturali negli *Onthophagus*. *Bollettino del Museo di Zoologia dell'Universita di Torino*, 1, 1–18.

Zunino, M. & Halffter, G. (1988) Analisis taxonomico ecologico y biogreografico de un grupo americano de *Onthophagus*. *Museo Regionale di Scienze Naturale Torino Monografia*, 9, 1–211.