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A cybertaxonomic revision of the new dung beetle tribe Parachoriini (Coleoptera: Scarabaeidae: Scarabaeinae) and its phylogenetic assessment using molecular and morphological data

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Table of contents

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Abstract

Two Oriental dung beetle genera: *Parachorius* Harold, 1873 and *Cassolus* Sharp, 1875 have long had an ambiguous tribal position in Scarabaeinae (Coleoptera: Scarabaeidae), but have never been considered as closely related. A recently discovered species representing the morphological link between the two genera gave a hint to their possible close affiliation. To assess phylogenetic and taxonomic placement of these genera, I conducted phylogenetic analyses of global dung beetle samples using morphological (134 taxa, 232 characters) and molecular (551 terminals, 8 gene regions) data. Both morphological and molecular analyses strongly support the monophyly of *Parachorius* + *Cassolus*. This leads to the synonymy of *Parachorius* with *Cassolus* **new synonymy**, and resulted in the new generic concept for *Parachorius*. The isolated phylogenetic position of *Parachorius* and its morphological distinctiveness from all other known Scarabaeinae tribes suggest recognition of a new tribe, Parachoriini **new tribe,** to maintain the stability of tribal classification in dung beetles. Investigation of old and recent material of *Parachorius* revealed a large number of undescribed species and the need for a taxonomic revision of this genus. The revision of *Parachorius***,** powered by the 3i cybertaxonomic tool, is presented in this study. The revised *Parachorius* is comprised of 19 species from the Oriental and southeastern Palaearctic Regions, of which seven are newly described (*P. asymmetricus* **new species**, *P. bolavensis* **new species**, *P. longipenis* **new species**, *P. newthayerae* **new species**, *P. pseudojavanus* **new species**, *P. schuelkei* **new species**, and *P. solodovnikovi* **new species**). Three species names in *Parachorius* are synonymized**,** namely, *P. fungorum* Kryzhanovsky & Medvedev, 1966 = *P. krali* Utsunomiya & Masumoto, 2001 **new synonymy**; *P. thomsoni* Harold, 1873 = *P. lannathai* Hanboonsong & Masumoto, 2001 **new synonymy**; and *P. peninsularis* (Arrow, 1907) = *C. pongchaii* Masumoto, 2001 **new synonymy**. Two species originally described in *Cassolus* (*C. sumatranus* and *C. minutus*) are transferred to the genus *Panelus* Lewis, 1895. The rank of the genus *Macropanelus* is lowered to a subgenus within *Panelus* (i.e. *Panelus* (*Macropanelus*) **new status**).

Key words: Dung beetles, Scarabaeinae, systematics, cybertaxonomy, new tribe

Introduction

Two dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) genera *Parachorius* Harold, 1873 and *Cassolus* Sharp, 1875 from the Oriental Region are rare in collections due to their cryptic lifestyle, which is primarily non-coprophagous and remains largely unknown. Although, *Parachorius* and *Cassolus* were described over a hundred years ago, their generic concepts have been considered well defined and these two genera have never been considered as closely related until recently. At the same time, the tribal placements of these genera have been unstable and different authors tended to classify them in different tribes (Table 1). For example, *Cassolus* was placed in Deltochilini (= Canthonini) according to the first large revision of the Oriental and Palaearctic scarabaeines (Balthasar 1963) and suggested to be a member of the Onthophagini in the morphology-based phylogenetic analysis (Philips 2005, 2016). At the same time, (Balthasar 1963) placed *Parachorius* in Pinotini (Dichotomiini), while subsequent studies placed this genus in Coprini (Vaz-de-Mello 2007, 2008). In spite of their inconstant tribal placement, these two genera have never been placed within the same tribe. A recent study (Tarasov & Keith 2011) found a new species representing a morphological link between the two genera and suggested a putative synonymy between *Parachorius* and *Cassolus* as well as their close affiliation with the New World genus *Canthon* Hoffmannsegg, 1817 (tribe Deltochilini). Further, the monophyly of the clade comprising species of *Parachorius* and *Cassolus* occurring in China was supported by the morphological phylogenetic analyses (Bai *et al.* 2011).

TABLE 1. History of *Parachorius* and *Cassolus* tribal placements in Scarabaeinae.

Genus/study	Balthasar (1963)	Philips (2005, 2016)	Vaz-de-Mello (2007, 2008)
Cassolus	Deltochilini	Onthophagini	—
Parachorius	Dichotomiini	—	Coprini

The taxonomic investigation of the museum specimens and additional recently-collected material of *Cassolus* and *Parachorius* from the Oriental Region revealed that a large portion of their species diversity is still undescribed. Two reasons—their unknown diversity and unclear phylogenetic affiliations—motivated me to taxonomically revise these genera and elucidate their phylogenetic placement. The taxonomic revision was powered by 3i Interactive Key and Taxonomic Database Software (http://dmitriev.speciesfile.org/index.asp). The phylogenetic assessment was performed using molecular and morphological data.

In the morphological phylogenetic analysis, all species of *Cassolus* and *Parachorius* were integrated into the largest matrix available for Scarabaeinae, comprising representatives of all dung beetle lineages (Tarasov & Génier 2015; Tarasov *et al.* 2016). The molecular phylogenetic analysis was based on the largest molecular matrix assembled recently for Scarabaeinae (Tarasov & Dimitrov 2016).

The morphological and molecular datasets were analyzed separately using the parsimony and likelihood methods. Both analyses converged suggesting that *Parachorius* + *Cassolus* form a monophyletic group and their current placement in two different genera is unwarranted. This synonymy *Parachorius* = *Cassolus* **new synonymy** and a new concept of the genus *Parachorius* marked as **sensu novo** are established here. Moreover, both analyses also suggest that the lineage of *Parachorius* **sensu novo** (i.e., *Parachorius* + *Cassolus*) is clearly separated from all Scarabaeinae tribes phylogenetically and morphologically. Since taxonomic concepts of the described Scarabaeinae tribes were recently discussed and ascertained (Tarasov & Dimitrov 2016), the separate position of *Parachorius* did not allow placing it in any of them. These facts support the recognition of a new tribe Parachoriini **new tribe** in order to accommodate the genus *Parachorius* and preserve stability of dung beetle classification. This new tribe is described in this study.

This revisionary work introduced substantial taxonomic changes in *Parachorius.* Prior to this study, *Parachorius* and *Cassolus* was comprised of eight and nine species respectively. Presently, *Parachorius* is comprised of 19 species, of which seven are described herein as new. The genus is distributed almost across the Oriental Region, except Borneo and the Philippines, with some representatives occurring in the southeastern Palaearctic region (southern China). The majority of species is concentrated in Indochina. Three species names in *Parachorius* are synonymized: *P. fungorum* Kryzhanovsky & Medvedev, 1966 = *P. krali* Utsunomiya & Masumoto, 2001 **new synonymy**; *P. thomsoni* Harold, 1873 = *P. lannathai* Hanboonsong & Masumoto, 2001 **new synonymy**; and *P. peninsularis* (Arrow, 1907) = *C. pongchaii* Masumoto, 2001 **new synonymy**. Two species originally described in *Cassolus*: *C. sumatranus* Lansberge, 1885 and *C. minutus* Boucomont, 1914 are removed to the Afro-Oriental genus *Panelus* Lewis, 1895. This transfer motivated me to undertake an investigation of *Panelus* morphology, which suggested its closest similarity to the genus *Macropanelus* Ochi, Kon, & Araya, 1998 occurring in Sumatra. From the latter, *Panelus* differs only by the significantly smaller body size. Here, I argue that the body size is not sufficient to treat *Macropanelus* as a separate genus and therefore lower its rank to a subgenus within the genus *Panelus* (*i.e.*, *Panelus* (*Macropanelus*) **new status**).

Materials and methods

Nomenclatural acts. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Commission on Zoological Nomenclature. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:8226E27D-E3A9-481A-B51B-558643BBB03A.

Taxa names and concepts. The tribal classification follows Scholtz *et al.* (2009), except tribes Coprini, Deltochilini, Dichotomiini, and Sisyphini whose concepts follow Tarasov and Dimitrov (2016). The nomenclature for family-group names follows Smith (2006) and Bouchard *et al.* (2011).

Material deposition. The depositories of the material examined in this paper are abbreviated as follows:

BMNH—The Natural History Museum, London, United Kingdom (M. Kerley, M. Barclay)
CST—Sergei Tarasov private collection
DEI—Senckenberg German Entomological Institute, Müncheberg, Germany (L. Zerche)
FMNH—The Field Museum of Natural History, Chicago, United States of America (M. Thayer, J. Boone)
ISNB—Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (A. Drumont)
MCSN—Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy (R. Poggi)
MHNG—Muséum d'Histoire Naturelle, Geneva, Switzerland (G. Cuccodoro)

MNHN—Museum national d'Histoire naturelle, Paris, France (O. Montreuil, A. Mantilleri)
NHMB—Naturhistorisches Museum, Basel, Switzerland (E. Sprecher)
NMPC—National Museum, Prague, Czech Republik (J. Hájek, M. Fikáček)
NMW—Naturhistorisches Museum, Wien, Austria (H. Schillhammer)
NSMT—National Science Museum (Natural History), Tokyo, Japan (S. Nomura)
OUMNH—Hope Entomological Collections, Oxford, United Kingdom (D. Mann)
RMNH—National Museum of Natural History, Leiden, The Netherlands (J. Krikken, J. Huijbregts)
ZIN—Zoological Institute, St.-Petersburg, Russia (A. Frolov)
ZMHB—Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (J. Frisch)
ZMUC—Natural History Museum of Denmark, Copenhagen, Denmark (A. Solodovnikov, S. Selvantharan).
ZMUM—Zoological Museum of Moscow State University, Moscow, Russia (A. Gusakov)

Morphological data and analyses. *Illustrations and abbreviations.* The majority of the photographs were taken with a Microptix photo system, and others were taken with a Canon EOS 500D digital camera attached to a Leica MZ16 microscope. Aedeagi, endophallic sclerites, and some skeletal structures were photographed in an alcohol-based hand sanitizer that was used to fix the position of structures for photography. The color schemes of the endophallic sclerites were drawn in Adobe Illustrator. The original figure illustrations are available at Figshare https://doi.org/10.6084/m9.figshare.5405563.v1.

Examined taxa. For this study I examined almost all species (except *C. minutus* Boucomont, 1914 and *P. maruyamai* Masumoto, Ochi, & Sakchoowong, 2012) previously assigned to *Cassolus* and *Parachorius*, in addition to new material. In total approximately 200 specimens of the genus *Parachorius* were examined.

Morphological principles and terminology. The morphological terms used in the present study follow Edmonds (1972), Tarasov and Solodovnikov (2011), and Tarasov and Génier (2015). The abbreviations used in describing morphology and illustrations (Figs. 1, 4) expand as follows:

A—axial sclerite
FLP—fronto-lateral peripheral sclerite
LC—lamella copulatrix
LFP—long fork-like process
R—metasternal ridge
SA—subaxial sclerites
SRP—superior right peripheral sclerite
Tub—phallobase basal tubercles

Character matrix. All 19 *Parachorius* species were scored into the character matrix that was previously developed for Scarabaeinae (Tarasov & Génier 2015; Tarasov *et al.* 2016). The species *P. maruyamai* was scored from the original description. In addition to them, a representative of the Afro-Oriental genus *Panelus,* putatively representing a taxon closely related to *Parachorius,* was also integrated into the matrix. The integration of these species into the previous matrix required the inclusion of 27 additional characters listed in the Character Report section. The original character statements remained unchanged and can be found in the original paper (Tarasov & Génier 2015).

The character matrix was constructed using Mesquite version 3.03 (Maddison & Maddison 2015) and includes 134 taxa and 232 characters; it can be downloaded from MorphoBank (www.morphobank.org project 2286). The character report is given below.

Phylogenetic analyses. The phylogenetic inference was performed under the maximum parsimony approach (MP) using TNT version 1.1 (Goloboff *et al.* 2008). The analyses were run omitting all ambiguous characters (characters 122, 71, 73, 74, 161, 204) as was suggested in Tarasov and Génier (2015).

Both the parsimony analyses under equal (EW) and implied weights (IW) were performed. The EW analysis was run using the following TNT settings: traditional search with 5000 replications and up to 200 trees saved per replication, tree buffer set to store 1M trees, TBR, the default collapsing rule, trees automatically condensed after search. The IW analyses were run under the same options except with number of replications = 1000. To explore the sensitivity of the results, three IW analyses were run under different values of the concavity factor, k = (40, 70, 100). The limited set of concavity factor was selected on the ground that its extensive range was shown to insignificantly affect tree topology in the previous phylogeny (Tarasov & Génier, 2015) that served as basis for present study.

To assign branch support values, I calculated Bremer support (BS) by searching suboptimal trees up to five steps longer than the shortest one using TBR swapping on the shortest trees.

Molecular data and analyses. Present molecular dataset and analytical procedures are based on recent large-scale molecular study on Scarabaeinae (Tarasov & Dimitrov 2016).

Taxon sample and vouchers. For the present study, two representatives corresponding to the original definition of *Parachorius* and one representative corresponding to the original definition of *Cassolus* were sequenced and integrated in the molecular dataset of Tarasov and Dimitrov (2016). In addition, a species of *Panelus* from Monaghan *et al.* (2007) was also included. In total, the molecular dataset comprised 551 terminals and eight gene regions. The information on the voucher specimens used in this study is summarized in Table 2.

TABLE 2. Species of *Parachorius* sequenced for the study and their GenBank (www.ncbi.nlm.nih.gov/genbank) accession numbers.

Species/genes	*18s*	*28sD2*	*28sD3*	*Tp1*
P. thomsoni	KX898975	KX898978	KX898981	KX898973
P. sp. (female, *P. thomsoni* or *P. fungorum*)	KX898976	KX898979	KX898982	KX898974
P. longipenis	KX898977	KX898980	NA	NA

Molecular markers. The previous study (Tarasov & Dimitrov 2016) that serves as a backbone for the present analytical procedure used eight phylogenetically informative markers: 16s ribosomal RNA (*16s*), 18s ribosomal RNA (*18s*), 28s ribosomal RNA domain 2 (*28sD2*), 28s ribosomal RNA domain 3 (*28sD3*), cytochrome c oxidase I (*COI*), carbamoylphosphate synthethase (*CAD*), topoisomerase I (*TP1*), and wingless (*Wg*). For the species of *Cassolus* and *Parachorius* used in the present molecular analysis, it was possible to sequence four gene regions (*18s*, *28sd2*, *28sd3*, *and TP1)*. DNA extraction, PCR amplification, and sequencing were done as detailed in Tarasov and Dimitrov (2016).

Sequence alignment, site selection, and partitioning. The sequences were managed and arranged into the final datasets in Geneious version R6 (Kearse *et al*. 2012). The alignment was performed with the web-based version of MAFFT (Katoh & Standley 2013) using Q-INS-i option, which takes into account secondary structure for rDNA genes with less than 300 sequences (*18s, 28sD2*), and L-INS-i for the rest. The secondary structure for rDNA genes was reconstructed in RNAalifold (Bernhart *et al*. 2008) based on the alignments obtained from MAFFT.

The next steps in data preparation are the same as those implemented in the recent backbone study of Scarabaeinae (Tarasov & Dimitrov 2016). For details, I refer the reader to that work, although the main steps are summarized below.

That study tested the performance of the gene regions using the Bayesian models adequacy assessment method of Brown and ElDabaje (2009) and suggested that exclusion of the partitions that failed the model adequacy evaluation has a potential to improve phylogenetic inference. Herein, I follow this approach and exclude "inadequate" partitions from the molecular analysis. The list of these partitions is given in Tarasov and Dimitrov (2016). In addition to them, the gap-rich sites containing gaps in more than 20% of the sequences were also removed (Tarasov & Dimitrov 2016). The partitioning scheme used here is the same as the one elucidated in the abovementioned backbone work (dataset DT3) using Partition Finder (Lanfear *et al.* 2014).

Rogue taxa exclusion. Specifically for this study, in order to increase the support and informativeness of the final tree, we excluded rogue taxa using RogueNaRok web-based software (Aberer *et al.* 2013). The RogueNaRok was run on the set of 1000 bootstrap trees from the maximum likelihood (ML) analysis, with droplet size = 1 using RogueNaRok algorithm to optimize support with the respect to the majority consensus tree. One hundred and five terminals were identified as rogues and were subsequently excluded from the final ML run.

Maximum likelihood (ML). The computations were performed on the Abel Cluster, owned by the University of Oslo and the Norwegian metacenter for High Performance Computing (NOTUR)

Two runs of the ML analyses were performed using RAxML version 8.0.26 (Stamatakis 2014) running on the High Performance Computing cluster Abel at the University of Oslo. Both runs used *–f a* option to perform rapid

Bootstrap analysis (1000 replicates) and search for best scoring ML tree in one program run and the GTRCATX model *(-m GTRCATX)* applied to each partition; the final tree was evaluated under GTRGAMMA model.

The set of the bootstrap trees from the first run was used to elucidate the rogue taxa (see Rogue taxa exclusion section) and then the second run was conducted using the dataset where the rogue taxa were excluded. The phylogeny from the second run is used here in further discussion.

Using cybertaxonomy for the* Parachorius *revision. The taxonomic revision of the genus *Parachorius* was performed using the 3i Interactive Key and Taxonomic Database Software (http://dmitriev.speciesfile.org/index.asp). This software represents a powerful tool for cybertaxonomy that substantially facilitates and accelerates production of taxonomic revisions. Herein, I used this software to manage taxonomic and distributional data, generate species description, formulate differential diagnoses, draw distribution maps, and construct key to species. The web version of the revision is available from http://dmitriev.speciesfile.org/key.asp?key=parachorius&lng=En&i=1&keyN=1.

Results of phylogenetic analyses

Analysis of morphological data. The EW parsimony analysis of the complete morphological matrix yielded 48026 most parsimonious trees (MPT) of length 528 whose, generally unresolved, strict consensus is provided in Fig. 1A. Although all *Cassolus* and *Parachorius* species are recovered as a separate monophyletic group with Bremer support of 3, this clade forms a polytomy with other dung beetle lineages. Implied-weights analyses even with extended range of the concavity factor (k = 40, 70, 100, 500, 1000) and 10000 replications surprisingly did not manage to recover MPT(s) of the same length as those of EW analysis. All MPT(s) from IW analyses were longer than MPT(s) of EW analysis. In order to obtain a better-resolved tree under IW, I selected all *Parachorius* and *Cassolus* species along with other 33 species from the matrix representing the phylogenetic diversity of scarabaeines (total 51 terminals). The analysis of this reduced dataset under IW yielded MPT(s) of the same length (L = 255) as the analysis of the reduced dataset under EW. Under IW, the analyses with concavity factor k = 40, 70, and 100 were run to test the sensitivity of the result. All three analyses yielded from 34 to 44 MPTs with similar strict consensuses. The analyses with k = 70 and 100 resulted in the same consensus trees (Fig. 1B). The consensus of the analysis with k = 40 differed slightly in arrangement of basal lineages while linkage within *Parachorius* and *Cassolus* was the same as that in the analyses with k = 70 and 100.

Implied-weights analyses of the reduced dataset are better resolved and consistent with the analysis of the full dataset (Fig. 1A–B). In these results *Parachorius* and *Cassolus* also form a monophyletic group, which is sister to the clade comprising *Sinapisoma*, *Ateuchus*, *Generidium*, *Copris*, and *Dichotomius*. The clade *Parachorius* + *Cassolus* is defined by five synapomorphies—1:0, 122:1, 213:1, 217:1, 225:1 (see Character report). In the *Parachorius* + *Cassolus* clade, the previous concepts of these genera are not monophyletic with *Parachorius* species being nested within *Cassolus* ones. Specifically, clade *Parachorius* + *Cassolus* splits into three subclades (Fig. 1B): subclade (A) comprising two closely related species from Java, of which one was formerly attributed in *Cassolus*; subclade (B) comprising species that were previously placed in *Parachorius*; and subclade (C) largely uniting species from the genus *Cassolus*.

Analysis of molecular data. The inferred molecular tree is almost the same with the one inferred in the backbone study of Tarasov and Dimitrov (2016). Thus, I do not overview the main results of the molecular phylogeny as this is summarized in the aforementioned work. The present molecular tree strongly supports (bootstrap support of 100%) monophyly of *Cassolus* + *Parachorius* (Fig. 2A–B). This clade emerges sister to the clade comprising the New World tribe Eurysternini and the lineage formed by the genera *Ochicanthon*, *Madaphacosoma*, and *Epactoides* that occur in the Oriental Region, the Eastern Arc Mountains, and Madagascar, respectively. In turn, this larger clade comprising *Cassolus* + *Parachorius,* Eurysternini, *Ochicanthon*, *Madaphacosoma*, and *Epactoides* comes up as sister to the primarily Old World tribe Sisyphini (clade *P* in Fig. 2A–B). The bootstrap support for this clade is < 50, though.

Unfortunately, the limited number of included *Cassolus* and *Parachorius* species does not allow assessment of the phylogenetic relationships within the clade *Parachorius* + *Cassolus* using molecular data.

Discussion of the phylogenetic results. Both molecular and morphological analyses converged in supporting monophyly of *Parachorius* + *Cassolus* with high support values (morphology: Bremer support value 3; molecules:

100% bootstrap support) that is consistent with the previous morphological analysis (Bai *et al.* 2011). The morphological analysis (Fig. 1A–B) that also aimed at resolving the relationships within *Parachorius* + *Cassolus* clade suggests that the species formerly included in *Parachorius* are nested among *Cassolus*, thereby supporting the synonymy between *Cassolus* and *Parachorius*, which is established here. This synonymy results in a new concept of the genus that is marked as *Parachorius* **sensu novo** (see details in Taxonomic results and discussion section).

Molecular and morphological analyses show different linkage between *Parachorius* and other Scarabaeinae lineages (Figs. 1B, 2A–B). In the molecular results *Parachorius* forms a clade with the tribes Eurysternini, Sisyphini, and the genera *Ochicanthon, Madaphacosoma*, and *Epactoides*, while morphological analyses support its sister affiliation with a clade including *Sinapisoma*, *Ateuchus*, *Generidium*, *Copris*, and *Dichotomius.* Nevertheless, both molecular and morphological results are consistent in placing *Parachorius* separately from all other described scarabaeine tribes. Thus, the phylogenetic results suggest that *Parachorius* cannot be placed in any of them. This is graphically shown in Fig. 2A where the concepts of the existing tribes are mapped onto the phylogeny.

Previous hypothesis (Tarasov & Keith 2011) that *Parachorius* can be closely affiliated with the tribe Deltochilini was not supported by the present study. Additionally, the present study does not find any evidence for close affiliation between *Parachorius* and somewhat similarly looking *Panelus*. In the molecular analysis, *Panelus* was identified as a rogue taxon and excluded from the final run. However, in the molecular run of the full dataset (*i.e.*, rogue taxa included), *Panelus* is recovered as sister to the tribe Coprini, and in turn, they two emerge as sister to the African genus *Pedaria* (*i.e.*, *Pedaria* + [*Panelus* + Coprini]). The clade *Pedaria* + *Coprini* is remotely related to *Parachorius* in the analyses with and without rogue taxa (Fig. 2A). In the morphological analysis, *Panelus* emerges as sister to the Oriental genus *Ochicanthon* (Fig. 1B) and this clade is remotely placed from *Parachorius* as well. Such incompatible positions of *Panelus* between molecular and morphological trees can be either a result of convergent morphological evolution in *Panelus* or incorrect identification of "*Panelus*" voucher deposited at GenBank. If the latter is the case, then the close affiliation of *Ochicanthon* and *Panelus* in the morphological analysis along with the close affiliation of *Ochicanthon* and *Parachorius* in the molecular analysis, may well indicate that *Panelus* and *Parachorius* are closely related as well (*i.e.*, *Panelus* can be a putative member of the clade (P) in Fig. 2). However, regardless of the relationships based on molecular data, morphological analysis unequivocally indicates that *Parachorius* and *Panelus* are drastically dissimilar in their morphological characters.

Presently, the scarabaeines are classified into 12 tribes. The majority of these tribes or tribal groups, namely Gymnopleurini, Scarabaeini, Onitini, Eucraniini, Eurysternini, Phanaeini, Oniticellini + Onthophagini, and Sisyphini are well diagnosed and considered monophyletic (Tarasov & Dimitrov 2016). At the same time, the taxonomic limits, and diagnosis of the tribes Deltochilini, Dichotomiini, Ateuchini, and Coprini have long been contentious. Recently Tarasov and Dimitrov (2016) defined new concepts and diagnoses for those problematic tribes (except Ateuchini that is not critical for present study), which, at the same time, placed many dung beetle genera in *incertae sedis* category, *i.e.*, unassigned to any existing tribe. Given these results, new tribes may need to be established to accommodate the generic diversity of Scarabaeinae, thus invoking need for the new dung beetle classification (Tarasov & Dimitrov 2016).

The isolated phylogenetic position of *Parachorius* outside every existing tribe is supported by both molecular and morphological analyses, which along with its distinct morphological diagnosis point out that this genus has to be separated into the new tribe Parachoriini, which is described here (see Systematics section). Although, the tribe Parachoriini is monotypic, its description is a logical step to the new phylogeny-based classification of dung beetles with morphologically diagnosable taxonomic units.

In the IW morphological analysis Parachoriini is defined by five synapomorphies (1:0, 122:1, 213:1, 217:1, 225:1) of which only two are not subjected to reversal changes within Parachoriini and hence shared by all its members. These synapomorphies shown in Fig. 1C–E are 1:0 (phallobase basal area with two tubercles dorsally) and 225:1 (metasternum with either long or short transverse basal ridge). Since the unique combination of these two states unequivocally diagnoses Parachoriini, I use only them to diagnose this tribe and exclude the three remaining synapomorphies (basal sclerite of galea longitudinally elongate, apical spur of protibia in males reaches middle of protarsomere 3, and protibia with first and second teeth distinctly separated from each other) from further discussion.

Taxonomic results and discussion

Below, I briefly summarize the main taxonomic results and actions taken in the present study.

1. ***Parachorius* (= *Cassolus* new synonymy).** The synonymy of *Parachorius* and *Cassolus* is supported by the phylogenetic analyses. The earlier name *Parachorius* takes precedence over *Cassolus*. This new concept includes 19 species, of which six were moved from *Cassolus* and seven described as new. *Parachorius* is comprised of the following species (see Fig 1A–B):

P. asymmetricus Tarasov **new species**
P. bolavensis Tarasov **new species**
P. fukiensis (Balthasar, 1960) **new combination**
P. fungorum Kryzhanovsky & Medvedev, 1966
P. globosus Arrow, 1931
P. gotoi (Masumoto, 1986) **new combination**
P. hookeri Arrow, 1931
P. humeralis (Arrow, 1907) **new combination**
P. javanus (Boucomont, 1914) **new combination**
P. longipenis Tarasov **new species**
P. maruyamai Masumoto, Ochi, & Sakchoowong, 2012
P. newthayerae Tarasov **new species**
P. nudus (Sharp, 1875) **new combination**
P. peninsularis (Arrow, 1907) **new combination**
P. pseudojavanus Tarasov **new species**
P. schuelkei Tarasov **new species**
P. semsanganus Tarasov & Keith, 2011
P. solodovnikovi Tarasov **new species**
P. thomsoni Harold, 1873

2. ***Parachorius* species names synonymized**. Two species names of *Parachorius* and one of *Cassolus* are synonymized based on the study of their morphology: *P. fungorum* Kryzhanovsky & Medvedev, 1966 = *P. krali* Utsunomiya & Masumoto, 2001 **new synonymy**, *P. thomsoni* Harold, 1873 = *P. lannathai* Hanboonsong & Masumoto, 2001 **new synonymy**, and *P. peninsularis* (Arrow, 1907) = *C. pongchaii* Masumoto, 2001 **new synonymy**.

3. ***Parachorius species inquirenda.*** The identity of *Panelus quadridentatus* (Balthasar, 1952) described from Vietnam and regarded as the synonym of *Parachorius nudus* (Balthasar 1963) needs further research. The type of the species is lost while the original description is poor that precludes any reliable inference of the species identity. Thus, I formally treat it as *species inquirenda* (see *Parachorius nudus* description for details).

4. **Parachoriini new tribe.** Morphological and molecular phylogenetic analyses suggest that the genus *Parachorius* has to be assigned to a separate new tribe Parachoriini, which is described below.

5. **Synonymy of *Panelus* and *Macropanelus***. The genus *Macropanelus* Ochi, Kon, & Araya, 1998 occurs in Sumatra and is comprised of three species (Ochi *et al.* 1998, 2008). The original description of *Macropanelus* lists six characters, mainly of the leg, abdomen, and metasternum morphology, which separate this genus from *Panelus* Lewis, 1895. The latter totals around three dozen species distributed in the Afrotropical and Oriental Regions. The generic level for *Macropanelus* is not phylogenetically supported (Ochi *et al.* 1998). Moreover, the differential characters of metasternum and leg morphology listed in the original description (Ochi *et al.* 1998) fall within the limits of the variation in the genus *Panelus*. The only reliable character that separates *Macropanelus* from *Panelus* is the larger body size in *Macropanelus*. Such important characters as elytral striation, aedeagal shape, and structure of aedeagus sclerite, which usually differ between Scarabaeinae genera, are identical in *Macropanelus* and *Panelus.* Given this evidence and the lack of phylogenetic support for the generic identity of *Macropanelus*, I lower its rank to subgeneric within the genus *Panelus*. Since the name *Panelus* takes the precedence, the name *Macropanelus* should have subgeneric status (*i.e.*, *Panelus* (*Macropanelus*) **new status**)

6. **Species transferred from *Cassolus* to *Panelus.*** Two species, previously placed in *Cassolus* are moved to the genus *Panelus* in this study. These species are treated below.

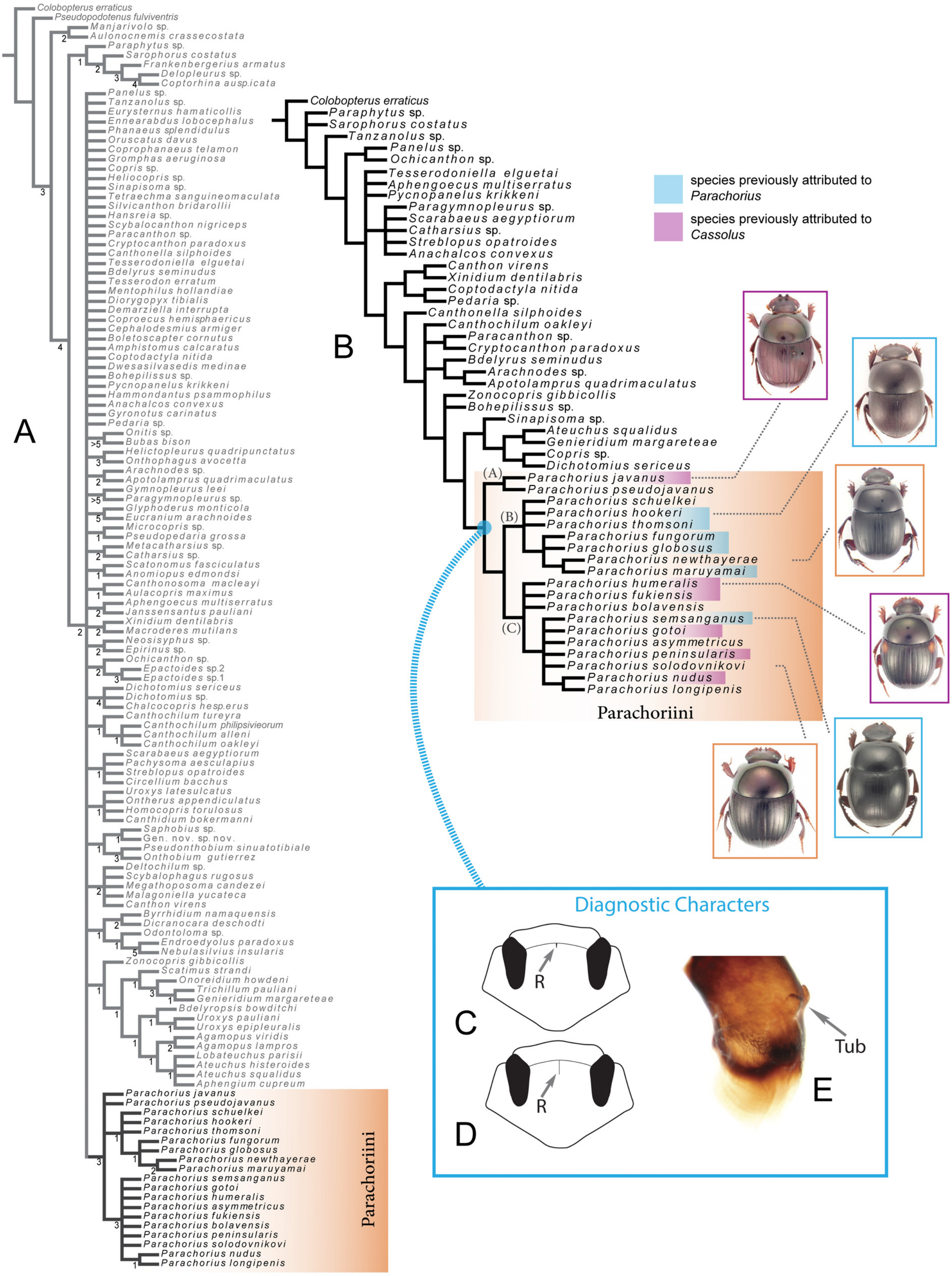

FIGURE 1. Diagnostic characters and phylogenetic position of the tribe Parachoriini **new tribe** (highlighted in orange) in morphological phylogeny of Scarabaeinae. (A) The strict consensus tree with Bremer support values comprising all analyzed taxa from equal weight analysis. (B) The strict consensus tree inferred using reduced taxon sample under implied weights option (k = 70 and 100). The species previously placed in *Cassolus* and *Parachorius* are highlighted in purple and blue respectively. (C–E) Diagnostic characters of the tribe Parachoriini. (C–D) Short and long ridges of metasternum respectively. (E) Phallobase with basal tubercles.

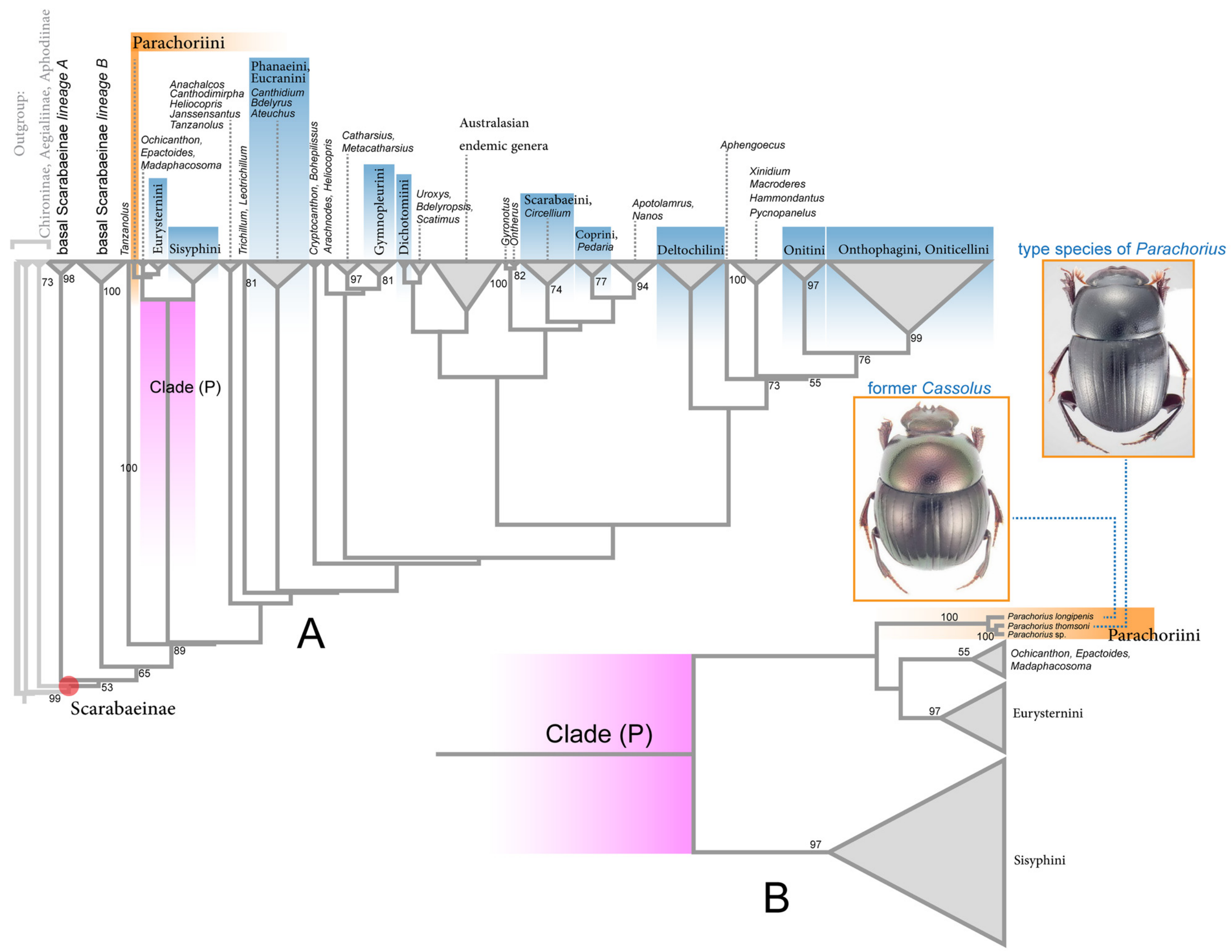

FIGURE 2. Phylogenetic position of the tribe Parachoriini **new tribe** (highlighted in orange) in global molecular phylogeny of Scarabaeinae. (A) Maximum likelihood tree of 446 Scarabaeinae terminals (rogue taxa excluded). The terminals are stylized based on taxonomy, with the size of the cone corresponding to the number of analyzed terminals. The clades corresponding to scarabaeine tribes are highlighted in blue. Values above branches indicate bootstrap support that is shown only if value > 50%. Clade "P" is shown in purple. (B) Clade P magnified.

***Panelus* (*Macropanelus*) *sumatranus* (Lansberge, 1885) new combination**
(Fig. 3A–D)

Cassolus sumatranus Lansberge, 1885: 2
Cassolus sumatranus; Boucomont 1914: 251
Cassolus sumatranus; Balthasar 1963: 263

Type locality. Sungei-Bulu, Sumatra

Comments. The species *Cassolus sumatranus* Lansberge, 1885 was originally placed in the genus *Cassolus*. Its overall similarity with the species of *Panelus* was first noticed by Boucomont (1914). The examination of the type series revealed that this species shares the diagnostic characters of the representatives from the genus *Panelus* subgenus *Macropanelus*. These characters are the asymmetrical shape of aedeagus, structure of endophallic sclerites, and the striation of elytra (some of them are provided in Fig. 3). Given this evidence, I transfer *Cassolus sumatranus* to *Panelus.* The formal inclusion of this species in the phylogenetic analysis was beyond the scope of present work since morphological characters unambiguously identify the taxonomic position of this species in *Panelus*.

Material examined. Holotype: male, "Sumatra Sungei-Bulu Seft 1878 O. Beccari / Typus / sumatranus Lansb.

/ Cassolus Sumatranus Lansbge. Type / Museo Civic di Genova / Holotype Cassolus sumatranus Lansberge, 1885 S. Tarasov det. 2010 / Panelus sumatranus (Lansberge, 1885) S. Tarasov det. 2010", 1°44'10"S, 105°23'30"E (MCSN).

Indonesia: 1 male, Sumatra Sungei-Bulu Seft 1878, 1°44'10"S, 105°23'30"E (O. Beccari) (MNHN). **1 female**, Sumatra Sungei-Bulu Seft 1878, 1°44'10"S, 105°23'30"E (O. Beccari) (MCSN).

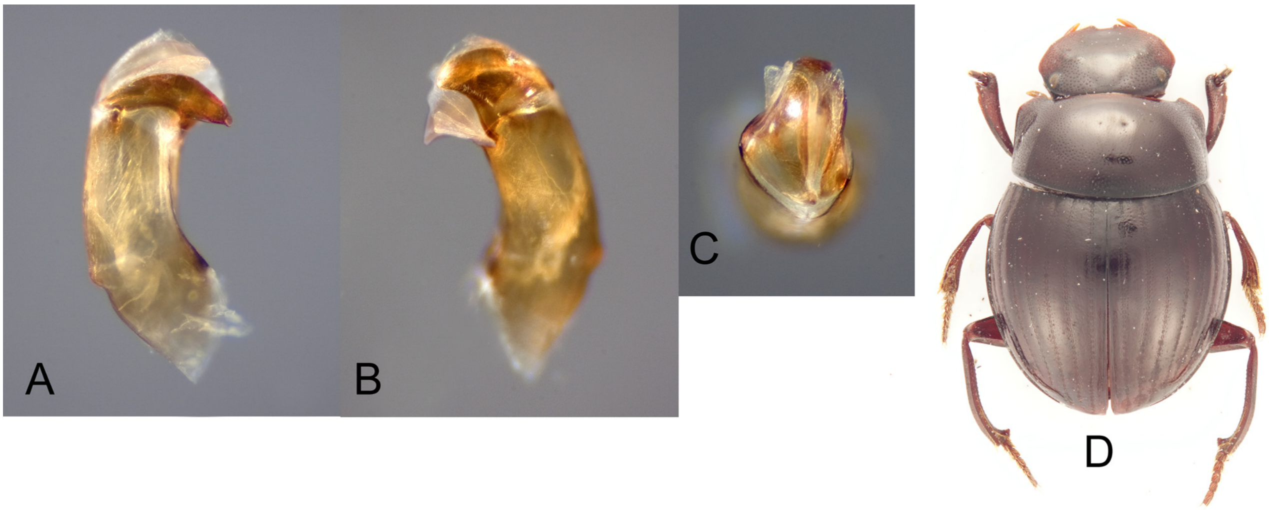

FIGURE 3. Morphology of *Panelus sumatranus*. (A–B) aedeagus in lateral view. (C) Parameres in dorsal view. (D) Habitus.

Panelus (*Panelus*) *minutus* (Boucomont, 1914) new combination

Cassolus minutus Boucomont, 1914: 252
Cassolus minutus; Balthasar 1963: 263

Type locality. Mt. Gedeh, Java

Comments. This species was originally described in *Cassolus*. Unfortunately, I was not able to locate the type specimen of this species in the collection of MNHN where it was presumably deposited. However, the original description of Boucomont (1914) includes evidence allowing the taxonomic assessment of this species. In that paper, Boucomont gives two important notes: (1) the species *C. minutus* is so similar to *Panelus parvulus* Waterhouse, 1874 that can be confused with it, and (2) both *C. sumatranus* [*i.e.*, *Panelus sumatranus*] and *C. minutus* remarkably resemble *Panelus* in their body shape, epistome, tarsi, and protibia. Additionally, Boucomont (1914) mentioned that *C. minutus* is significantly smaller in size than *C. sumatranus*. Boucomont's findings of the close affiliations between *C. sumatranus* and the members of *Panelus* are supported by this study. I follow the mentioned evidences for similarity between *C. minutus* and the members of *Panelus,* and thereby transfer *C. minutus* to *Panelus* as well.

Systematics

Tribe Parachoriini Tarasov new tribe

Type genus. ***Parachorius*** **Harold, 1873 here designated.**
urn:lsid:zoobank.org:act:BEC3CB84-5E85-4AA9-842C-7F2A02BC0C62

Description. Body coloration usually more-or-less uniform, dark, sometimes dark brown with reddish tinge, and/or elytral humeral area with yellow spot; clypeus with two teeth; gular ridges invaginated almost along entire area of gula; gular ridges form sclerotized roof over gula and dorsal process of tentorium posteriorly.

Pronotum laterally rounded or, with varying degree between males and females, angulate in anterior half. Anterior portion of hypomera depressed; hypomera anterior ridge stretches toward lateral margin of hypomera.

Elytron with eight distinctly visible striae. Wings usually normally developed, one species has reduced wings. Wing *MPa* vein present.

Metasternum with transverse basal ridge that is either short or long.

Protibia apical spur and protarsus present in both males and females; mesotibia with two apical spurs, metatibia with one spur; mesotarsal and metatarsal claws simple, present; in males profemur anterior margin and metafemur posterior margin usually produced in angle, while metatibia is strongly curved, notched, and/or denticulate.

Pygidium not grooved and without medial pit. Male parameres either symmetrical or not, in some species with horn-like upper lobes. Dorsal basal area of phallobase with two tubercles.

Endophallic sclerites*:* axial and SA sclerites present; SRP sclerite ring-shaped, FLP sclerite can be present or absent (Fig. 4A–C).

Body length 3.5–10.6 mm.

Diagnosis. The tribe Parachoriini is easily separated from all other dung beetle lineages and tribes by the combination of two morphological character: (1) phallobase basal area with two tubercles dorsally (Fig. 1E) and (2) metasternum with either short or long transverse basal ridge (Fig. 1C–D).

Taxonomical note. The tribe is monotypic**.**

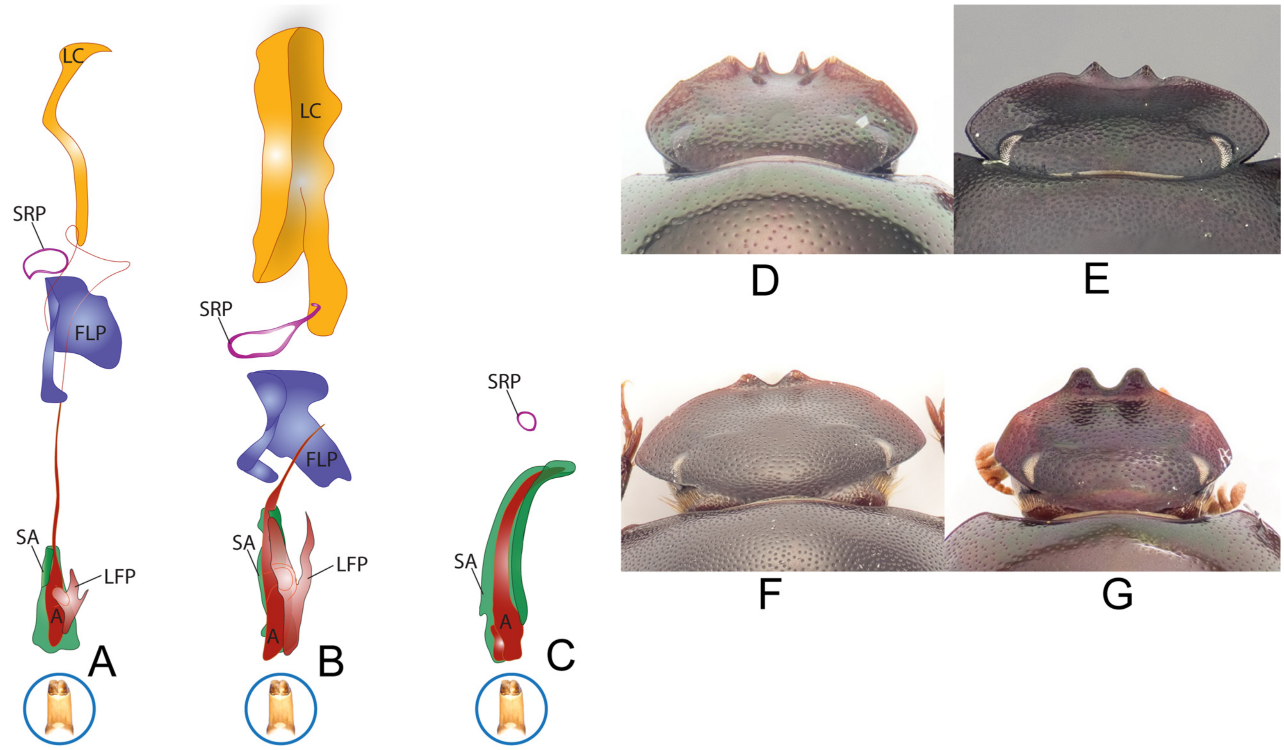

FIGURE 4. Morphological elements of *Parachorius***.** (A–C) Endophallic sclerites; aedeagus icon in blue circle indicates position of aedeagus in relation to endophallic sclerite. (D–G) Head in dorsal view. (A, D) *Parachorius longipenis*. (B) *Parachorius fungorum*. (C, G) *Parachorius pseudojavanus*. (E) *Parachorius gotoi*. (F) *Parachorius globosus*.

Genus *Parachorius* Harold, 1873 *sensu novo*

Parachorius Harold, 1873: 103 (type species*: Parachorius thomsoni* Harold, 1873)
Cassolus Sharp, 1875: 40 (type species: *Cassolus nudus* Sharp, 1875), **new synonymy**
Heteroateuchus Paulian, 1935: 115 (type species*: Heteroateuchus oberthueri* Paulian, 1935), synonym

Description. Since *Parachorius* is the only genus of the tribe Parachoriini, the description of the genus is the same as given for Parachoriini**.** In addition, I provide some relevant comparative information below.

Diagnosis. See diagnosis for Parachoriini.

Sexual dimorphism. Males are separated from females in most species by some sexually dimorphic characters. Namely, in comparison to females, males of some species may have (1) protibia with modified apical spur and/or modified first anterior tooth, (2) profemur anterior margin produced in angle, (3) angulate lateral margin and/or frontal angles of pronotum, (4) dilated metafemur posterior margin, and (5) curved and/or denticulate posterior margin of metatibia.

Morphology of endophallic sclerites. The morphology of endophallic sclerites in *Parachorius* varies across species. Three morphological ground plans of sclerites can be distinguished**:** (1) most of the endophallic sac lack sclerites, axial and SA sclerites simple, FLP absent, SRP small, LC absent (*P. javanus* and *P. pseudojavanus*) (Fig. 4C); (2) inferior portion of axial sclerite with long fork-like process (LFP), axial sclerites enlarged inferiorly with moderately short filiform process extending superiorly that reaches only FLP, inferior portion of axial sclerite with LFP, SA small (*P. globosus, P. fungorum, P. thomsoni, P. hookeri, P. maruyamai, P. newthayerae, P. pseudojavanus, P. javanus* and *P. schuelkei*) (Fig. 4B); and (3) inferior portion of axial sclerite with long fork-like process (LFP), axial sclerites enlarged inferiorly with long filiform process extending superiorly that reaches LC, inferior portion of axial sclerite with LFP, SA small (*P. longipenis, P. solodovnikovi, P. nudus, P. peninsularis, P. bolavensis*, and *P. fukiensis*) (Fig. 4A). The endophallic sclerites of three species fall outside of the provided ground plans. In *P. semsanganus* the structure of endophallic sclerites resembles a transitional state between ground plan 2 and 3. In *P. humeralis* and *P. asymmetricus* the FLP sclerite is absent and the endophallic sclerites are similar to those in ground plan 3. The diversity of aedeagal parameres shapes is shown in Fig. 5.

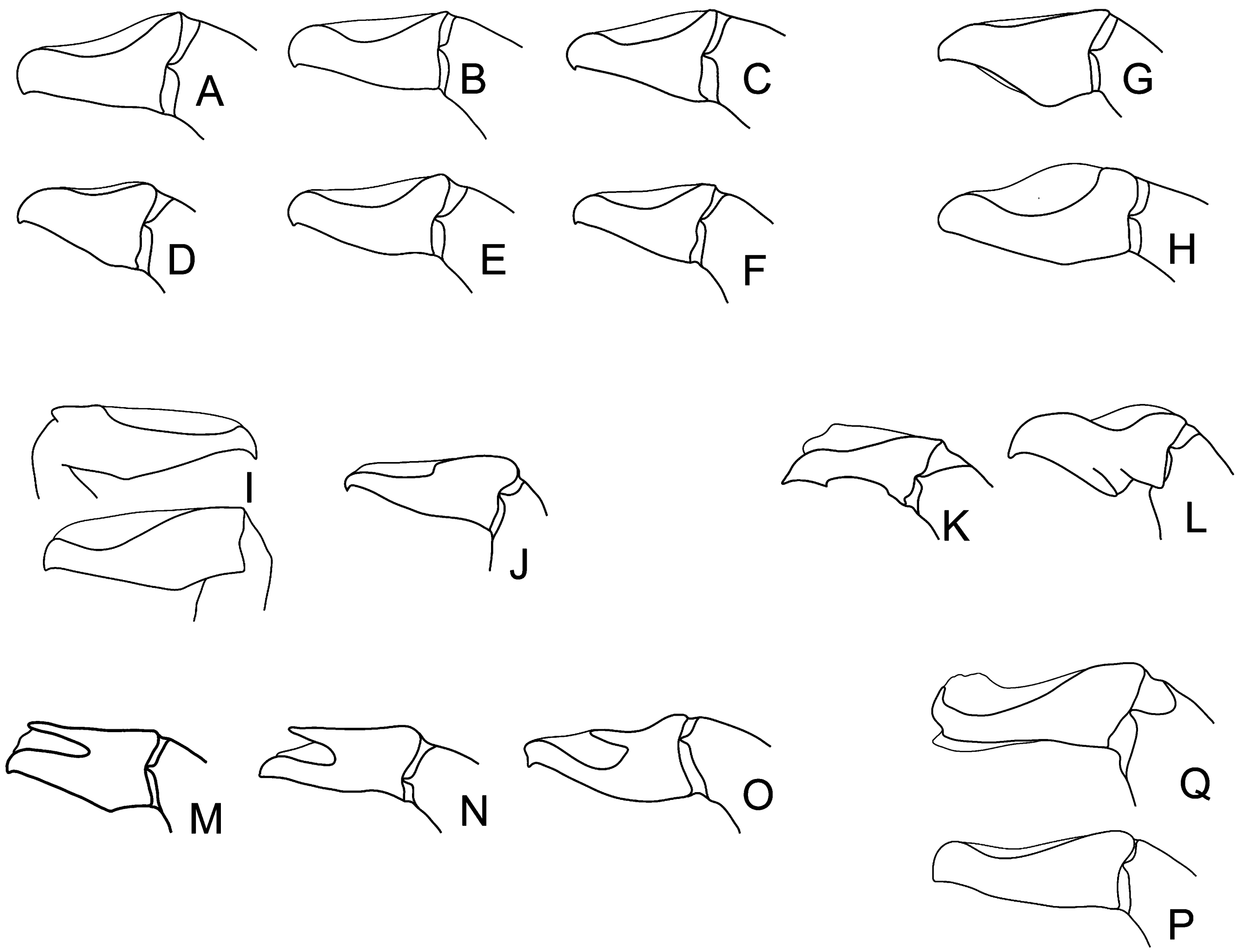

FIGURE 5. Diversity of aedeagal parameres in *Parachorius*. (A) *Parachorius fungorum.* (B) *Parachorius hookeri.* (C) *Parachorius schuelkei.* (D) *Parachorius thomsoni.* (E) *Parachorius globosus.* (F) *Parachorius newthayerae.* (G) *Parachorius bolavensis.* (H) *Parachorius fukiensis.* (I) *Parachorius nudus.* (J) *Parachorius peninsularis.* (K) *Parachorius pseudojavanus.* (L) *Parachorius javanus.* (M) *Parachorius solodovnikovi.* (N) *Parachorius longipenis.* (O) *Parachorius humeralis.* (P) *Parachorius semsanganus.* (Q) *Parachorius gotoi.*

Taxonomical note. The genus *Cassolus* is synonymized with *Parachorius* based on the result of phylogenetic analyses. Currently, *Parachorius* includes 19 species. A key to species and the descriptions of the new species are provided below.

Ecology. *Parachorius* species are quite rare in collections. In this study, I examined approximately 200 specimens, the majority of which came from recent collecting in Indochina. Their rare occurrence in collections is mainly due to their non-coprophagous feeding habits, which prevents massive collecting using dung traps. The vast majority of the specimens with known ecological data were collected in forest using flight intercept traps, carrion traps, or fruit traps.

Distribution. The genus is widespread in the Oriental and southeastern Palaearctic Regions, from Indian subcontinent in the west through Myanmar, Indochina, and southern China to Taiwan in the east. It also occurs in Sundaland, namely Malay Peninsula, Sumatra, and Java. The Philippines and Borneo lack any known species of *Parachorius*.

Key to males of *Parachorius*

Parachorius species are reliably identified only using males. A separate key to the identifiable females is provided in the next section. The species are illustrated in Figs. 6–24 and their distribution maps are given in Figs. 25–27.

1 Clypeus with two teeth, outer margin of each tooth not notched basally (Fig. 4F–G) 2
- Clypeus with two teeth, outer margin of each tooth distinctly or slightly notched basally (Fig. 4D–E) 10
2 Clypeus with two distinctly produced teeth (Fig. 4G) 3
- Clypeus with two less produced teeth (Fig. 4F 5
3 Body black; parameres widely rounded; head triangularly shaped (Fig. 21); size 6.5–6.8 mm; southern China. . . . . *P. schuelkei* Tarasov **new species**
- Body reddish brown, rarely dark brown; parameres either claw shaped or apically acute but not widely rounded; head more rounded and not as distinctly triangular as in *P. schuelkei* 4
4 Protibia with first tooth somewhat modified in male—slightly thickened and spatulate; parameres notched basally and claw shaped in lateral view (Fig. 14); length 6.7 mm; known only from the holotype; Java . . . . *P. javanus* (Boucomont, 1914)
- Protibia first tooth not modified in males; parameres medially narrowed (in lateral view), apically acute (Fig. 20); length 6–7 mm; Java . . . . *P. pseudojavanus* Tarasov **new species**
5 Metatibia strongly curved and notched medially (Figs. 16C, 17D); frontal angles of pronotum from moderately to distinctly sharp (Figs. 16B, 17C, E–F) 6
- Metatibia slightly sinuate (Fig. 24E); frontal angles of pronotum rounded (Fig. 24G) 7
6 Middle part of metafemur dilated posteriorly and produced as a large, rounded angle; pronotum distinctly angulate laterally with frontal angles moderately sharp (Fig. 17); length 7.8–8.0 mm; southern Laos . . . . . .*P. newthayerae* Tarasov **new species**
- Metafemoral posterior margin simple, metafemur not dilated; pronotum presumably (as none of the specimens were studied) not angulate laterally with frontal angles distinctly sharp (Fig. 16); length 6.5–6.8 mm; central Thailand. . . . . *P. maruyamai* Masumoto, Ochi, & Sakchoowong, 2012
7 Elytra covered with dense contiguous and rugose punctures (Fig. 10F); pronotum almost as long as elytra; wings reduced (Fig. 10); 6–7 mm; northeastern India. . . . . *P. globosus* Arrow, 1931
- Elytra covered with sparse (not contiguous) punctures (Fig. 24F); pronotum notably shorter than elytra; wings normally developed 8
8 Metafemoral posterior margin with two distinct denticles, apical denticle is produced and spur-like; metatibial inner margin excavated apically; metafemoral posterior margin not serrate; parameres of aedeagus simple, apex slightly rounded, triangularly shaped (Fig. 24); length 6.5–9.0 mm; eastern India, Myanmar, Thailand, Laos . . . . *P. thomsoni* Harold, 1873
- Metafemoral posterior margin without pair of distinct denticles, simple or dilated, either serrate or not; metatibial inner margin not excavated apically; parameres of aedeagus simple, apex widely rounded and inferiorly angulate 9
9 Metafemoral posterior margin serrate (sometimes slightly) and varies from simple, not modified, to dilated; metatibial inner margin produced in small angle apically (Fig. 9); length 6.5–9.0 mm; southern China, Myanmar, Indochina . . . . *P. fungorum* Kryzhanovsky & Medvedev, 1966
- Metafemoral posterior margin simple, not serrate, not dilated; metatibial inner margin straight, not produced apically (Fig. 12); size 6.0 mm; northern India . . . . *P. hookeri* Arrow, 1931
10 Outer margin of each clypeal tooth slightly notched basally (Fig. 4E). 11
- Outer margin of each clypeal tooth distinctly notched basally (Fig. 4D) 12
11 Inner margin of metatibia denticulate with relatively small teeth; protibia with apical tooth wide, nearly merging with second tooth; parameres elongate and rounded apically; length 5–6 mm (Fig. 11); Taiwan . . . . *P. gotoi* (Masumoto, 1986)
- Inner margin of metatibia denticulate with large teeth (sometimes denticulation obliterated); protibia with apical and second teeth distinctly separated from each other; parameres bear membranous lobes and bent upward apically; length 8.2–10.6 mm (Fig. 22); northern Laos . . . . *P. semsanganus* Tarasov & Keith, 2011

12 Parameres asymmetrical; humeral area of elytron usually with yellow spot, sometimes yellow spot absent and elytra uniformly colored (Fig. 6); length 4.5–4.7 mm; India .... *P. asymmetricus* Tarasov **new species**

- Parameres symmetrical; humeral area of elytron with or without yellow spot 13

13 Parameres with horn-like upper lobes dorsally (Fig. 5M–O) 14

- Parameres normal, without horn-like upper lobes (Fig. 5G–H) 16

14 Humeral area of elytron usually (but not always) with yellow spot; inner margin of metatibia not denticulate; metafemoral posterior margin usually greatly dilated apically, less often dilation reduced; aedeagus as in Fig. 5N, length 3.8–5.0 mm (Fig. 13); northeastern India .... *P. humeralis* (Arrow, 1907)

- Humeral area of elytron without yellow spot, elytra uniformly colored; inner margin of metatibia denticulate with relatively small teeth; metafemoral posterior margin either simple or dilated and produced in a slight angle 15

15 Parameres longer than in next species (Fig. 15A–D); protibia with apical tooth spatulate, bent downward and notably larger than second tooth; first tooth wide, nearly merging with second tooth; metafemoral posterior margin simple, not modified or dilated and produced in slight angle in basal half (Fig. 15); length 3.8–5.0 mm; Indochina .... *P. longipenis* Tarasov **new species**

- Parameres shorter than in previous species (Fig. 23A–C); protibia with apical tooth approximately twice as wide as second tooth; first and second teeth distinctly separated from each other; metafemoral posterior margin simple, not modified, sometimes slightly dilated but not produced in angle; length 3.9–5.0 mm (Fig. 23); Indochina .... *P. solodovnikovi* Tarasov **new species**

16 Apical spur of protibia equal or longer than first protibial tooth and first three protarsomeres combined (Fig. 7E); inner margin of metatibia not denticulate (Fig. 7G) 17

- Apical spur of protibia shorter than first protibial tooth and first three protarsomeres combined (Fig. 18E); inner margin of metatibiae with relatively small teeth (Fig. 19F–H) 18

17 Parameres widened basally (lateral view), apex acute; metafemoral posterior margin dilated near middle; dilation widely rimmed (Fig. 7); length 4.2–4.5 mm; southern Laos .... *P. bolavensis* Tarasov **new species**

- Parameres emarginate superiorly (*i.e.*, dorsally in lateral view, Fig. 8A–C), apex rounded; metafemoral posterior margin simple or dilated in apical third, but not rimmed (Fig. 8); length 3.5–4.6 mm; southeastern China, Laos, Vietnam .... *P. fukiensis* (Balthasar, 1960)

18 Protibia with apical tooth spatulate, bent downward and notably larger than second tooth; first tooth wide, appearing bifurcate as it merges with denticles located between first and second teeth; metafemoral posterior margin simple, not dilated; aedeagus as in Fig. 5H; length 4.8 mm (Fig. 18); Cambodia .... *P. nudus* (Sharp, 1875)

- Protibia with apical tooth approximately twice as wide as second tooth, first and second teeth distinctly separated from each other; metafemoral posterior margin simple, not modified or slightly dilated in apical forth and produced in rounded angle preapically; aedeagus as in Fig. 5I; length 4.0–5.5 mm (Fig. 19); Thailand, Malay Peninsula, Sumatra .... *P. peninsularis* (Arrow, 1907)

Key to females of *Parachorius*

Twelve out of 19 *Parachorius* species cannot be reliably identified using females. Therefore, the key below contains some couplets that refer to several species at the same time. In such ambiguous cases the distribution criterion should be used to separate species. This criterion is not always reliable as many species have overlapping distributional areas.

1 Clypeus with two teeth, outer margin of each tooth not notched basally (Fig. 4F–G) 2

- Clypeus with two teeth, outer margin of each tooth distinctly or slightly notched basally (Fig. 4D–E) 6

2 Clypeus with two distinctly produced teeth (Fig. 4G) 3

- Clypeus with two less produced teeth (Fig. 4F) 4

3 Body black; head triangularly shaped (Fig. 21); length 6.5–6.8 mm; southern China .... *P. schuelkei* Tarasov **new species**

- Body reddish-brown, rarely dark brown; head more rounded not as distinctly triangular as in *P. schuelkei*; length 6–7 mm .... *P. javanus* (Boucomont, 1914) and *P. pseudojavanus* Tarasov **new species**

4 Elytra covered with dense contiguous and rugose punctures (Fig. 10F); pronotum almost as long as elytra; wings reduced (Fig. 10); 6–7mm; northeastern India .... *P. globosus* Arrow, 1931

- Elytra covered with sparse (not contiguous) punctures (Fig. 24F); pronotum notably shorter than elytra; wings normally developed 5

5 Length 6 mm (Fig. 12); northern India .... *P. hookeri* Arrow, 1931

- Length 6.5–9.0 mm. This couplet contains four species with morphologically undistinguishable females. Their identity can be, to certain extent, determined from the geographical distribution (see species descriptions for details). .... *P. newthayerae* Tarasov **new species**, *P. maruyamai* Masumoto, Ochi, & Sakchoowong, 2012, *P. thomsoni* Harold, 1873, *P. fungorum* Kryzhanovsky & Medvedev, 1966

6 Outer margin of each clypeal tooth slightly notched basally (Fig. 4E) 7

- Outer margin of each clypeal tooth distinctly notched basally (Fig. 4D) 8

7 Clypeal teeth acute; length 5–6 mm (Fig. 11); Taiwan .... *P. gotoi* (Masumoto, 1986)

- Clypeal teeth rounded; length 8.2–10.6 mm (Fig. 22); northern Laos .... *P. semsanganus* Tarasov & Keith, 2011

8 Humeral area of elytron usually with a yellow spot, sometimes the yellow spot is absent and elytra uniformly colored; India . 9

\- Humeral area of elytron without yellow spot, elytra uniformly colored; southeastern China, Indochina, Malay Peninsula, and Sumatra 10

9 Species from southern and central India (Fig. 6); length 4.5–4.7 mm . . . . *P. asymmetricus* Tarasov **new species**

\- Species from northeastern India (Sikkim, Assam, Meghalaya); length 3.8–5.0 mm (Fig. 13). . . . . . *P. humeralis* (Arrow, 1907)

10 Body shape rectangular and less convex (Figs. 7D, 8F); length 3.5–4.6 mm. . . . . *P. bolavensis* Tarasov **new species** and *P. fukiensis* (Balthasar, 1960)

\- Body shape round and distinctly convex (Fig. 15F); length 3.8–5.4 mm. This couplet comprises four species with largely overlapping distributional areas and undistinguishable females. Nevertheless, species identity can be, to certain extent, determined from the geographical distribution (see species descriptions for details) . . . . *P. longipenis* Tarasov **new species**, *P. solodovnikovi* Tarasov **new species,** *P. nudus* (Sharp, 1875), and *P. peninsularis* (Arrow, 1907)

Species descriptions

The species descriptions are alphabetically ordered.

Parachorius asymmetricus Tarasov new species

(Figs. 6, 25A)
urn:lsid:zoobank.org:act:F032F403-82AA-4A56-A085-3E8771794696

Type locality. Nilgiri Hills [India].

Etymology. The name of this species derives from the word "asymmetrical" referring to the asymmetry of aedeagal parameres in this species. The name should be treated as an adjective in the nominative singular.

Distribution. The species is known from southern and central India.

Taxonomic notes. One female with uniformly black elytra from Malabar (included in material examined) is excluded from the type series since exact identification requires examination of male genitalia. However, the shape of protibia and locality of this female are consistent with that of *P. asymmetricus*.

Diagnosis. The species is most similar to *P. humeralis* from which it differs by asymmetrical male genitalia and widened protibia with first tooth nearly merging the second tooth in males. *Parachorius asymmetricus* is the only *Parachorius* species with drastically asymmetrical parameres and it can be easily separated from the rest of *Parachorius* species using this character.

Description. *Body.* Body dark, length 4.5–4.7 mm. Elytra usually with yellow humeral spots.

Head. Clypeus with two teeth, outer margin of each tooth distinctly notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1–3 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with almost straight or sinuate anterior margin. Protibia with apical spur reaching protarsomere 2; first tooth normal, notably modified in males, nearly merging with second tooth and approximately twice as wide as second tooth. First tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, largely dilated in apical half and produced into a sharp angle; dilation steeply reduced near apex. Metatibia slightly sinuate, inner margin not denticulate, produced in small angle apically.

Metasternum. Transverse basal ridge of metasternum reduced and extremely short.

Aedeagus. Parameres distinctly asymmetrical.

Holotype. Male (Fig. 6E). Elytra with yellow humeral spots.

Material examined. Holotype: **male**, "Nilgiri Hills. H.L. Andrewes. / Nilgiri Hills / Andrewes Bequest. B.M. 1922-221 / Cassolus humeralis Determined by G.J. Arrow. / HOLOTYPE Parachorius asymmetricus S. Tarasov det. 2010", 11°25'1"N, 76°30'1"E (BMNH). **Paratypes (1 male, 1 female)**: **India**: **1 male paratype**, Mandar (Beng) 1/91 (P. Cardon) (ISNB); Chota Nagpore, Palkot, on vi–vii/1897, (R.P. Cordon) (NMPC); **1 female paratype**, Malabar, Walayar forests, on ix/1956 (P.S. Nathan) (ISNB). **Additional specimen: 1 female**, Malabar, Walayar forests, on IX.1956, (P.S. Nathan) (ISNB).

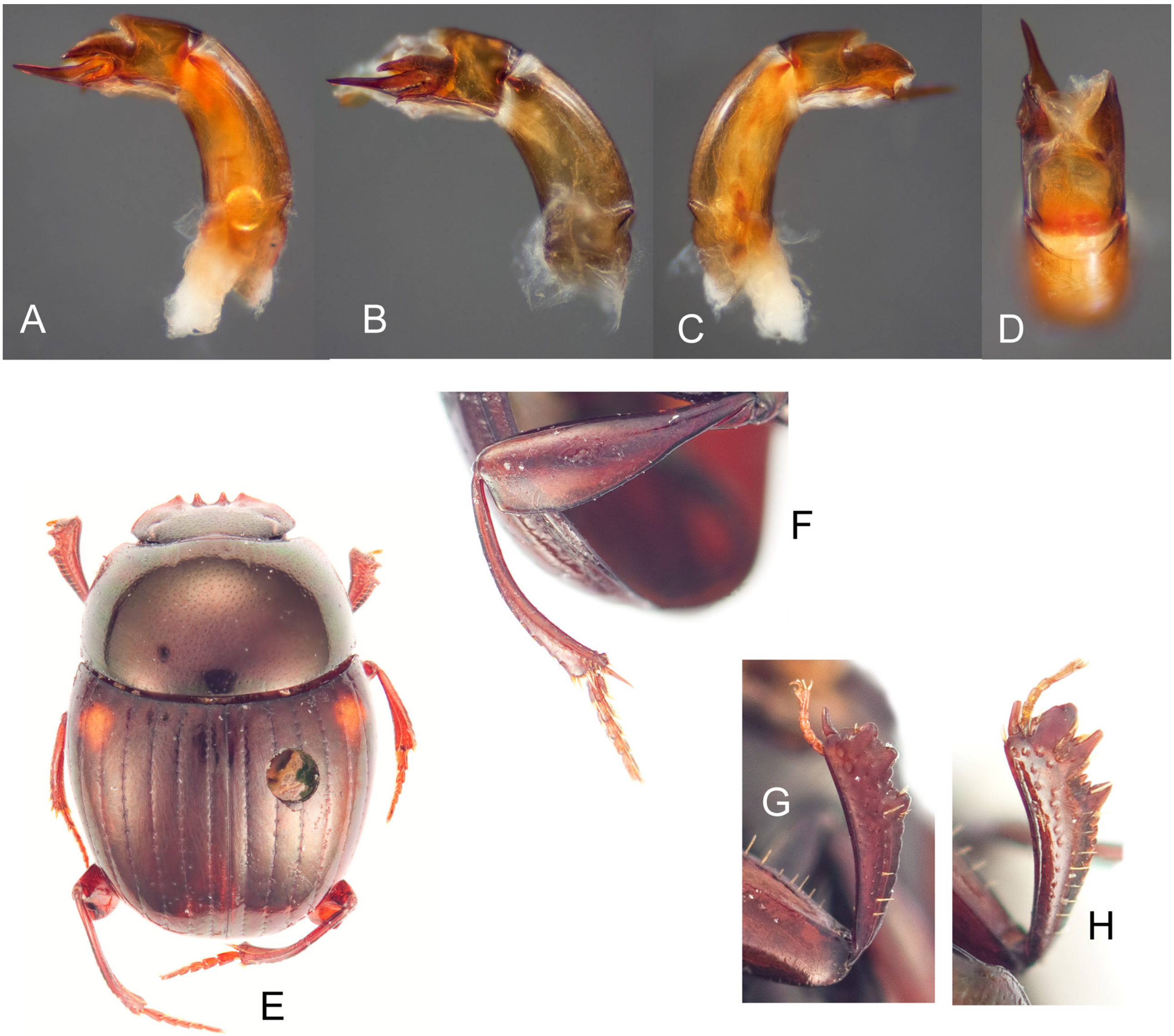

FIGURE 6. Morphology of *Parachorius asymmetricus*. (A) aedeagus, left lateral view (holotype). (B) aedeagus, left lateral view (paratype). (C) aedeagus, right lateral view (holotype). (D) aedeagus, dorsal view (holotype). (E) habitus (male, holotype). (F) right metafemur (male, holotype). (G) protibia (putative female). (H) protibia (male, holotype).

Parachorius bolavensis **Tarasov new species**
(Figs. 7, 25B)
urn:lsid:zoobank.org:act:A116D60D-8D17-434E-8AAD-84A0C331C23E

Type locality. Bolaven Plateau, Laos

Etymology. The name of this species is derived from its type locality in Bolaven plateau, southern Laos.

Distribution. The species is known only from the two localities on Bolaven plateau in southern Laos where the type series was collected. Presumably, this species is endemic to Bolaven plateau that has unique climatic conditions due to its elevation (average height is approximately 1000 m) over the lowlands.

Diagnosis. This species is most closely related to *P. fukiensis*. It differs from *P. fukiensis* and the remaining *Parachorius* species by the shape of aedeagus (parameres widened basally, their apices acute) and by the widely rimmed middle dilation of the posterior metafemoral margin.

Description. *Body.* Body black, length 4.2–4.5 mm. Elytra uniformly colored, mostly black.

Head. Clypeus with two teeth, outer margin of each tooth distinctly notched basally.

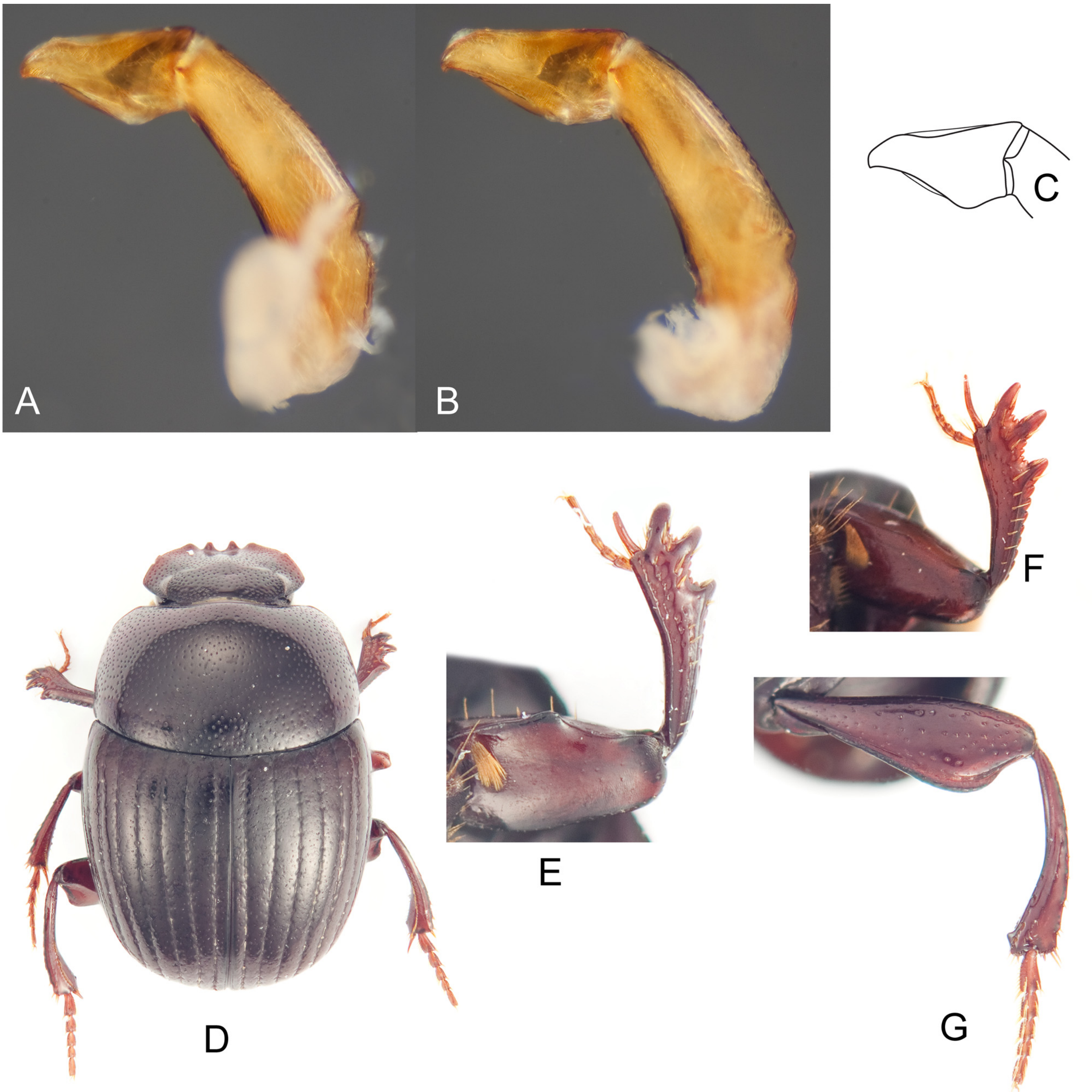

FIGURE 7. Morphology of *Parachorius bolavensis*. (A) aedeagus, lateral view (holotype). (B) aedeagus, lateral view (paratype). (C) aedeagus. (D) habitus (male, holotype). (E) protibia (male, paratype). (F) protibia (female, paratype). (G) left metafemur (male, paratype).

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1–2 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with anterior margin medially produced in angle or with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth normal, notably modified in males, approximately twice as wide as second tooth; first and second teeth distinctly separated from each other, first tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, dilated medially, dilation widely rimmed. Metatibia slightly sinuate, inner margin not denticulate, produced into a small angle apically.

Metasternum. Transverse basal ridge of metasternum reduced and extremely short.

Aedeagus. Parameres symmetrical, widened basally (lateral view), apex acute.

Holotype. Male (Fig. 7D). Profemur with anterior margin medially produced in angle.

Material examined. Holotype: **Laos**: **male**, "S[outhern] Laos, Bolaven plateau, Ban Houayteuay h1200m N15°4.655' E106°16.848' disturb montane forest pitfall traps leg. S. Tarasov 6.5-14.6.2008 / HOLOTYPUS Parachorius bolavensis S. Tarasov det. 2010", 15°4.655'N, 106°16.848'E (ZMUC). **Paratypes** (**10 males**, **10 females**): **8 male paratypes, 6 female paratypes**, Champasak Province: Bolaven Plateau, Ban Thôngvay (=Xékatam) vicinity, old logging road N of village, FMHD#2008-037, ANMT site 1231, 15°14.288'N, 106°31.891'E, 1095 m, selectively logged forest, on 8–16/vi/2008 (A. Newton, M. Thayer) (FMNH); **1 male paratype**, **3 female paratypes**, Champasak Province: Bolaven Plateau, Ban Thôngvay (=Xékatam) vicinity, old logging road N of village, FMHD#2008-040, ANMT site 1232, 15°14.494'N, 106°31.807'E, 1170 m, selectively logged forest, on 8–16/vi/2008, (A. Newton, M. Thayer) (FMNH); **1 male paratype**, **1 female paratype**, Champasak Province, Bolaven Plateau, Ban Houayteuay, 15°4.655'N, 106°16.848'E, 1200 m, disturb montane forest, on 6/v–14/vi/2008 (S. Tarasov) (CST).

Parachorius fukiensis (Balthasar, 1960) new combination
(Figs. 8, 25C)

Cassolus fukiensis Balthasar, 1960: 90
Cassolus fukiensis; Balthasar 1963: 261

Type locality. Kuatun, Fújiàn Province, China.

Distribution. The species is known from southeast China (Fújiàn Province), Laos, and Vietnam. The locality in Fújiàn province is the northernmost one among all the species in the genus *Parachorius*. Given the large extent of occurrence, this species is probably widespread in Indochina and southern China.

Taxonomic notes. The known localities of this species are quite distantly located from each other, which is uncommon for the members of *Parachorius***.** Therefore, this distributional pattern may suggest that *P. fukiensis* represents a complex of similar species and requires additional material and a more detailed study to resolve the issue.

Diagnosis. This species is most similar to *P. bolavensis*. It differs from *P. bolavensis* in aedeagal parameres emarginate superiorly (*i.e.*, dorsally in lateral view, Fig. 8A–C), rounded aedeagal apex, and metafemoral posterior margin not rimmed. *Parachorius fukiensis* can be separated from the rest of *Parachorius* species by the shape of aedeagus.

Description. *Body.* Body black, length 3.5–4.6 mm. Elytra uniformly colored, mostly dark.

Head. Clypeus with two teeth, outer margin of each tooth distinctly notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1–2 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with anterior margin produced in angle medially or with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth normal, notably modified in males, approximately twice as wide as second tooth; first and second teeth distinctly separated from each other; first tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, simple, or dilated in apical third of metafemur and produced in angle. Metatibia slightly sinuate, inner margin not denticulate, produced in small angle apically.

Metasternum. Transverse basal ridge of metasternum reduced and extremely short.

Aedeagus. Parameres symmetrical, emarginate superiorly (*i.e.*, dorsally in lateral view, Fig. 8A–C), apex rounded.

Material examined. Holotype: **China**: **male**, "Kuatun (2300m) 27.40n. Br. 117.40ö. L. Klapperich 29.4.1938 (Fukien) / Cassolus fukiensis n.sp. Balth. Holotypus / Holotpus Parachorius fukiensis Balthasar S. Tarasov det. 2011", 27°40'N, 117°40'E (NMPC). **Laos**: **1 male**, Xieng Khouang Province, Phonsavan, Plain of Jars N3, 19°17.33'N, 103°9.17'E, 1100 m, disturb montane forest, on 3–16/viii/2008 (S. Tarasov) (CST). **Vietnam**: **1 male**, Gialai Contum, Buonluoi, 14°20'N, 108°36'E, 12/vi/1982 (L. Medvedev) (ZIN). **2 males**, SW Donghoi, 17°28'N, 106°35'E, 300 m, 27/iii/1963 (O. Kabakov) (ZIN).

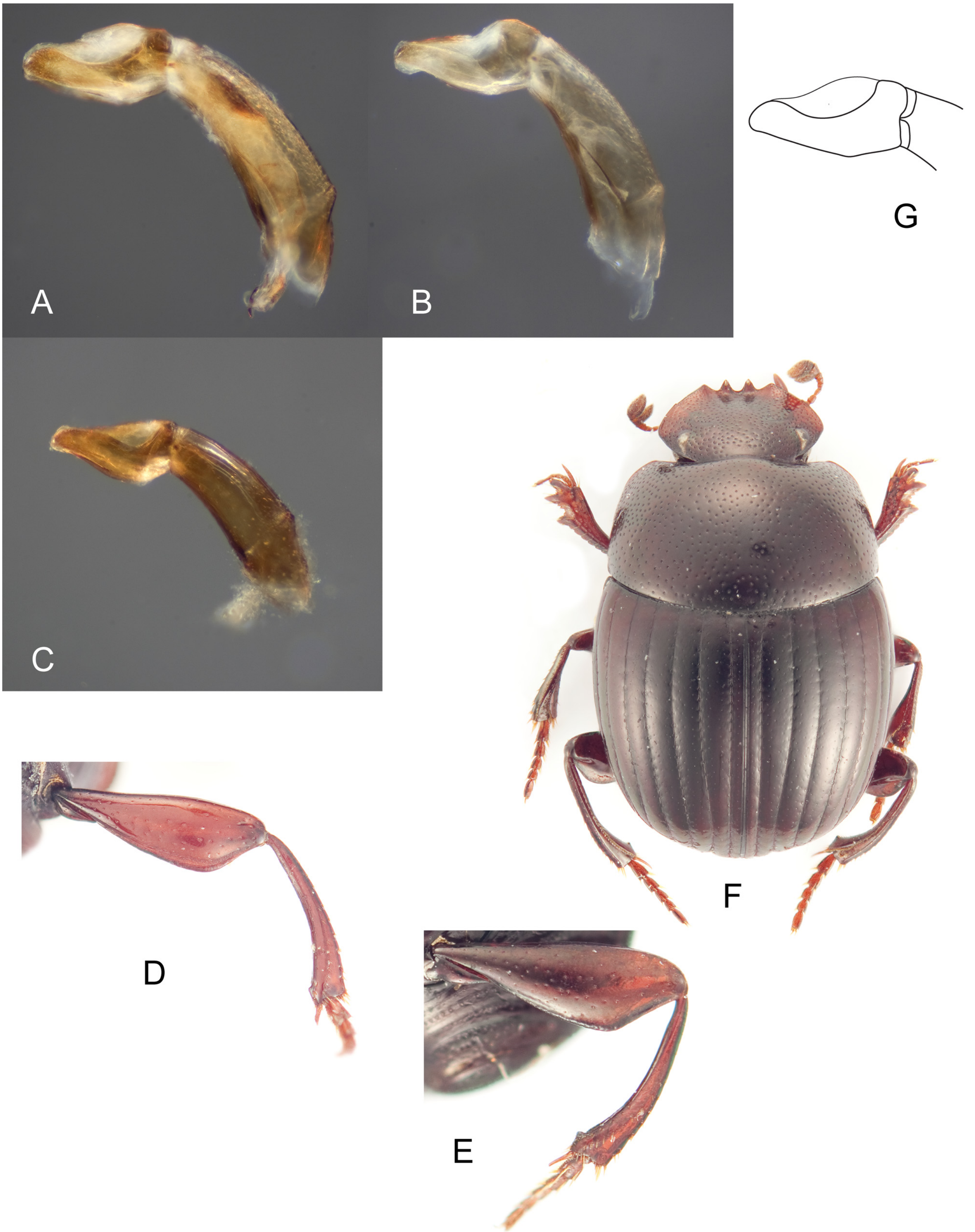

FIGURE 8. Morphology of *Parachorius fukiensis*. (A) aedeagus, lateral view (holotype). (B) aedeagus, lateral view (paratype, Laos, Phonsavan). (C) aedeagus, lateral view (paratype, Vietnam, Donghoi). (D) left metafemur (male, paratype, Laos, Phonsavan). (E) left metafemur (male, paratype, Vietnam, Donghoi). (F) habitus (male, holotype). (G) aedeagus.

Parachorius fungorum Kryzhanovsky & Medvedev, 1966
(Figs. 9, 25D)

Parachorius fungorum Kryzhanovsky & Medvedev, 1966: 394
Parachorius krali Utsunomiya & Masumoto, 2001: 125 (**new synonymy**)

Type locality. Yunnan, Daweishan, 1900 m, vicinity of Binbjan, China (*Parachorius fungorum*); Yunnan 1800–2000 m, Yipinslang. China (*Parachorius krali*)

Distribution. Southern China (Kuatun, Yunnan), Myanmar, Laos, and Vietnam.

Taxonomic notes. The original description of *P. fungorum* is based on two females (Kryzhanovsky & Medvedev 1966). The publication mentions that all primary types of the described species were deposited in the Institute of Zoology in Beijing, while paratypes were shared between both Institute of Zoology in Beijing and the Zoological Institute in St.-Petersburg. Any specific information about the deposition of paratype of *P. fungorum* is lacking in that paper. The paratype could not be located in the Zoological Institute in St.-Petersburg, and it was not possible to check the collection in Beijing due to the lack of access. Nevertheless, I consider the identity of the specimens examined here with the types of *P. fungorum* certain and provide arguments below to support this statement.

Given that the type series of *P. fungorum* only includes females the set of characters listed in the original description is uninformative since females of *P. fungorum* are not distinguishable from those of its closest relative *P. thomsoni*. At the same time, males and females of *P. thomsoni* and *P. fungorum* can be easily separated from all other species of *Parachorius*.

The studied material suggests that *P. fungorum* occurs in southern China, Indochina, and Myanmar, while *P. thomsoni* tends to populate more western areas - northeast India, Myanmar, and western Indochina. Although, the distribution of *P. thomsoni* and *P. fungorum* overlaps in Myanmar, Thailand, and Laos, only *P. fungorum* occurs in southern China. Based on the fact that only one species of this pair is found in southern China, I conclude that the examined specimens from China are conspecific with the types of *P. fungorum*. Thus, I synonymize *P. lannathai* - the recently described species from Yunnan - with *P. fungorum*.

Additionally, another species, *P. hookeri,* known only from the holotype collected in northeastern India, may be conspecific with *P. fungorum* (for details, see *P. hookeri* description).

Diagnosis. The species is most similar to *P. thomsoni* and *P. hookeri*. It differs from them and other species of *Parachorius* in the following combination of characters: (1) parameres simple, their apices widely rounded and inferiorly angulate, (2) metafemoral posterior margin serrate (sometimes slightly), and (3) shape of metafemoral posterior margin varies from simple, not modified to dilated.

Description. *Body.* Body black, length 6.5–9.0 mm. Elytra uniformly colored, black.

Head. Clypeus with two indistinct teeth, outer margin of each tooth not notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 0.5–2.0 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with anterior margin medially produced in angle or with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth almost not modified in males, approximately as wide as second tooth; first and second teeth distinctly separated from each other; first tooth normal, distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin serrate (sometimes slightly), simple, not modified or dilated in apical third of metafemur and produced in angle. Metatibia slightly sinuate, inner margin not denticulate, produced in small angle apically.

Metasternum. Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length.

Aedeagus. Parameres symmetrical, simple, apex widely rounded and inferiorly angulate.

Material examined. Holotype of *Parachorius krali*: China: male, "Holotype Parachorius krali Uts. & Mas./ Coll. Masumoto 2000/Yunnan 1800-2000m 25.04N 101.555E Yipinslang 17-20.6.1994 Vit Kuban leg.", 25°4'N, 101°55'E (NSMT). **1 male**, Kuatun, Fukien (Tschung Sen.), 27°40'N, 117°40'E, on 11/v/1946 (NMPC). **1 male**, Yunnan Province (NMPC). **1 male**, southern China, Yunnan Province, Vallis flimin, Soling-ho, B.M. 1931-358 (NMPC). **2 males**, Sichuan Province, Xichang environs, 1600 m, on 1/vii/2002 (A. Gorodinski) (OUMNH). **1 male**, Ynnan, Recu de Lou-Nan, on 1931 (MNHN). **2 males**, Yunnan, Baoshan City environs, 2000 m, on 10/vii/

1998 (A. Gorodinski) (ZIN). **Laos**: **1 male**, Xieng Khouang, Phonsavan, Nong Pet, 19°34.657'N, 103°23.313'E, 1300 m, disturb montane forest, on 1–3/viii/2008 (S. Tarasov) (CST). **Myanmar**: **1 male**, Carin Cheba, L. Fea, 900–1100 m, on 5/x/1988 (MNHN). **Vietnam**: **1 male**, Hoa-Binh, Tonkin (MNHN). **1 male**, Tam Dao, rotten fish, 900 m, on 2/ix/1963 (O. Kabakov) (ZIN). **1 male**, Tonkin Hoa-Binh, 20°49.7'N, 105°20'E (J. Clermont) (NMPC).

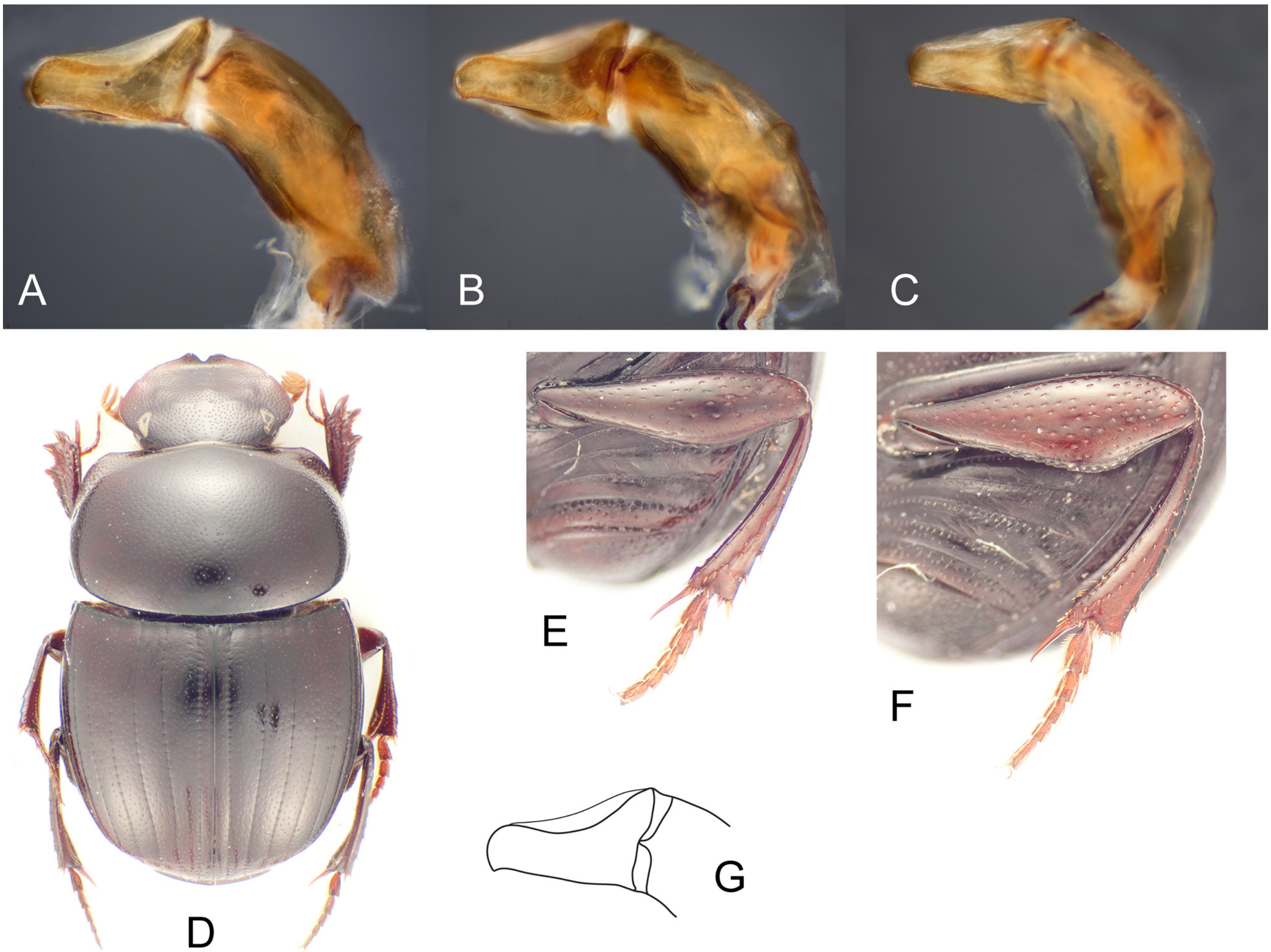

FIGURE 9. Morphology of *Parachorius fungorum*. (A–C, G) aedeagus, lateral view. (D) habitus (male). (E-F) left metafemur (male).

Parachorius globosus Arrow, 1931
(Figs. 10, 25E)

Parachorius globosus Arrow, 1931: 360
Heteroateuchus oberthueri Paulian, 1935: 115 (synonym)
Parachorius globosus; Balthasar 1963: 277
Parachorius globosus; Matthews 1974: 159
Parachorius globosus; Bacchus 1978: 103

Type locality. Darjeeling, India (*Parachorius globosus*); Darjeeling, India (*Heteroateuchus oberthueri*)

Distribution. Northeastern India.

Diagnosis. *Parachorius globosus* differs from other species of *Parachorius* by rugose punctation of elytra, reduced wings, and pronotum being almost as long as elytra in anterior-posterior direction.

Description. *Body.* Body, brown, length 6–7 mm. Elytra uniformly colored.

Head. Clypeus with two indistinct teeth, outer margin of each tooth not notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 0.5–2.0 puncture diameter(s). Pronotum in anterior-posterior direction almost as long as elytra.

Elytra. Elytra covered with dense contiguous and rugose punctures.

Wings. Wings reduced, approximately as long as 1/2 of normally developed wings.

Legs. Profemur with anterior margin produced in angle medially or with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth almost not modified in males, approximately as wide as second tooth; first and second teeth distinctly separated from each other; first tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin serrate (sometimes slightly), simple, not modified. Metatibia slightly sinuate, inner margin not denticulate, produced in small angle apically.

Metasternum. Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length.

Aedeagus. Parameres symmetrical, simple, apex widely rounded and inferiorly angulate.

Material examined. Holotype: **India**: **male**, "Holotype / N. India: Darjeeling. 5000 ft. 14.iii.1924. Maj. R.W.G. Hingston / Everest Exp. Brit Mus 1924-386 / Parachorius globosus, type arrow / Parachorius globosus arrow M.E. Bacchus det 1975. HOLOTYPE / Parachorius globosus Arrow, 1931 S. Tarasov det. 2010" (BMNH). **1 female**, Bengal, Darjeeling District, Ghoom-Lopchu, 2000 m, on 14/x/1978, (Besuchet-Lobl) (MNHN). **1 male**, Darjeeling, Ex Museo Harold (MNHN). **1 male**, Darjeeling, Ghoom, B.M. 1931-452 (M. Cameron) (BMNH). **1 male**, **3 females**, Museum Paris, Sikkim, on 1891 (Harmand) (MNHN).

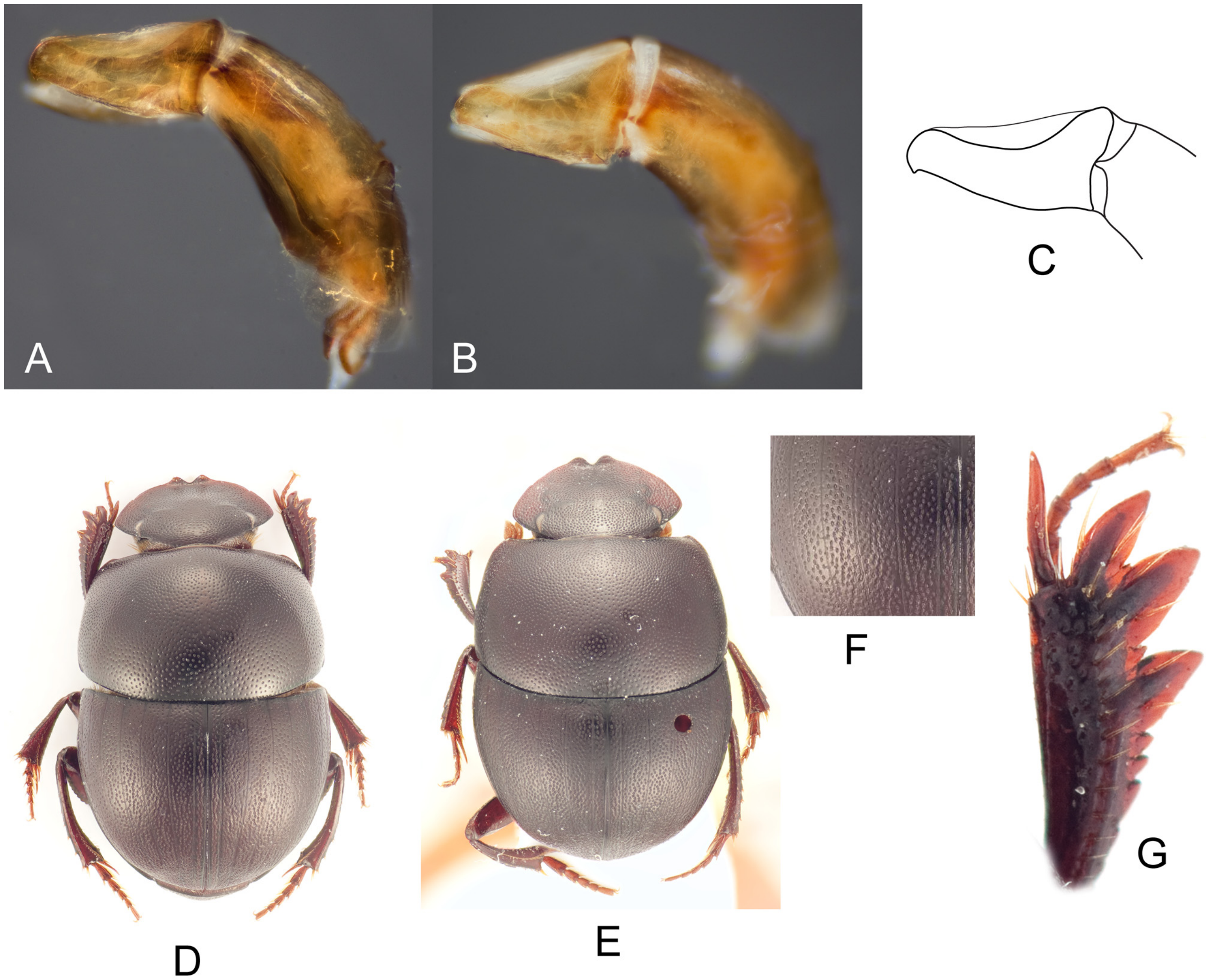

FIGURE 10. Morphology of *Parachorius globosus*. (A–C) aedeagus. (D) habitus (male). (E) habitus (female, holotype). (F) disc of left elytron. (G) protibia (female)

Parachorius gotoi **(Masumoto, 1986) new combination**
(Figs. 11, 25F)

Cassolus gotoi Masumoto, 1986: 85
Cassolus gotoi: Masumoto 1991: 156

Type locality. Hewanshan [Hewangshan, Nantou Hsien, Taiwan].

Distribution. This species is endemic to Taiwan where it is only known from two specimens collected in type locality and Fushan botanical garden.

Taxonomic notes. Since only two specimens were examined (only one of them was male), it was not possible to assess the intraspecific variation. Presumably male specific characters such as the shape of the metafemoral posterior margin may be variable and dilated in similar way as in other species of the genus.

Diagnosis. This species differs from the other *Parachorius* species by its parameres elongate and rounded apically.

Description. *Body.* Body black, length 5.5 mm. Elytra uniformly colored.

Head. Clypeus with two teeth, outer margin of each tooth slightly notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1.0–1.5 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

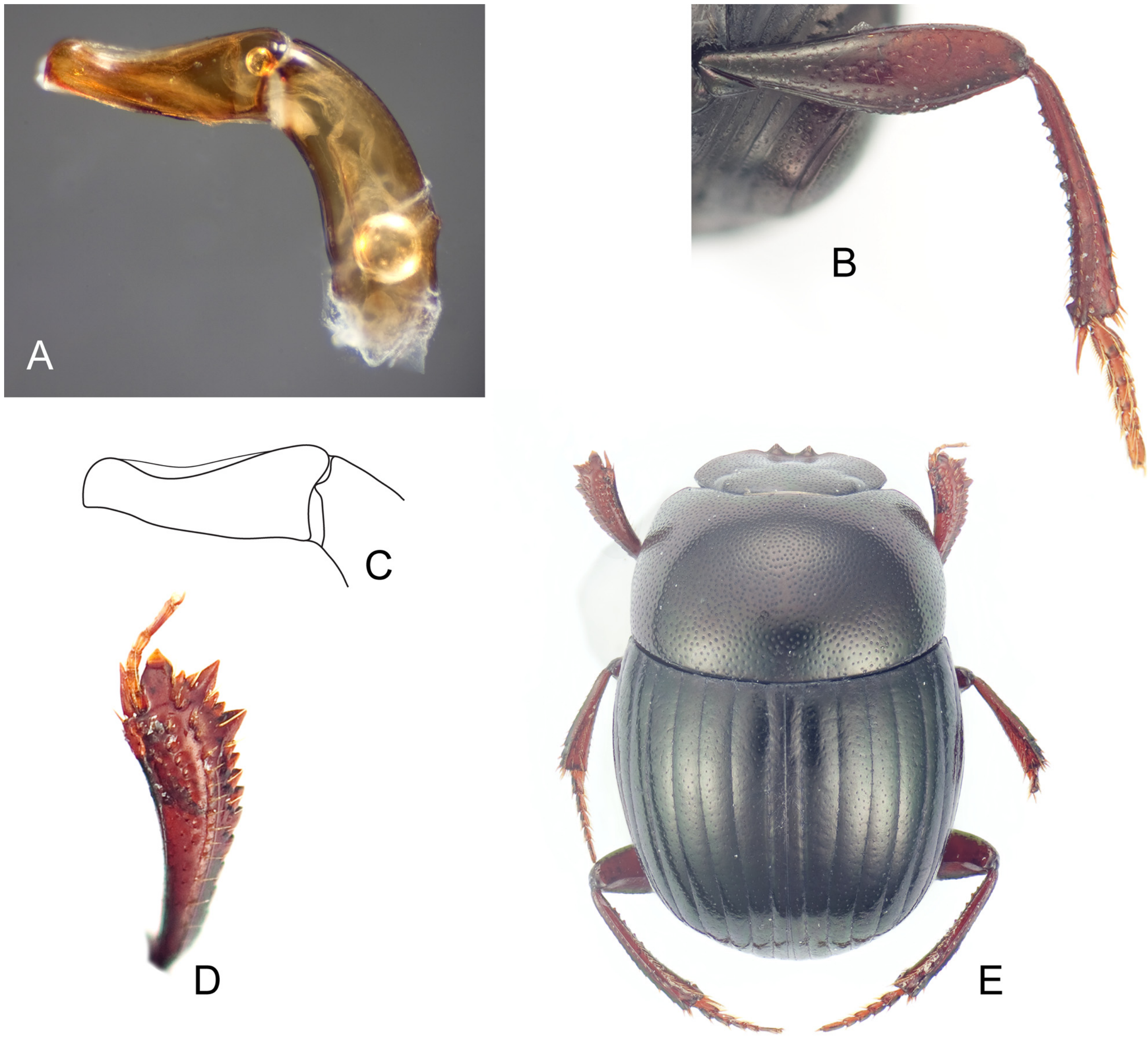

FIGURE 11. Morphology of *Parachorius gotoi*. (A, C) aedeagus. (B) left metafemur (male). (D) protibia (male). (E) habitus (male).

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with almost straight or sinuate anterior margin. Protibia with apical spur reaching protarsomere 2. First tooth notably modified in males, spatulate, bent downward and notably larger than second tooth with which it nearly merged; first tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin serrate, simple, not modified. Metatibia slightly sinuate, produced in small angle apically, inner margin denticulate with relatively small teeth.

Metasternum. Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length.

Aedeagus. Parameres symmetrical, elongate, and rounded apically.

Material examined. Holotype: **Taiwan**: **1 female**, "Holotype Cassolus gotoi Masumoto / Hewanshan Date: 20.VI.1985 [Hewangshan, Nantou Hsien] Luo Chinchih leg", 23°48.7'N, 120°55.1'E (NSMT). **1 male**, Fushan Botanical Garden, 24°45'N, 121°36'E, on 7–8/v/2004, (K. Masumoto) (NSMT).

***Parachorius hookeri* Arrow, 1931**

(Figs. 12, 26A)

Parachorius hookeri Arrow, 1931: 359
Parachorius hookeri; Balthasar, 1963: 277
Parachorius hookeri; Bacchus, 1978: 104

Type locality. Sikkim, northeast India.

Diagnosis. Given the shape of parameres with apex simple, widely rounded, and inferiorly angulate this species is similar to *P. fungorum*, *P. newthayerae*, *P. globosus*, and *P. shuelkei*. Based on external morphology this species is most similar to *P. fungorum*. The latter and *P. hookeri* can be differentiated from other species of abovementioned group by (1) clypeus with two indistinct teeth that are not notched laterally, (2) metatibia slightly sinuate, (3) frontal angles of pronotum rounded, and (4) wings normally developed. *Parachorius hookeri* subtly differs from *P. fungorum* by not having modified metathoracic legs and the absence of a serrate margin of the metatibia.

Taxonomic notes. The paramere shape in *P. hookeri*, *P. fungorum*, *P. newthayerae*, *P. globosus*, and *P. shuelkei* are almost identical. A larger series of specimens will be needed to assess intraspecific variation of *P. hookeri,* known only from a single male, in comparison to its close relative *P. fungorum*. *Parachorius hookeri* may just be a minor male of *P. fungorum*, with whom it has an identical shape of aedeagus, meaning that the two names should be synonyms.

However, I do not attempt to synonymize these names here, for the two reasons: (1) aedeagus shape is not an ultimate character for species delimitation in *Parachorius* as some species have similar aedeagus shapes despite being drastically different in external characters; (2) in addition, these two forms seems to have a disjunct distributions with *P. hookeri* occurring in northern India and *P. fungorum* occurring in southern China, Myanmar, and Indochina. Thus, at this point, given the distribution and characters differentiating *P. hookeri* and *P. fungotum*, I consider *P. hookeri* a separate species.

Description. *Body.* Body brown, dark, length 6 mm. Elytra uniformly colored.

Head. Clypeus with two indistinct teeth, outer margin of each tooth not notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 0.5–2.0 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth almost not modified in males, approximately as wide as second tooth, first and second teeth distinctly separated from each other; first tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, simple, not modified. Metatibia slightly sinuate, inner margin not denticulate, straight, not produced apically.

Metasternum. Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length.

Aedeagus. Parameres symmetrical, simple, apex widely rounded and inferiorly angulate.

Material examined. Holotype: **India**: **1 male**, “Holotype / n Ind / Parachorius hookeri type Arrow / Parachorius hookeri Arrow M.E. Bacchus det. 1975 HOLOTYPE / Parachorius hookeri Arrow, 1931 S. Tarasov det. 2010” [Sikkim] (BMNH).

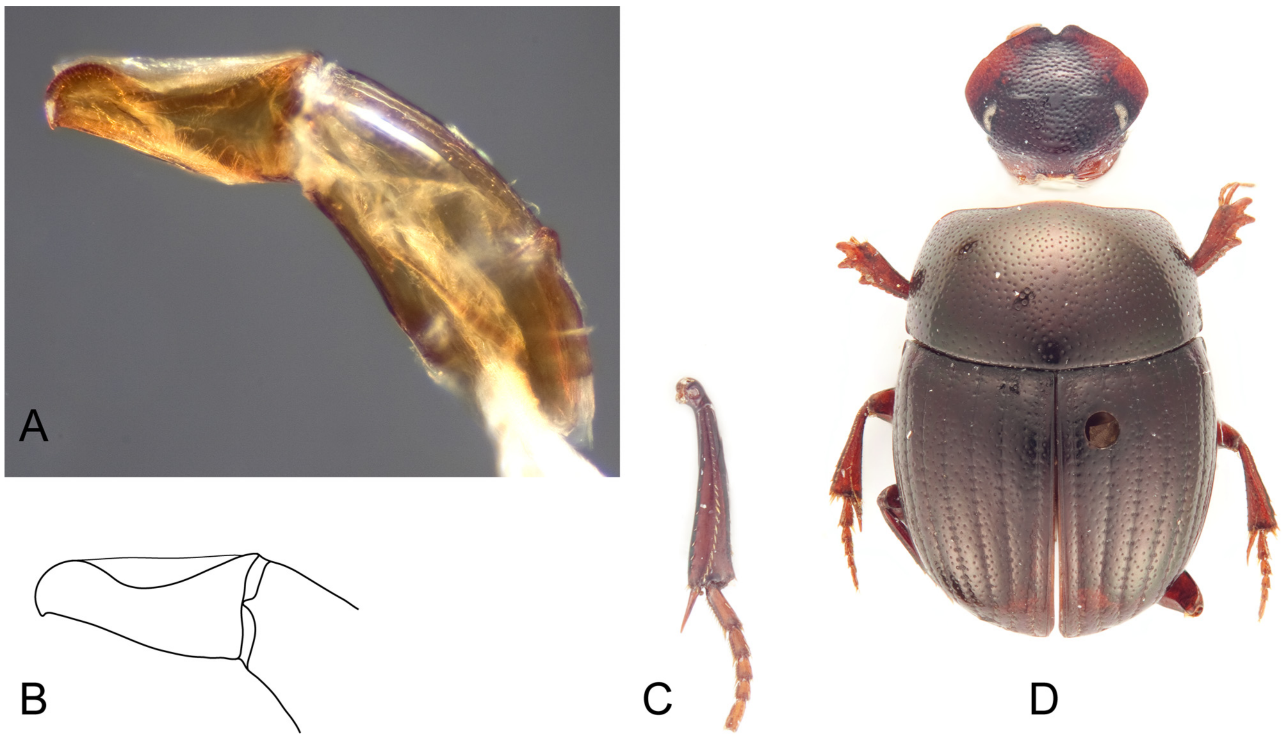

FIGURE 12. Morphology of *Parachorius hookeri*. (A) aedeagus, lateral view (holotype). (B) aedeagus lateral view. (C) left metafemur (male, holotype). (D) habitus (male, holotype)

Parachorius humeralis **(Arrow, 1907) new combination**
(Figs. 13, 26B)

Cassolus humeralis Arrow, 1907: 416
Cassolus humeralis; Gillet 1911: 39
Cassolus humeralis; Arrow 1931: 361
Cassolus humeralis; Balthasar 1963: 262
Cassolus humeralis; Kryzhanovsky & Medvedev 1966: 394
Cassolus humeralis; Bacchus 1978: 104
Cassolus humeralis; Paulian 1980: 57

Type locality. Assam Sudiya [Assa, northeastern India].

Distribution. The species is known only from northeastern India (Sikkim, Assam, Meghalaya).

Diagnosis. This species is most similar to *P. asymmetricus* from which it differs by the symmetrical aedeagus as well as first and second teeth of protibia being distinctly separated from each other. From other *Parachorius* species *P. humeralis* can be separated by (1) elytron usually bearing yellow humeral spot (rarely not), (2) aedeagus shape, (3) apical half of metafemoral posterior margin from slightly to largely dilated and produced in sharp or rounded angle, and (4) dilation of metafemur steeply reducing near apex.

Description. *Body.* Body, black or brown, dark, length 3.8–5.0 mm. Elytra with yellow humeral spot or uniformly colored.

Head. Clypeus with two teeth, outer margin of each tooth distinctly notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 0.5–2.0 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

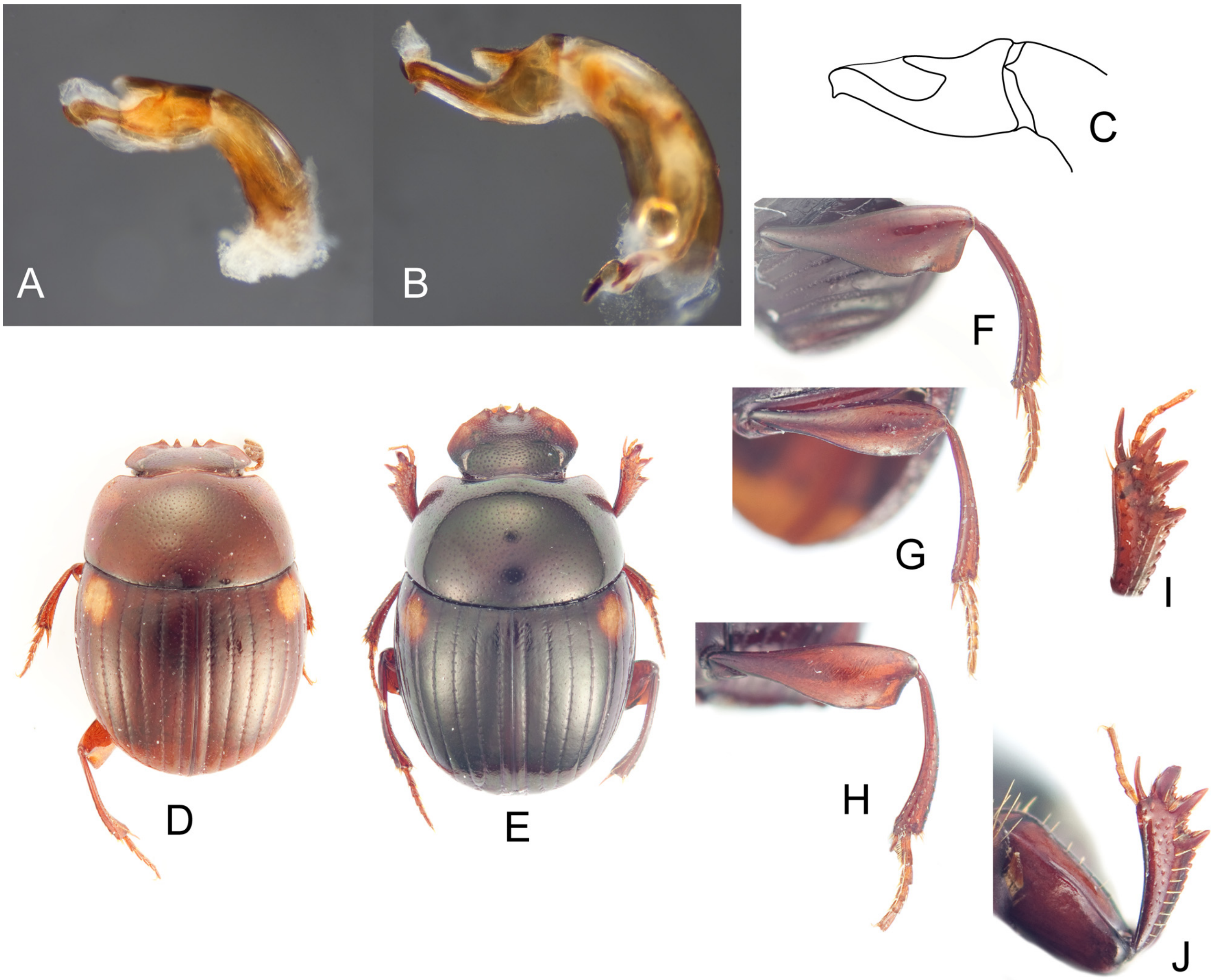

FIGURE 13. Morphology of *Parachorius humeralis*. (A–B) aedeagus (Darjeeling). (C) aedeagus. (D) habitus (male, holotype). (E) habitus (male). (F–H) right metafemur (male). (I) protibia (female). (J) protibia (male).

Wings. Wings normally developed.

Legs. Profemur with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth notably modified in males, approximately twice as wide as second tooth; first and second teeth distinctly separated from each other; first tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, largely dilated in apical half of metafemur and produced in sharp angle or slightly dilated in apical forth of metafemur and produced in rounded angle preapically; dilation gradually reducing preapically. Metatibia slightly sinuate, inner margin not denticulate, produced in small angle apically.

Metasternum. Transverse basal ridge of metasternum reduced and extremely short.

Aedeagus. Parameres symmetrical, with horn-like upper lobes dorsally.

Material examined. Lectotype: **India**: **1 male**, "? / LECTOTYPE / Doherty / Assam Sudiya / 60468 / Fry Coll. 1905-100 / Cassolus humeralis / Arrow type ? A. a. m., 1907 / Cassolus humeralis Arrow ? M.E. Bacchus det 1975. LECTOTYPE", 27°50'N, 95°45'E (BMNH). **Paralectotypes**: **1 male**, **1 female**, Assam, Patkai Hills (BMNH). **1 male**, Darjiling, Gopaldhara, Runbong Valley, Sikkim, British Museum 1922-307, 27°2.1'N, 88°15.8'E, on vii/1920 (H. Stevens) (BMNH). **1 male**, Gopaldhara, Runbong Valley, Sikkim, 1916-218, 27°2.1'N, 88°15.8'E (H. Stevens) (ISNB). **1 male**, Gopaldhara, Runbong Valley, Sikkim, 1916-218, 27°2.1'N, 88°15.8'E (H. Stevens) (BMNH). **1 male**, Gopaldhara, Runbong Valley, Sikkim, British Museum 1922-307, 27°2.1'N, 88°15.8'E (H. Stevens) (BMNH). **1 male**, Assam, Bhalukpong, 27°2'N, 92°35'E, 150 m, on 26/v–3/vi/2009 (P. Pocholatko) (BMNH). **1 male**, Darjeeling, Mungpo, B.M. 1931-452, 26°58.3'N, 88°22.3'E (M. Cameron) (BMNH). **1 male**, Meghalaya, SW of Cherrapunjee, 25°13.5'N, 91°40'E, 900 m, on 5–24/v/2005 (P. Pocholatko) (BMNH). **1 male**, Shilong, 25°33.9'N, 91°53' E, 6/iv/1918, (BMNH). **1 male**, W Bengal, Darjeeling, North Point, No 890, 27°2.1'N, 88°15.8'E, 1500 m, from traps with carcass, 23/x/1967 (G. Topal) (ZIN).

Parachorius javanus (Boucomont, 1914) new combination

(Figs. 14, 26C)

Cassolus javanus Boucomont, 1914: 251
Cassolus javanus; Balthasar, 1963: 263

Type locality. Sokabumi [West Java].

Diagnosis. Along with *P. schuelkei* and *P. pseudojavanus*, this species can be separated from all other *Parachorius* the two distinctly produced clypeal teeth whose outer margin is not notched basally. *Parachorius javanus* can be distinguished from *P. schuelkei* and *P. pseudojavanus* by a combination of characters: (1) body coloration is reddish brown, and (2) parameres are notched basally and claw shaped in lateral view. External morphology and endophallic sclerite characters place *P. javanus* as most closely related to *P. pseudojavanus.*

Taxonomic notes. The species is known only from the holotype. All other records of *P. javanus* are likely to refer to the newly described and closely related *P. pseudojavanus*. *Parachorius javanus* and *P. pseudojavanus* can only be reliably separated by the shape of aedeagus; the females of the two species are undistinguishable. Due to this, many females from various localities in West Java remain unidentified.

Description. *Body.* Body reddish brown, length 6.7 mm. Elytra uniformly colored.

Head. Clypeus with two distinctly produced teeth, their outer margin not notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1–4 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemora with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth notably modified in males, approximately twice as wide as second tooth; first and second teeth distinctly separated from each other; first tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, simple, not modified. Metatibia slightly sinuate, inner margin not denticulate, straight, not produced apically.

Metasternum. Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length.

Aedeagus. Parameres symmetrical, notched basally, and claw shaped in lateral view.

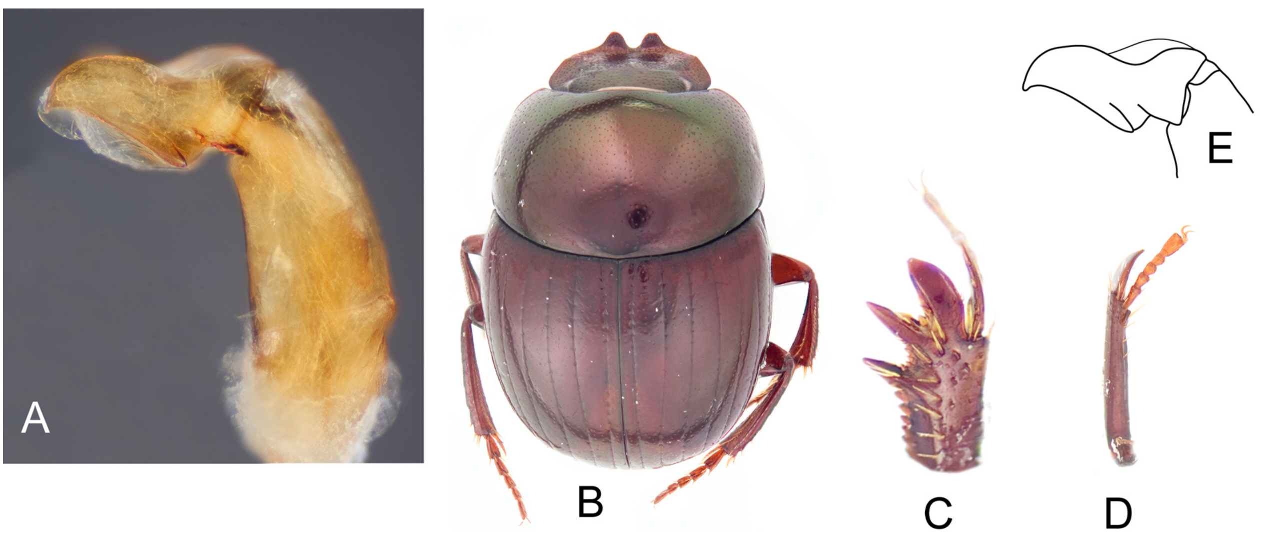

FIGURE 14. Morphology of *Parachorius javanus*. (A, E) aedeagus lateral view (male, holotype). (B) habitus (male, holotype). (C–D) protibia (male, holotype)

Material examined. Holotype: **1 male**, "Java occident Sukabumi 2000 1983 H. Fruhstorfer / EX MUSEO N. VAN DE POLL] / TYPUS / Boucomont det. 1914 Cassolus javanus n.sp. / MUSEUM PARIS Boucomont / J. Krikken 1969 compared with 5 PM (Amsterdam:ZMUA) which is comp[letely]. Rufous from Bogor", 6°55.1'S, 106°55.6'E (MNHN).

Parachorius longipenis **Tarasov new species**
(Figs. 15, 26D)
urn:lsid:zoobank.org:act:9BE1948F-A942-492A-A07A-278B88EE090D

Type locality. Hoa Binh, Vietnam.

Etymology. The name of this species derives from the Latin words "longus" and "penis" reflecting the fact that this species has a relatively elongated penis in comparison to the similar species *P. solodovnikovi*.

Distribution. The species is known from Vietnam, Laos, and Thailand. It is abundant in collections compared to other species of *Parachorius* and therefore, likely widespread in Indochina.

Diagnosis. This species is most similar to *P. nudus*, *P. solodovnikovi*, and *P. peninsularis*. From them and all other *Parachorius*, it can be separated by (1) protibia with first tooth spatulate, bent downward and notably larger than second tooth, (2) first tooth also looks bifurcated as it merged with denticles located between first and second teeth, (3) aedeagal parameres elongate with horn-like upper lobes dorsally.

Description. *Body.* Body black, length 3.8–5.6 mm. Elytra uniformly colored.

Head. Clypeus with two teeth, outer margin of each tooth distinctly notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 0.3–1.0 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemora with almost straight or sinuate anterior margin. Protibia apical spur reaching protarsomere 2. First tooth notably modified in males, spatulate, bent downward and notably larger than second tooth, with which it is almost merged; first tooth may look bifurcate because it is merged with denticles located between first and second teeth. Metafemoral posterior margin not serrate, it varies from simple to dilate with produced angle in basal half of metafemur. Metatibia produced in small angle apically, slightly sinuate, inner margin denticulate with relatively small teeth.

Metasternum. Transverse basal ridge of metasternum reduced and extremely short.

Aedeagus. Parameres symmetrical, with horn-like upper lobes dorsally.

Holotype. Male (Fig. 15F). Profemur with sinuate anterior margin. First tooth bifurcate. Metafemoral posterior margin dilated.

Material examined. Holotype: **Vietnam**: **1 male**, "Hoa Binh[,] Tonkin [northern Vietnam,] [leg.] de Cooman / 57 / HOLOTYPE Parachorius longipenis S. Tarasov det. 2010", 20°49.7'N, 105°20'E (MNHN). **Paratypes (45 males)**: **1 male paratype**, Laos ou Cambodge, on 1911 (Bonnote) (MNHN); **Laos**: **1 male paratype**, Houayang National Park, approximately 15 km N of Vientiane, ANIMT site 1225, carrion trap (squid), 18°5.923'N, 102°40.128' E, 190 m, tropical handwood forest, on 2-19/vi/2008 (J. Pedersen, M. Thayer, A. Newton) (FMNH); **1 male paratype**, Vientiane, Houayang forest, 18°5.86'N, 102°40.547'E, 200 m, disturbed forest, on 12–19/vi/2008 (A. Newton, M. Thayer) (FMNH); **Thailand**: **2 male paratypes**, Chaiyaphum province, Thep Sathit district, Pa Him Ngam, 15°42'N, 101°23'E, on 1/ix/2007 (H. Enghoff) (ZMUC); **1 male paratype**, Prae Siam, on 1929-33 (Poul Fogh) (ZMUC); **Vietnam**: **1 male paratype**, Bac Kan Province, Ba Be National Park, 22°25'3"N, 105°37'59"E, 290 m, Limestone Karst, disturbed forest, on 4/vii–6/ix/2005 (L. Hayes) (OUMNH); **1 male paratype**, Bac Kan Province, Ba Be National Park, 22°25'2"N, 105°38'1"E, 315 m, Limestone Karst, disturbed forest, on 4/vii–6/ix/2005 (L. Hayes) (OUMNH); **1 male paratype**, Dong Nai Province, Nam Cat Tien National Park, 11°25.1'N, 107°25.6'E, forest, on 21/v–16/vi/2005 (D. Fedorenko) (ZMUM) **13 male paratypes**, Hoa Binh, Tonkin [northern Vietnam], 20°49.7'N, 105°20'E, on [date specified only for two specimens: 1923 and 1928] (A. De Cooman) (MNHN); **1 male paratype**, Tonkin [northern Vietnam] Central Environs de Tuyen-quan[g], 21°49'N, 105°13'E, on vii–ix/1901 (A. Weiss) (MNHN); **Laos**: **16 male paratypes**, Houayang National Park, approximately 15 km N of Vientiane, 18°5.889'N, 102°40.521'E, 180 m, secondary rain forest, on 19–20/vi/2008

(A. Solodovnikov, J. Pedersen) (ZMUC); **Vietnam**: **6 male paratypes**, Hoa Binh, Tonkin [northern Vietnam], 20°49.7'N, 105°20'E, on [date specified only for two specimens: 1923 and 1928] (A. De Cooman) (MNHN).

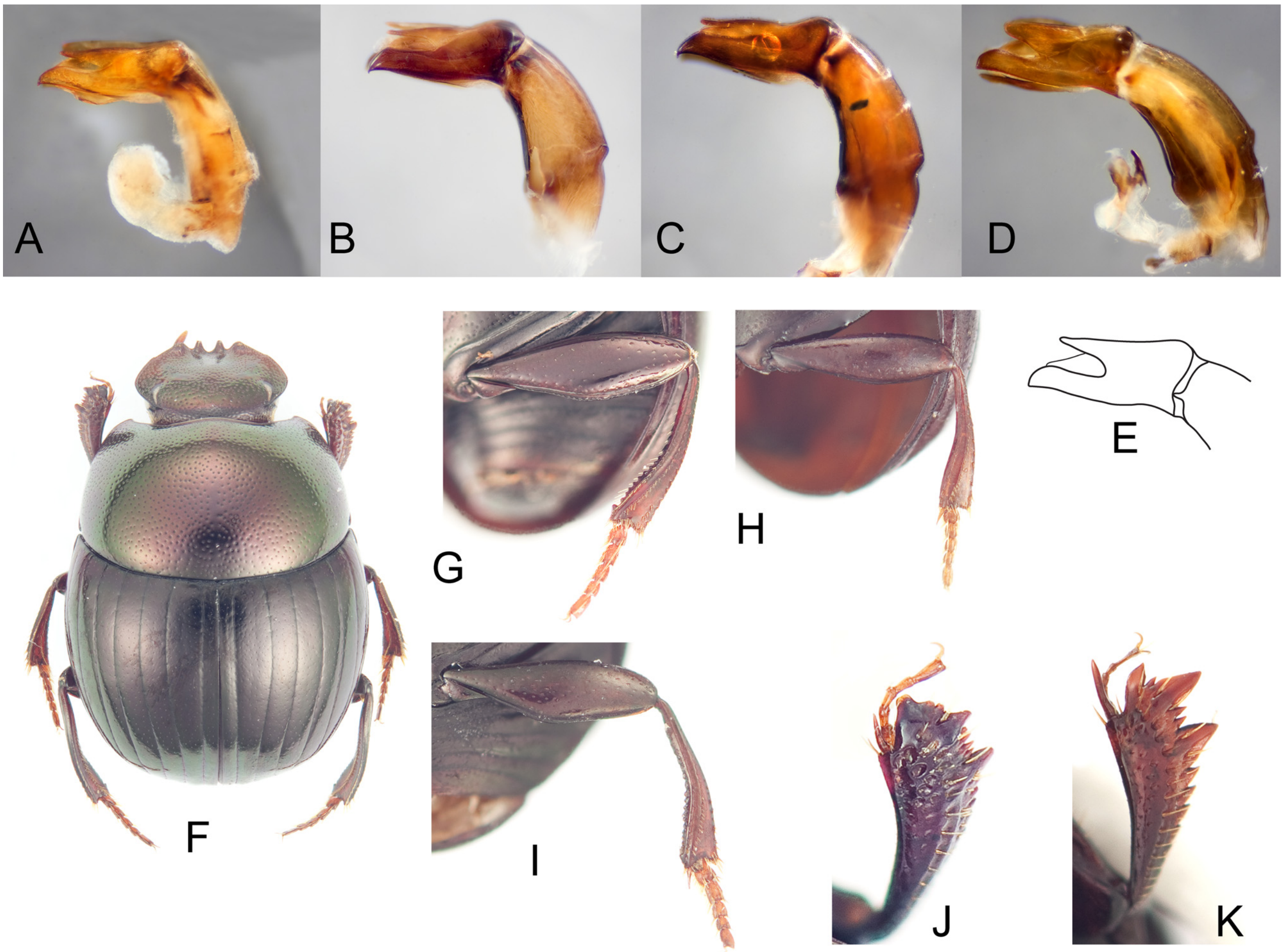

FIGURE 15. Morphology of *Parachorius longipenis*. (A) aedeagus, lateral view (paratype, Vietnam). (B) aedeagus, lateral view (paratype, Thailnd). (C) aedeagus, lateral view (paratype, Laos) (D) aedeagus, lateral view (holotype) (E) aedeagus. (F) habitus (male, holotype). (G) right metafemur (male, holotype). (H) right metafemur (male, paratype, Vietnam). (I) right metafemur (male, paratype, Thailand). (J) left protibia (flipped from original, male, holotype). (K) protibia (female, paratype, Laos).

***Parachorius maruyamai* Masumoto, Ochi, & Sakchoowong, 2012**
(Figs. 16, 26E)

Parachorius maruyamai Masumoto, Ochi, & Sakchoowong, 2012: 104

Type locality. Khao Yai National Park, Kong Kaew [central Thailand].

Distribution. Known only from Khao Tai National Park in central Thailand.

Taxonomic notes. Unfortunately, I was not able to study the type specimens of this species. However, the original description provides sufficient information to formulate its diagnosis and elucidate its phylogenetic position.

Diagnosis. Such characters as sharp frontal angles of pronotum and strongly curved metatibia suggest that this species is most closely related to *P. newthayerae*. **T**he aedeagus shape is similar in these two species, but *P. maruyamai* differs from *P. newthayerae* by strongly sharped frontal angles of pronotum and not dilated posterior margin of metafemur.

The identification using females is ambiguous, see *P. newthayerae* description for details.

Material examined in Masumoto *et al.* (2012). Holotype: **Thailand**: **1 male**, "Thai: Nakhon Ratchashima,/

Khao Yai National Park,/Kong Kaew (700m)/22-28 IX 2007, Maruyama/M. & Katayama Y.(FIT)", 14°26'20"N, 101°22'19"E (NSMT). **Paratype**: **3 females**, "Thai: Nakhon Ratchashima,/Khao Yai National Park,/Kong Kaew (700m)/22–28 IX 2007, Maruyama/M. & Katayama Y.(FIT)", 14°26'20"N, 101°22'19"E (NSMT).

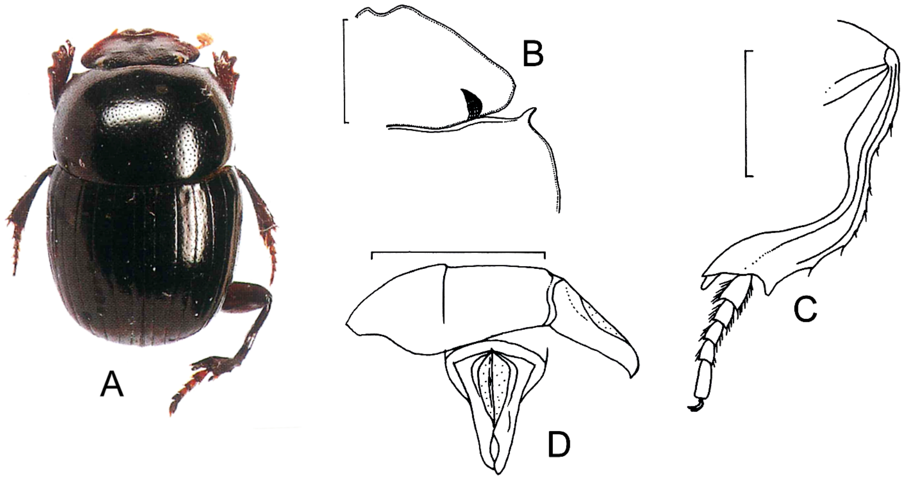

FIGURE 16. Morphology of *Parachorius maruyamai* according to Masumoto *et al.* (2012). (A) habitus (male, holotype). (B) head and pronotum (dorsal view, scale 1 mm). (C) left metafemur (male). (D) aedeagus.

Parachorius newthayerae **Tarasov new species**

(Figs. 17, 26F)

urn:lsid:zoobank.org:act:5DE8A2B0-44BC-43A0-B38F-B3483509F42F

Type locality. Bolaven plateau, Laos.

Etymology. The species is named after two great entomologists, Alfred Newton and Margaret Thayer, who collected the largest series of specimens of this new species in Laos. Alfred and Margaret kindly hosted me during a visit to the Field Museum where the largest part of this taxonomic work on *Parachorius* was conducted. The epithet "*newthayerae*" is the combination of their last names. This species name should be treated as a noun in apposition.

Distribution. This species seems endemic to Bolaven plateau in southern Laos.

Taxonomic notes. In females of *P. newthayerae* the secondary sexual characters of legs modification are not expressed, although anterior angles of pronotum can be very slightly angulate. As only the secondary sexual characters reliably separate *P. newthayerae* from *P. maruyamai*, *P. fingorum*, and *P. thomsoni*, the identification of *P. newthayerae* using females is ambiguous.

Diagnosis. This species is most closely related to *P. maruyamai.* Both species differ from all other *Parachorius* by sharped frontal angles of pronotum along with strongly curved metatibia in males. *Parachorius newthayerae* differs from *P. maruyamai* by dilated posterior margin of metafemur and angulate lateral margin of pronotum.

Description. *Body.* Body black, length 7.8–8.0 mm. Elytra uniformly colored.

Head. Clypeus with two indistinct teeth, outer margin of each tooth not notched basally.

Pronotum. Pronotum distinctly angulate laterally. Frontal angles sharp. Disc covered with punctures separated by 0.5–2.0 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth almost not modified in males, approximately as wide as second tooth; first and second teeth distinctly separated from each other; first tooth normal, distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin serrate (sometimes slightly) or not serrate, medially dilated, and produced in large rounded angle. Metatibia strongly curved and notched medially; inner margin not denticulate, produced in small angle apically.

Metasternum. Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length.
Aedeagus. Parameres symmetrical, simple, apex widely rounded and inferiorly angulate.
Holotype. Male. Profemur with sinuate anterior margin. Metafemoral posterior margin serrate.

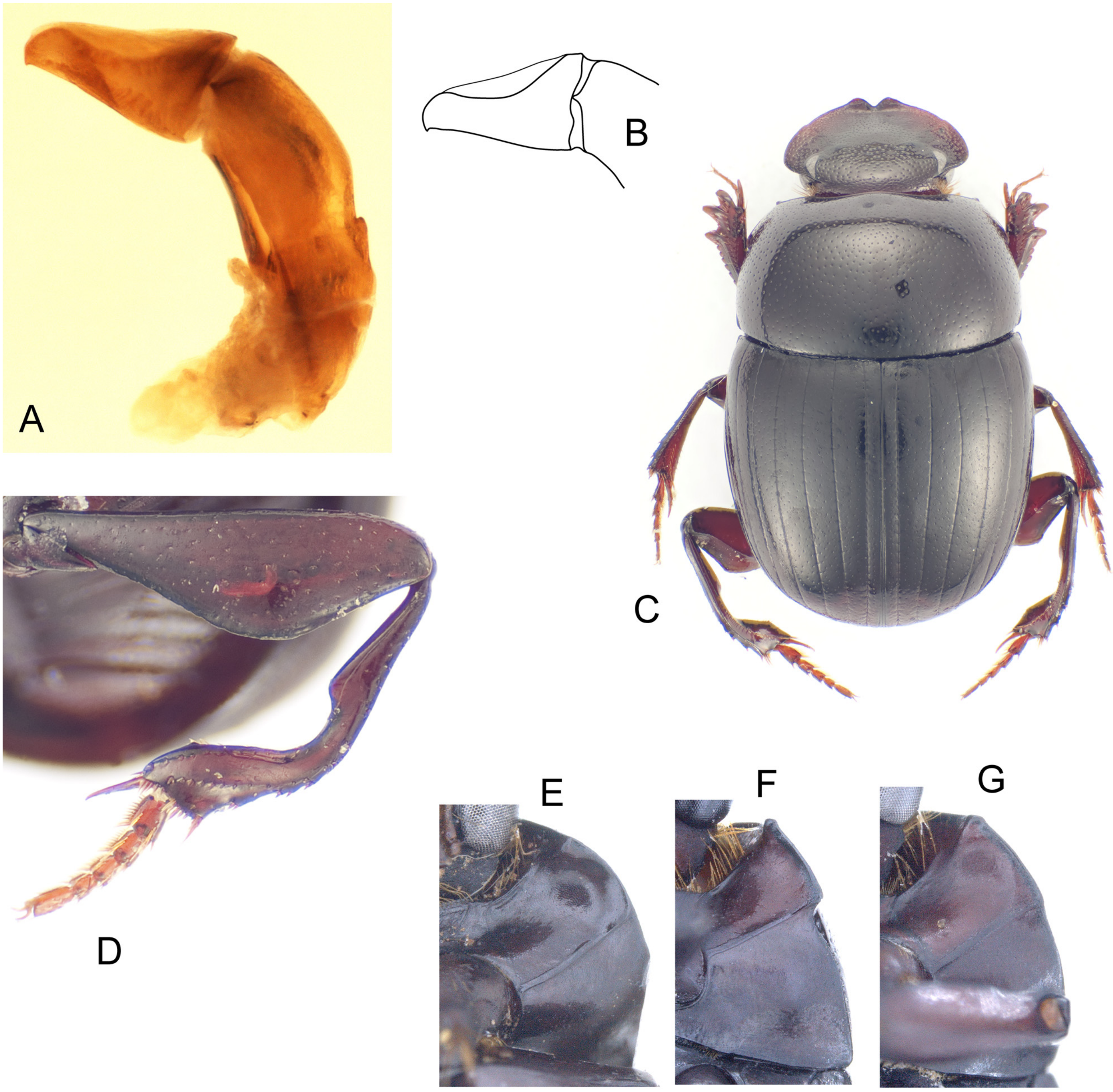

FIGURE 17. Morphology of *Parachorius newthayerae*. (A) aedeagus lateral view (paratype). (B) aedeagus lateral view. (C) habitus (male, paratype). (D) left metafemur (male, paratype). (E, G) propleuron (female). (F) propleuron (male, paratype).

Material examined. Holotype: **Laos**: **1 male**, "LAOS: Champasak Pr.: Bolaven Plateau, Ban Thôngvay (=Xékatam) vic., old logging road N of village1095m, 15°14.288'N 106°31.891'E,8-16.vi.2008 / selectively logged forest; FMHD#2008-037, flight intercept trap, A. Newton & M. Thayer; ANMT site 1231 ex 95% FIELD MUS. NAT. HIST. / HOLOTYPUS Parachorius newthayerae / S. Tarasov det. 2011", 15°14.288'N, 106°31.899'E (FMNH). **Paratypes (3 males, 3 females)**: **1 male paratype**, Champasak Province: Bolaven Plateau, Ban Thôngvay (=Xékatam) vicinity, old logging road N of village, FMHD#2008-034, ANMT site 1230, 15°13.96'N, 106°31.731'E, 1035 m, selectively logged forest, on 8–16/vi/2008 (A. Newton, M. Thayer) (FMNH); **1 male paratype**, Champasak Province: Bolaven Plateau, Ban Thôngvay (=Xékatam) vicinity, old logging road N of village, FMHD#2008-037, ANMT site 1231, 15°14.288'N, 106°31.899'E, 1095 m, selectively logged forest, on 8–16/vi/2008 (A. Newton, M. Thayer) (FMNH); **1 female paratype**, Champasak Province: Bolaven Plateau, Ban

Thôngvay (=Xékatam) vicinity, old logging road N of village, FMHD#2008-038, ANMT site 1231, 15°14.288'N, 106°31.891'E, 1095 m, selectively logged forest, on 8–16/vi/2008 (A. Solodovnikov, M. Thayer, A. Newton) (FMNH); **2 female paratypes**, Champasak Province: Bolaven Plateau, Ban Thôngvay (=Xékatam) vicinity, old logging road N of village, FMHD#2008-040, ANMT site 1232, 15°14.494'N, 106°31.807'E, 1170 m, selectively logged forest, on 8–16/vi/2008 (A. Newton, M. Thayer) (FMNH); **1 male paratype**, Champasak Province, Bolaven Plateau, Ban Thongvay, 15°14.741'N, 106°31.916'E, 1150 m, disturbed montane forest (S. Tarasov) (CST). **Additional specimen: 1 female**, Champasak Province: Bolaven Plateau, Ban Thôngvay (=Xékatam) vicinity, old logging road N of village, FMHD#2008-035, ANMT site 1230, 15°13.96'N, 106°31.731'E, 1035 m, selectively logged forest, on 8–16/vi/2008 (A. Solodovnikov, M. Thayer, A. Newton) (FMNH).

Parachorius nudus (Sharp, 1875) new combination
(Figs. 18)

Cassolus nudus Sharp, 1875:40
Cassolus nudus; Gillet 1911: 39
Cassolus nudus; Boucomont & Gillet 1921: 4
Cassolus nudus; Paulian 1945: 58
Panelus quadridentatus Balthasar, 1952: 223 (*species inquirenda*)
Cassolus quadridentatus; Balthasar 1963: 260
Cassolus nudus; Balthasar 1963: 260
Cassolus nudus; Masumoto, 1987: 127
Cassolus nudus; Hanboonsong & Masumoto 2001: 135
Cassolus nudus; Masumoto *et al*. 2012: 105

Type locality. Cambodia (*Cassolus nudus*); Hoa-Binh, Vietnam (*Panelus quadridentatus*)

Distribution. The species is known only from the holotype specimen collected in Cambodia, which lacks any detailed information on the type locality.

Diagnosis and taxonomic notes. In external morphology this species is most similar to *P. solodovnikovi*, *P. longipenis*, and *P. peninsularis.* Reliable species identification in this group requires examination of the parameres. The squeezed aedeagus of the holotype, the only available specimen of this species, does not allow reconstructing the real shape of the aedeagus. This imposes problems on the identity of this species and its separation from the similar species. Although the aedeagus is squeezed, the examination suggests that its parameres seem to lack horn-like dorsal lobes that are present in *P. solodovnikovi* and *P. longipenis*. Given current state of knowledge, this indicates that *P. nudus* is a separate species. At the same time, due to squeezing the separation of the paramere shape between *P. nudus* and *P. peninsularis* does not seem possible. However, from the latter, *P. nudus* can be reliably distinguished by the modified first tooth of the protibia, where *P. nudus* is bifurcate, spatulate, bent downward, and notably larger than the second tooth with which the first tooth is almost merged. These facts support the species identity of *P. nudus*.

Panelus quadridentatus, the synonym of *P. nudus,* is described from Vietnam ("Tonkin: Hoa-Binh, A. de Cooman leg."). All studied material from Vietnam suggests that *P. nudus* does not likely occur there, which points out that *P. quadridentatus* is probably conspecific with either *P. solodovnikovi* or *P. longipenis*, which are known from the same collecting events. Unfortunately, the type of *Panelus quadridentatus* deposited in NMPC is probably lost (Bezdek & Hajek 2011). Moreover, the original description of *Panelus quadridentatus* does not list any characters enabling reliable separation of this species from other *Parachorius*. Hence, being unable to examine the type and separate *P. quadridentatus* from other *Parachorius*, I follow Balthasar (1963) and tentatively treat *P. quadridentatus* as a synonym of *P. nudus*. The elucidation of *P. quadridentatus* identity needs further investigation and this species has to be formally regarded as *species inquirenda*.

The type of *P. nudus* is the only *Parachorius* known from Cambodia. Additional sample of *Parachorius* from Cambodia is needed to assess diagnosis and identity of *P. nudus*.

Description. *Body.* Body dark, length 4.8 mm. Elytra uniformly colored.

Head. Clypeus with two teeth, outer margin of each tooth distinctly notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1.0–1.5 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with almost straight or sinuate anterior margin. Protibia with apical spur reaching protarsomere 2. First tooth notably modified in males, spatulate, bent downward and notably larger than second tooth, with which it almost merged; first tooth may look bifurcated as it is merged with denticles located between first and second teeth. Metafemoral posterior margin not serrate, simple, not modified. Metatibia slightly sinuate, inner margin denticulate with relatively small teeth, produced in small angle apically.

Metasternum. Transverse basal ridge of metasternum reduced and extremely short.

Aedeagus. Parameres symmetrical, simple, and narrowed toward apex (lateral view).

Material examined. Holotype of *Cassolus nudus*: Cambodia: 1 male, "Cassolus nudus type DS / Camb Mouhot [Cambodia] / Ex Musæo D.Sharp 1890 / G.J. Arrow vidit 1901 / Museum Paris ex. coll. R. Oberthur / Type / Holotypus Cassolus nudus S. Tarasov det. 2010 / Parachorius nudus S. Tarasov det. 2011 " (MNHN).

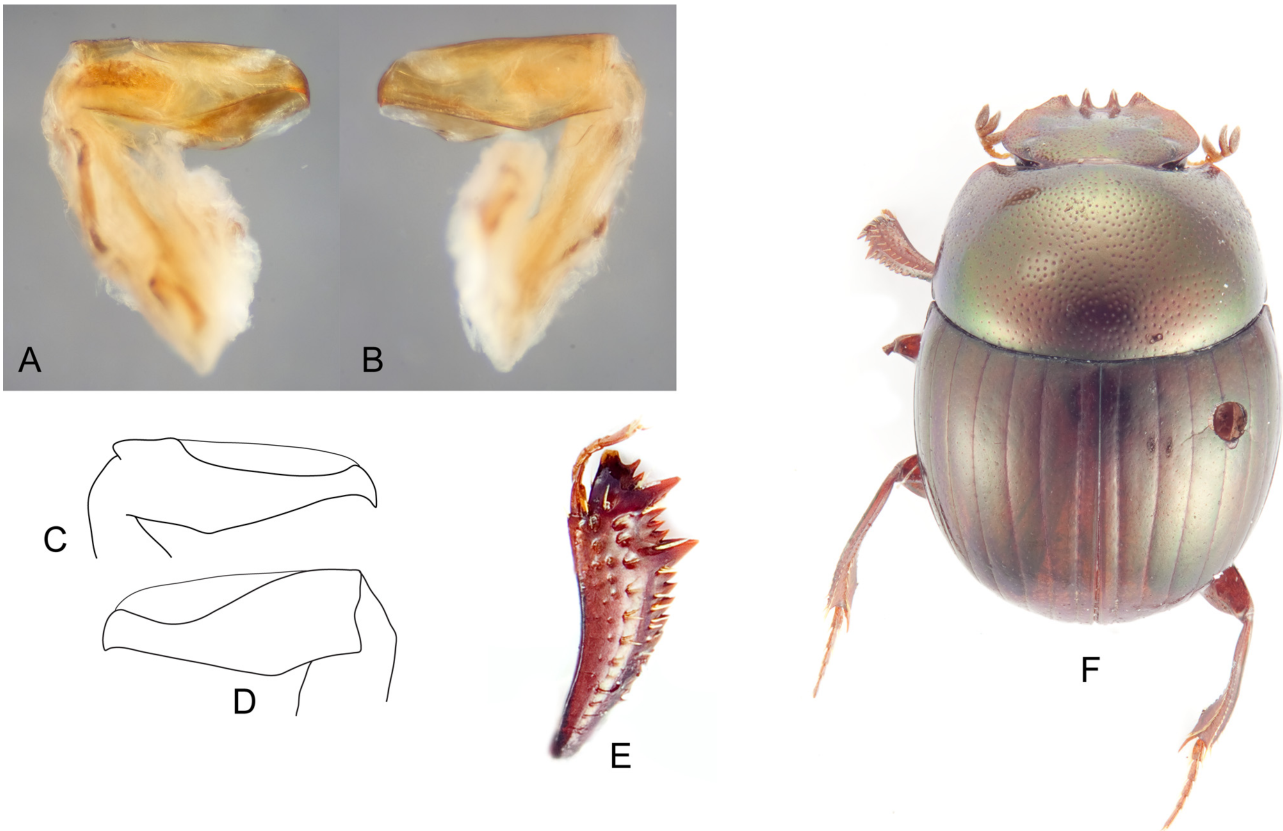

FIGURE 18. Morphology of *Parachorius nudus*. (A, C) aedeagus, right lateral view (holotype). (B, D) aedeagus, left lateral view (holotype). (E) protibia (male, holotype). (F) habitus (male, holotype).

Parachorius peninsularis (Arrow, 1907) new combination

(Figs. 19, 27A)

Cassolus peninsularis Arrow, 1907: 437
Cassolus peninsularis; Gillet 1911: 39
Cassolus peninsularis; Boucomont 1914: 250
Cassolus peninsularis; Balthasar 1963: 260
Cassolus peninsularis; Bacchus 1978: 106
Cassolus pongchaii Masumoto, 1989: 31 **(new synonymy)**
Cassolus pongchaii; Hanboonsong & Masumoto 2001: 135

Type locality. Perak, Penang [Malay Peninsula] (*Cassolus peninsularis*); Doi Suthep/Pui, Chiang Mai Province, Thailand (*Cassolus pongchaii*)

Distribution. Central Thailand, Malay Peninsula, and Sumatra.

Taxonomic notes. *Cassolus pongchaii* is synonymized with *P. peninsularis* based on the similarity in external morphology and male genitalia. The types of *C. pongchaii* were not studied; however, I examined a specimen from the type locality of *C. pongchaii* that was identified by K. Masumoto as *C. pongchaii*.

The specimens of *P. peninsularis* examined here demonstrate variation in the shape of genitalia and external morphology. Most likely this variation suggests that *P. peninsularis* represents a complex of closely related species; however, the material deficiency does not allow adequately assessing it. Therefore, pending a more detailed study, in this paper I assume the concept of *P. peninsularis* sensu lato.

I examined two *Parachorius* females from Sulawesi (Tondano, Minahassa) deposited in MNHN, which are likely mislabeled specimens of *P. peninsularis* (species identification using females is ambiguous in *Parachorius*). This is supported by the fact that the Oriental genus *Parachorius* does not occur in Sulawesi and some other scarabaeine specimens from those two localities were identified to be mislabeled as well (Krikken & Huijbregts 2007).

Diagnosis. *Parachorius peninsularis* differs from all other members of *Parachorius* by the following combination of characters: clypeus with two teeth, outer margin of each tooth distinctly notched basally; protibia with apical spur reaching protarsomere 2, its first tooth approximately twice as wide as second tooth; metatibia with inner margin denticulate with relatively small teeth; parameres simple, narrow toward apex (lateral view).

Description. *Body.* Body ranges from black to reddish brown, length 4.0–5.5 mm. Elytra uniformly colored.

Head. Clypeus with two teeth, outer margin of each tooth distinctly notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by or 1–3 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemora with almost straight or sinuate anterior margin. Protibia with apical spur reaching protarsomere 2. First tooth notably modified in males, approximately twice as wide as second tooth, with which it is almost merged or first and second teeth distinctly separated from each other; first tooth normal, distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, simple, or slightly dilated in apical forth of metafemur and produced in rounded angle preapically, dilation gradually reducing toward apex. Metatibia slightly sinuate, its inner margin denticulate with relatively small teeth, and produced in small angle apically.

Metasternum. Transverse basal ridge of metasternum reduced and extremely short.

Aedeagus. Parameres symmetrical, simple and narrowed toward apex (lateral view).

Material examined in this study and records from other sources. Lectotype of *Cassolus peninsularis*: Malaysia: **1 male**, “LECTOTYPE / 66473 / Doherty / ? / Perak L.C. / Fry Coll. 1905-1007 / Cassolus peninsularis type m# A. a. m., 1907 / Cassolus peninsularis Arr m# M.E. Bacchus det 1975 LECTOTYPE", 4°48.4'N, 100°48'E (BMNH). **Paralectotype**: **1 male**, Penang Lamb. 93.60, 5°15.794'N, 100°29'E (BMNH). **Paralectotype**: **2 females**, Perak, 4°48.4'N, 100°48'E (BMNH). **Holotype of *Cassolus pongchaii***: **Thailand**: **1 male**, Doi Suthep/ Pui, Chiang Mai Province, 18°48.951'N, 98°54.015'E, on 30/vii–5/vii/1988 (K. Masumoto) (NSMT) (this record is from Masumoto 1989). **Paratype**: **Thailand**: **9 specimens**, Doi Suthep/Pui, Chiang Mai Province, 18°48.951'N, 98°54.015'E, on 30/vii–5/vii/1988 (K. Masumoto) (NSMT) (this record is from Masumoto 1989). **1 male**, 90891 [locality is illegibly written] (ZMHB). **Indonesia**: **1 male**, North Sumatra, Serdang, Tandjong, Morawa, 5°14.8'N, 96°3'E (B. Hagen) (RMNH). **1 male**, northeastern Sumatra, Deli, Bukit Pandjang Est. Langsa, lowland forest, on ix/1954 (A. Sollaar) (RMNH). **1 male**, northeastern Sumatra, Deli, Kuala Simpang, 4°17.1'N, 98°3.5'E, lowland forest, on viii/1953 (A. Sollaart) (RMNH). **1 male**, northeastern Sumatra, Deli, Kuala Simpang, 4°17.1'N, 98°3.5'E, lowland forest, on ix/1953 (A. Sollaart) (RMNH). **2 males**, northeastern Sumatra, Tebing-tinggi, 3°19.16'N, 99°9.13'E (Dr. Schultheiss) (DEI). **1 male**, Sumatra (ZMHB). **1 male**, Sumatra, Bedagei, collection of V. de Poll (MNHN). **Malaysia**: **1 male**, Malay Peninsula, Kedah, near Jitra, catchment area, 5°52.9'N, 100°31.7'E, 4/vii/1928 (H.M. Pendlebury) (BMNH). **1 male**, Perak, Batang Padang, Jor Camp, 1800 feet, on 6/vi/1923 (H.M. Pendlebury) (BMNH). **Thailand**: **2 specimens**, Doi Inthanon, Chiang Mai Prov., 18°35.325'N, 98°29.066'E, on 30/ vii–3/viii/1988 (K. Masumoto) (NSMT) (this record is from Masumoto 1989). **3 specimens**, Doi Inthanon, Chiang Mai Province, 18°35.325'N, 98°29.066'E, 11/xii/1988 (Y. Manit) (NSMT) (this record is from Masumoto 1989). **1 specimen**, Doi Pui, Chiang Mai Province, 18°48.951'N, 98°54.015'E, 10/ii/1987 (Y. Manit) (NSMT) (this record is from Masumoto 1989). **1 male**, Doi Suthep, Barber F., 18°48.95'N, 98°54.015'E, on iii/1986 (P. Scwedinger)

(MHNG). **1 specimen**, Doi Suthep/Pui, Chiang Mai Province, 18°48.951'N, 98°54.015'E, 20/xi/1988 (Y. Manit) (NSMT) (this record is from Masumoto 1989). **1 specimen**, Phrao Chiang Dao, Chiang Mai Province, 19°21.891'N, 98°57.96'E, 10/ix/1988 (Y. Manit) (NSMT) (this record is from Masumoto 1989). **1 male**, Phukhet Island, 7°56.8'N, 98°20.3'E, 25/iv/2007 (S. Romantsov) (ZIN). **1 male**, Tak Province, Umphang District, Mae Chan/Mae Klong confluence, Thung Yai Wildlife Sanctuary, 15°30'N, 98°48'E, 300 m, oak/bamboo forest, on 24/iv–6/v/1988 (M.J.D. Brendell) (RMNH). **1 male**, Tak Province, Umphang District, Mae Chan/Mae Klong confluence, Thung Yai Wildlife Sanctuary, 15°30'N, 98°48'E, 300 m, oak/bamboo forest, on 24/iv–6/v/1988 (M.J.D. Brendell) (BMNH).

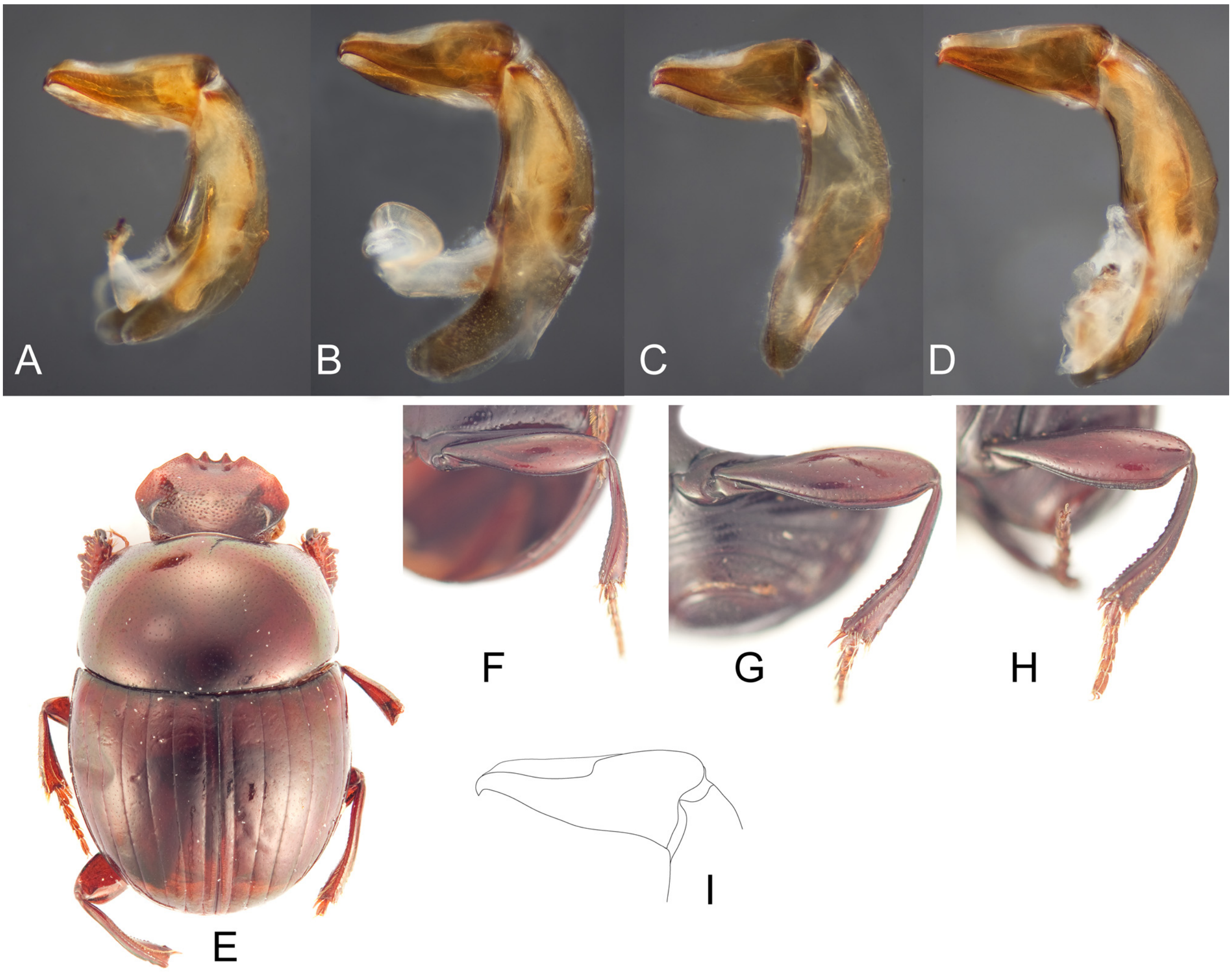

FIGURE 19. Morphology of *Parachorius peninsularis*. (A) aedeagus, lateral view (lectotype). (B) aedeagus, lateral view (Malay, Kedah). (C) aedeagus, lateral view (Sumatra). (D) aedeagus, lateral view (Thailand, Thung Yai). (E) habitus (male, lectotype). (F–H) right metafemur (male). (I) aedeagus, lateral view.

***Parachorius pseudojavanus* Tarasov new species**
(Figs. 20, 27A)
urn:lsid:zoobank.org:act:00ABB56D-BAAA-4C05-862A-0E1359DA03E5

Type locality. Goenoeng Tangkoeban [Gunung Trangkuban, West Java].

Etymology. The name reflects close similarity of this species with *P. javanus*.

Distribution. West Java.

Taxonomic notes. This species is most closely related to *P. javanus* from which it can be separated by the shape of the parameres. All other previous records of *P. javanus* (except the holotype) have to be attributed to *P. pseudojavanus*, which is substantially more frequent in the collections.

Diagnosis. This species is most closely related to *P. javanus*. It can be separated from *P. javanus* and all other *Parachorius* by the following combination of characters (1) parameres medially narrowed (in lateral view), apically acute, (2) protibia with first tooth not noticeably modified in males, approximately as wide as second tooth.

Description. *Body.* Body reddish brown or rarely dark brown, length 6–7 mm. Elytra uniformly colored.

Head. Clypeus with two distinctly produced teeth, their outer margin not notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1–4 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemora with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth almost not modified in males, approximately twice as wide as second tooth; first and second teeth distinctly separated from each other; first tooth normal, distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, simple, not modified. Metatibia slightly sinuate, inner margin not denticulate, straight, not produced apically.

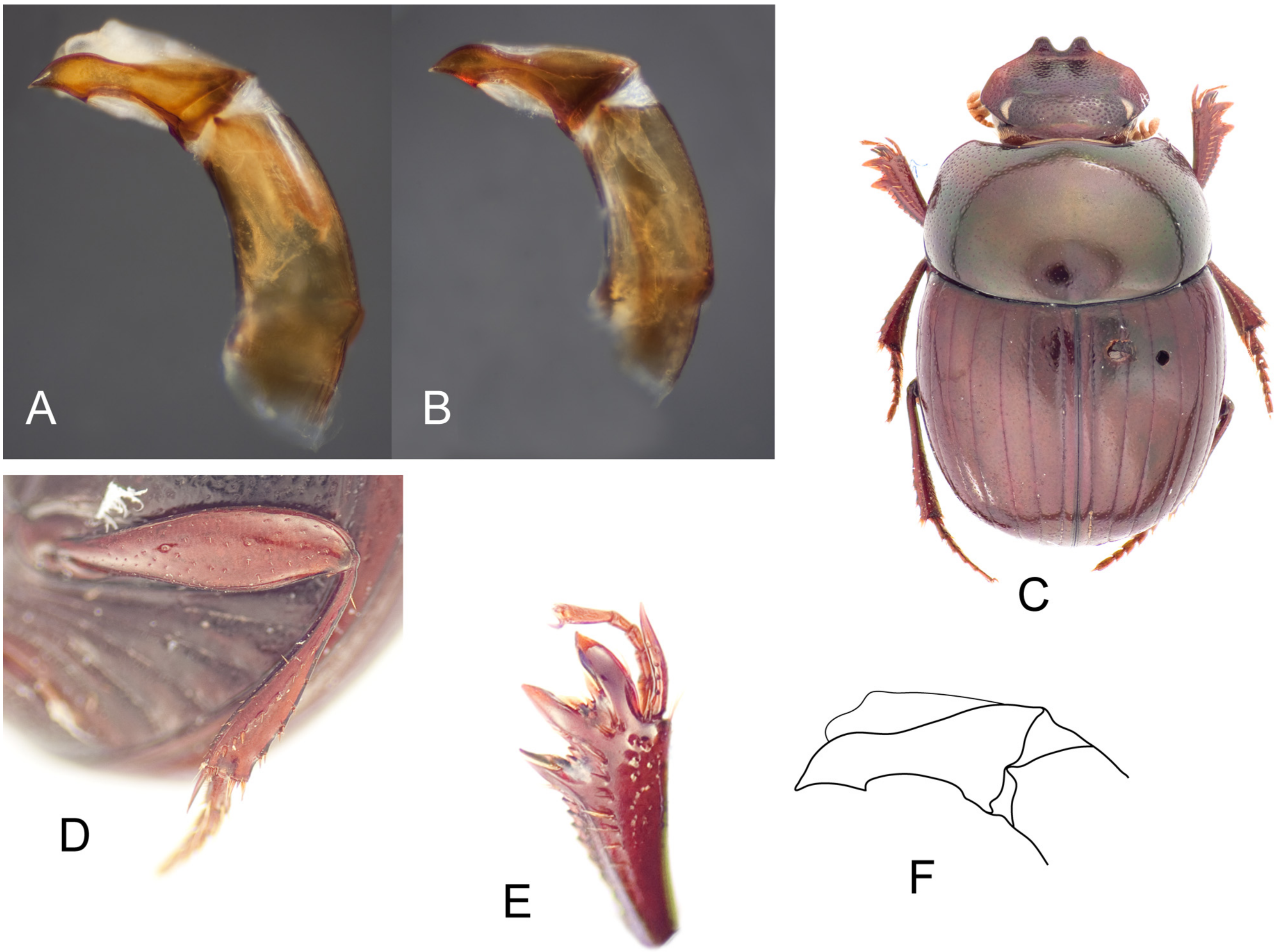

FIGURE 20. Morphology of *Parachorius pseudojavanus*. (A) aedeagus lateral view (male, holotype). (B) aedeagus lateral view (male, paratype). (C) habitus (male, holotype). (D) right metafemur (male). (E) protibia (male). (F) aedeagus lateral view.

Metasternum. Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length.

Aedeagus. Parameres symmetrical, medially narrowed (in lateral view), apically acute.

Holotype. Male (Fig. 20C). Body reddish brown. Profemur with sinuate anterior margin.

Material examined. Holotype: **Indonesia**: **1 male**, "Java, Goenoeng Tangkoeban [Gunung Trangkuban] Prahoe 7.1933 / F.C. Drescher leg. Dr.Ed. Jacobson ded. Eing. Nr. 79, 1934. / MUSEUM PARIS Boucomont / HOLOTYPE Parachorius pseudojavanus S. Tarasov det. 2010", 6°45.7'S, 107°36.3'E (MNHN). **Paratypes (4**

males): **1 male paratype**, Java (ZMHB); **2 male paratypes**, Java, Goenoeng Tangkoeban [Gunung Trangkuban] Prahoe, vii/1933, 6°45.7'S, 107°36.3'E (E. Jacobson) (MNHN). **1 male paratype**, West Java, Mount Gedeh, Tjibodas, 6°47'S, 106°59'E, 1500 m (RMNH).

Parachorius schuelkei Tarasov new species

(Figs. 21, 27C)
urn:lsid:zoobank.org:act:CA113116-C954-450D-8576-5D92D379C637

Type locality. Baoshan Pref., Gaoligong Shan, Yunnan, China.

Etymology. This species is names after Michael Schülke the collector of the type series.

Distribution. China, Yunnan.

Diagnosis. The external morphology of this species is most similar to *P. javanus* and *P. pseudojavanus*, but it can be easily distinguished from both of these species by the black coloration and simple, apically rounded shape of aedeagal parameres. In addition, *P. javanus* and *P. pseudojavanus* are known from Java and *P. schuelkei* is distributed in southern China.

Description. *Body.* Body black, length 6.5–6.8 mm. Elytra uniformly colored.

Head. Clypeus with two distinctly produced teeth, their outer margin not notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 0.5–2.0 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

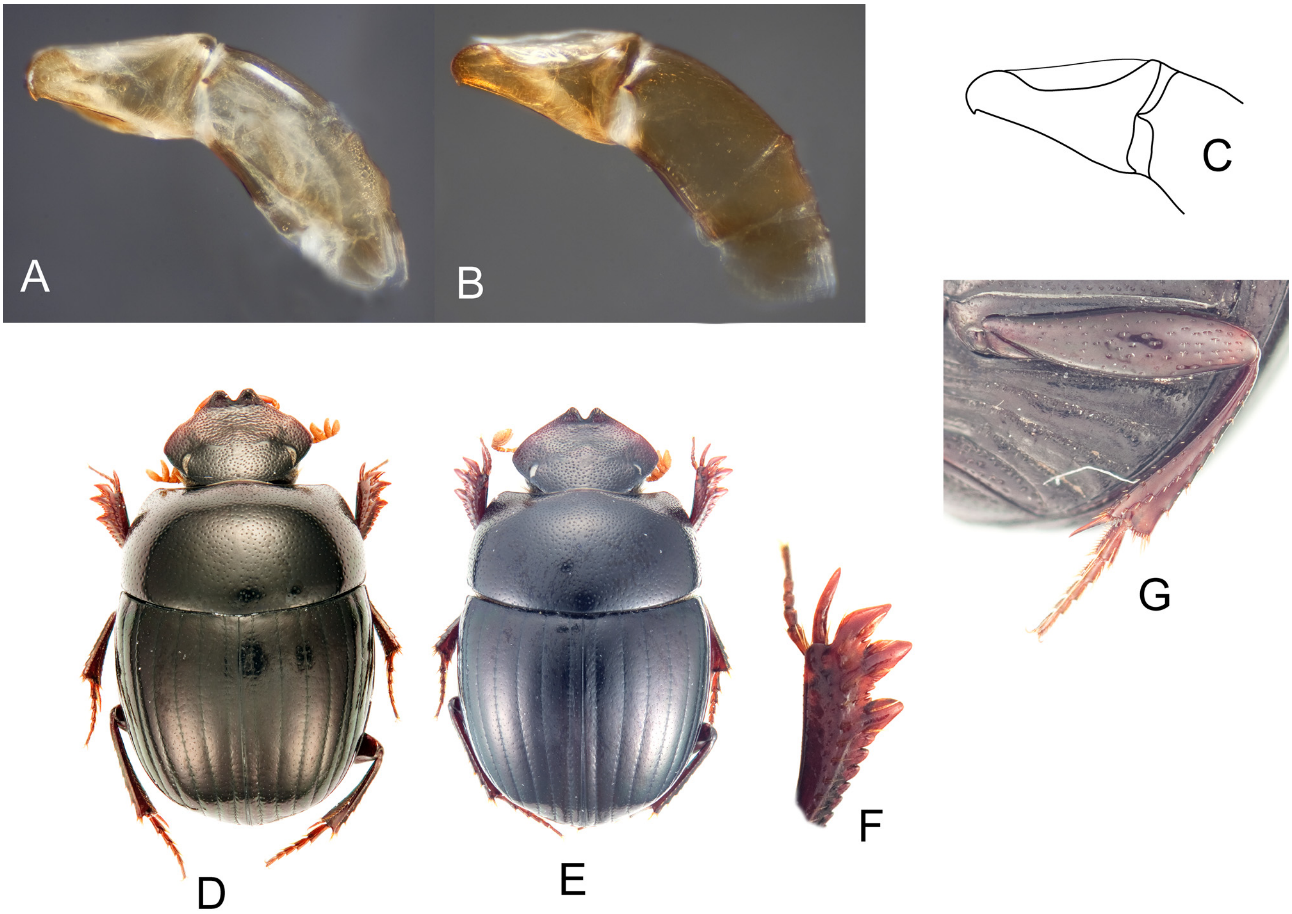

FIGURE 21. Morphology of *Parachorius schuelkei*. (A) aedeagus, lateral view (paratype). (B) aedeagus, lateral view (holotype). (C) aedeagus lateral view. (D) habitus (male, holotype). (E) habitus (female, paratype). (F) protibia (female, paratype). (G) left metafemur (male, holotype).

Legs. Profemur with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth almost not modified in males, approximately as wide as second tooth; first and second teeth distinctly separated from each other; first tooth normal, distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, simple, not modified. Metatibia slightly sinuate, inner margin not denticulate, straight, not produced apically.

Metasternum. Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length.

Aedeagus. Parameres symmetrical, simple, apex widely rounded and inferiorly angulate.

Holotype. Male (Fig. 21D). Profemur with sinuate anterior margin.

Material examined. Holotype: **1 male**, "CHINA: Yunnan [CH07-13], Baoshan Pref., Gaoligong Shan, E pass, 36km SE Tengchong, 2200m, 24°49'32"N, 98° 46'06"E, decid. forest, litter, wood, fungi sifted, 31.V.2007, M. Schülke / HOLOTYPE Parachorius schuelkei S. Tarasov det. 2010", 24°49'32"N, 98°46'6"E (ZMHB). **Paratypes (1 male, 2 females)**: **China**: **1 female paratype**, CHINA: Yunnan [CH07-11], Baoshan Prefecture, Gaoligong Shan, m. Xiaheishan, 35 km SE Tengchong, 24°50'16"N, 98°45'43"E, 2110 m, deciduous forest, on 30/v/2007 (M. Schülke) (ZMHB); **1 female paratype**, CHINA: Yunnan [CH07-13], Baoshan Prefecture, Gaoligong Shan, E pass, 36 km SE Tengchong, 24°49'32"N, 98°46'6"E, 2200 m, deciduous forest, on 31/v/2007 (M. Schülke) (ZMHB); **1 male paratype**, CHINA: Yunnan [CH07-19], Dehong Dai Autonomous Prefecture, mountain range 31 km E Luxi, 24°29'31"N, 98°52'58"E, 2280 m, secondary pine forest with old deciduous trees, on 3/vi/2007 (M. Schülke) (ZMHB).

***Parachorius semsanganus* Tarasov & Keith, 2011**

(Figs. 22, 27D)

Parachorius semsanganus Tarasov & Keith, 2011: 51

Type locality. Phou Sane Mountain, northern Laos.

Distribution. Northern Laos, Phou Sane Mountain.

Diagnosis. This species stands out in being the largest representative of *Parachorius*. It can be separated from all other species of *Parachorius* by metatibia with large teeth in males and inner margin denticulate and parameres with apex bent upward and membranous lobes.

Description. *Body.* Body black, length 8.2–10.6 mm. Elytra uniformly colored.

Head. Clypeus with two teeth, outer margin of each tooth very slightly notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1–2 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with almost straight or sinuate anterior margin. Protibia with apical spur reaching protarsomere 2. First tooth notably modified in males, approximately twice as wide as second tooth; first and second teeth distinctly separated from each other; first tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin serrate (sometimes slightly), simple, not modified. Metatibia slightly sinuate, inner margin denticulate with large teeth on inner margin, produced with a small angle apically.

Metasternum. Transverse basal ridge of metasternum reduced and extremely short.

Aedeagus. Parameres symmetrical, bearing membranous lobes and bending upward apically.

Material examined. Holotype: **Laos**: **1 male**, "LAOS-NE, Xieng Khouang prov., 19°38.20'N 103°20.20'E, Phonsavan (30 km NE): PHOU SANE Mt., 1420 m, 10.-30.v.2009, D. Hauck leg. / HMB Basel, NMPC Prague Laos 2009 Expedition: M. Brancucci, M. Geiser, Z. Kraus, D. Hauck, V. Kubán / HOLOTYPE Parachorius semsanganus D. Keith & S. Tarasov det. 2011", 19°38.2'N, 103°20.2'E (NHMB). **Paratypes**: **4 males**, **3 females**, Xieng Khouang Province, 30 km NE Phonsavan: Ban Na, Lam Phou Sane Mountain, 19°38'N, 103°20'E, 1300–1500 m, on 10–30/v/2009 (M. Brancucci) (NHMB). **Paratypes**: **2 males**, Xieng Khouang Province, Phonsavan (30 km NE): Phou Sane Mountain, Laos 2009 Expedition: M. Brancucci, M. Geiser, Z. Kraus, D. Hauck, V. Kubán, 19°38.2'N, 103°20.2'E, 1420 m, on 10–30/v/2009 (Z. Kraus) (NHMB). **Paratypes**: **9 females**, Xieng Khouang Province, Phonsavan (30 km NE): Phou Sane Mountain, Laos 2009 Expedition: M. Brancucci, M. Geiser, Z. Kraus, D. Hauck, V. Kubán, 19°38.2'N, 103°20.2'E, 1420 m, on 10–30/v/2009 (D. Hauck) (NHMB).

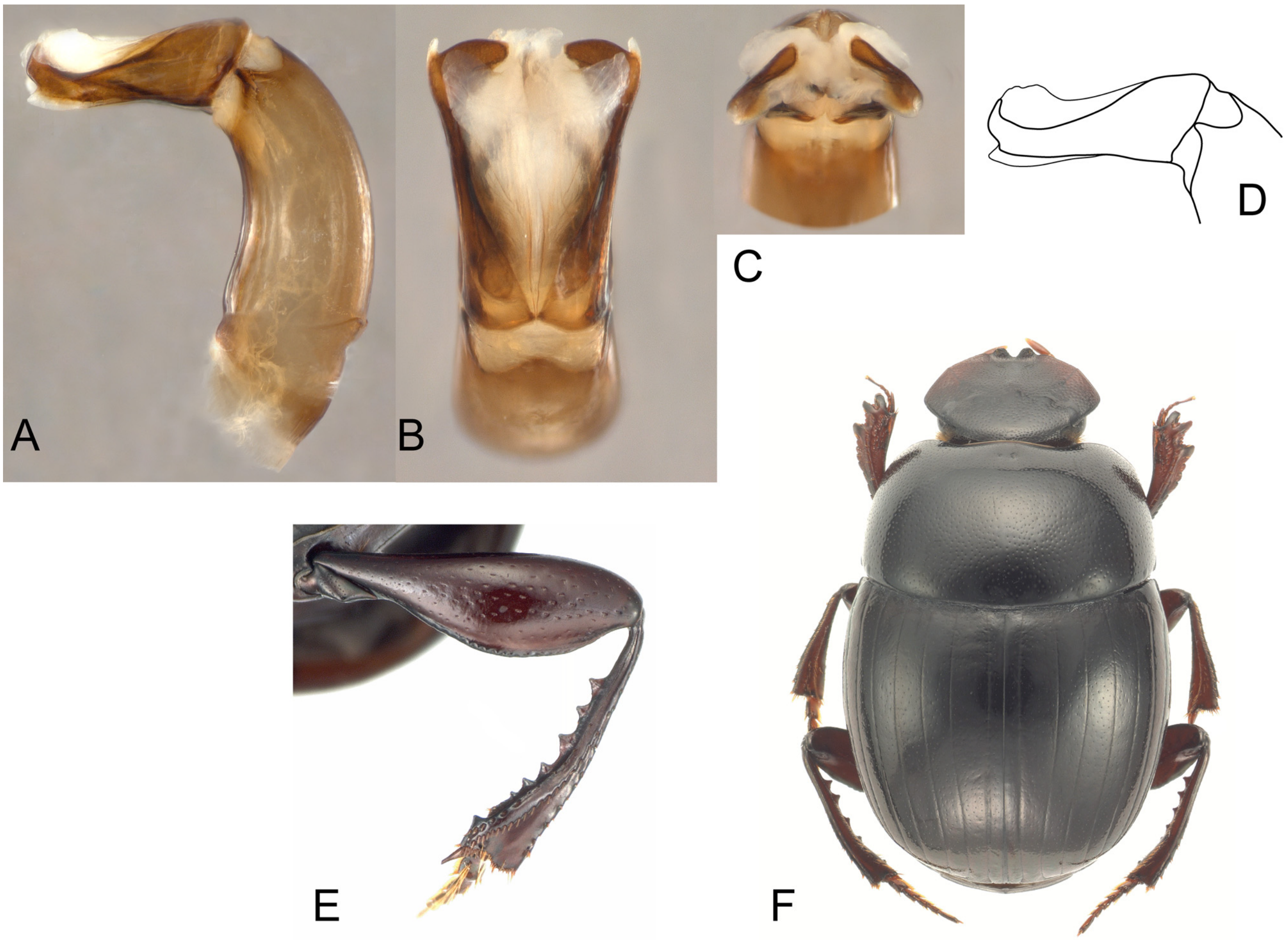

FIGURE 22. Morphology of *Parachorius semsanganus*. (A) aedeagus, lateral view (paratype). (B) aedeagus, dorsal view (paratype). (C) aedeagus, apical view (paratype). (D) aedeagus lateral view. (E) right metafemur (male, paratype). (F) habitus (male, holotype).

Parachorius solodovnikovi **Tarasov new species**
(Figs. 23, 27E)
urn:lsid:zoobank.org:act:4E27796A-EA33-425A-B0FE-F9D100FD799D

Type locality. Vientiane, Houayang forest, Laos.

Etymology. This species is named after the great entomologist and staphylinid specialist, Alexey Solodovnikov, who was also my MSc thesis advisor.

Distribution. The species is known only from few localities in Vietnam, Laos, and Thailand. It is presumably widespread in Indochina.

Diagnosis. This species is most similar to *P. nudus*, *P. longipenis*, and *P. peninsularis*. From those species and all other *Parachorius*, it can be separated by the following combination of characters (1) protibia with apical spur reaching protarsomere 2, (2) first tooth approximately twice as wide as second tooth, (3) metatibia inner margin denticulate with relatively small teeth, (4) parameres with dorsally horn-like upper lobes.

Description. *Body.* Body black, length 3.9–5.0 mm. Elytra uniformly colored.

Head. Clypeus with two teeth, outer margin of each tooth distinctly notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1–2 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with almost straight or sinuate anterior margin. Protibia with apical spur reaching protarsomere

2. First tooth notably modified in males, approximately twice as wide as second tooth; first and second teeth distinctly separated from each other; first tooth distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, simple, not modified. Metatibia slightly sinuate, inner margin denticulate with relatively small teeth, produced in small angle apically.

Metasternum. Transverse basal ridge of metasternum reduced and extremely short.

Aedeagus. Parameres symmetrical, with dorsally horn-like upper lobes.

Holotype. Male (Fig. 23E). Profemur with sinuate anterior margin.

Material examined. Holotype: **Laos**: **male**, "LAOS, Vientiane[,] Houayang forest, N18° 5.860' E102° 40.547' h=200m, carrion trap & pitfall traps, disturb forest 10.3-24.5.2008 leg. S Tarasov / HOLOTYPE Cassolus solodovnikovi S. Tarasov det. 2010", 18°5.86'N, 102°40.547'E (ZMUC). **Paratypes (5 males)**: **1 male paratype**, Vientiane province, National Park Phu Khao Khouay, Ban Vangheua, 18°19.552'N, 102°48.692'E, 880 m, pine forest, on 30/ix–28/xi/2007 (S. Tarasov) (CST); **1 male paratype**, Vientiane, Houayang forest, 18°5.86'N, 102°40.547'E, 200 m, disturb forest, on 30/viii–11/ix/2007 (S. Tarasov) (CST); **Thailand**: **1 male paratype**, Na Haeo (secondary forest), 17°30.231'N, 100°56.363'E, on 5–12/v/2001 (Constant, Grootaert) (ISNB); **Vietnam**: **1 male paratype**, Tonkin [northern Vietnam], region of Hoa-Binh, 20°49.7'N, 105°20'E, on 1928, (A. De Cooman) (MNHN); **1 male paratype**, Tonkin [northern Vietnam], region of Hoa-Binh, 20°49.7'N, 105°20'E, on 1927 (A. De Cooman) (MNHN).

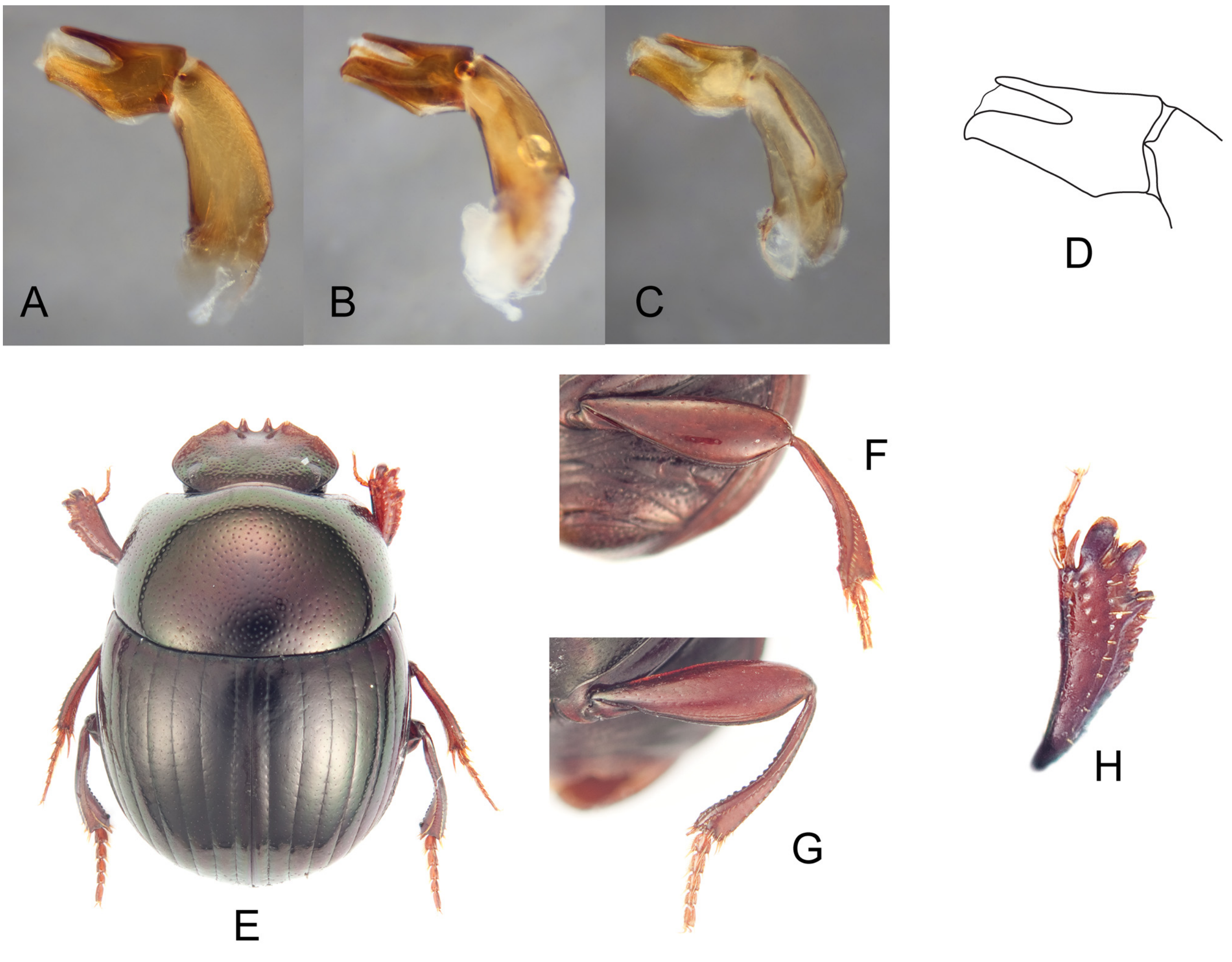

FIGURE 23. Morphology of *Parachorius solodovnikovi*. (A) aedeagus, lateral view (holotype). (B) aedeagus, lateral view (paratype, Thailand). (C) aedeagus, lateral view (paratype, Vietnam). (D) aedeagus, lateral view (E) habitus (male, holotype). (F) left metafemur (male, paratype, Vietnam) (G) left metafemur (male, holotype). (H) left protibia (male, holotype, original image flipped).

Parachorius thomsoni Harold, 1873
(Figs. 24, 27F)

Parachorius thomsoni Harold, 1873: 103
Parachorius thomsoni; Gillet 1911: 54
Parachorius thomsoni; Boucomont 1929: 761
Parachorius thomsoni; Arrow 1931: 358
Parachorius thomsoni; Paulian 1945: 59
Parachorius thomsoni; Balthasar 1963: 276
Parachorius thomsoni; Kryzhanovsky & Medvedev 1966: 394
Parachorius thomsoni; Masumoto 1987: 127
Parachorius lannathai Hanboonsong & Masumoto, 2001: 138 (**new synonymy**)

Type locality. India or. [eastern India] (*Parachorius thomsoni*); Maesa Valley Chiang Mai, Thailand (*Parachorius lannathai*)

Taxonomic notes. *Parachorius lannathai* described from Thailand is synonymized with *P. thomsoni* based on external morphology and the shape of aedeagus.

Distribution. Eastern India, Myanmar, Thailand, and Laos.

Diagnosis. The species is most similar to *P. fungorum* and *P. hookeri*. It differs from them by the following combination of characters (1) metafemoral posterior margin with two distinct denticles of which the apical denticle is spur-like, produced; (2) parameres simple, apex slightly rounded forming triangle.

Description. *Body.* Body black or dark brown, length 6.5–9.0 mm. Elytra uniformly colored.

Head. Clypeus with two indistinct teeth, outer margin of each tooth not notched basally.

Pronotum. Pronotum rounded laterally. Frontal angles rounded. Disc covered with punctures separated by 1–2 puncture diameter(s). Pronotum in anterior-posterior direction notably shorter than elytra.

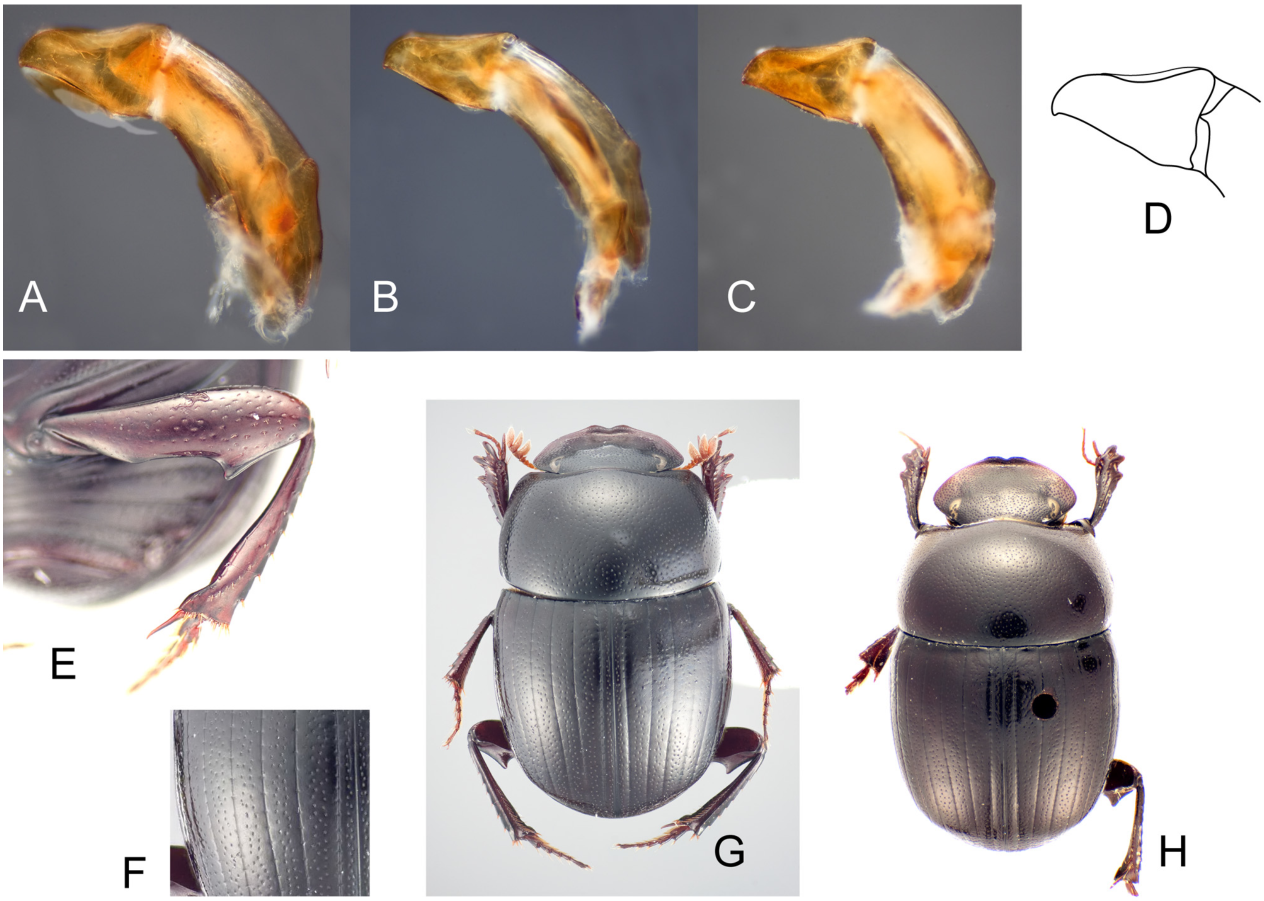

FIGURE 24. Morphology of *Parachorius thomsoni*. (A) aedeagus, lateral view (*P. thomsoni* holotype, male) (B) aedeagus, lateral view (*P. lannathai*, holotype, male). (C–D) aedeagus, lateral view. (E) left metafemur (*P. lannathai*, holotype, male). (F) disc of left elytron (G) habitus (*P. lannathai*, holotype, male). (H) habitus (*P. thomsoni*, holotype, male).

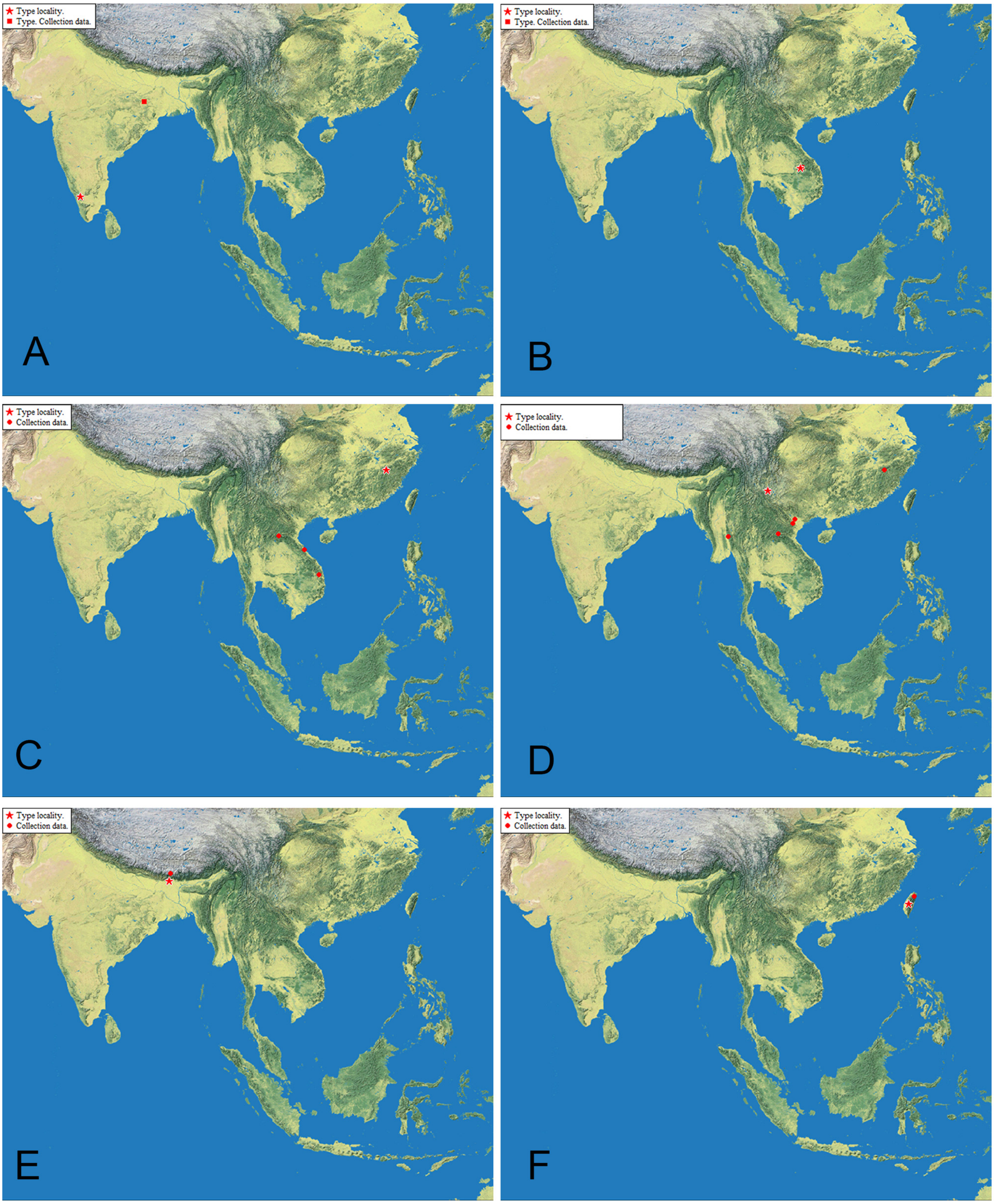

FIGURE 25. Distribution maps of *Parachorius* species. (A) *Parachorius asymmetricus.* (B) *Parachorius bolavensis.* (C) *Parachorius fukiensis.* (D) *Parachorius fungorum.* (E) *Parachorius globosus.* (F) *Parachorius gotoi. Type locality*—type locality of species (holotype or lectotype); *Type. Collection data*—localities of type specimens associated with species (paratypes or paralectotypes); *Collection data*—localities of other specimens examined in this study.

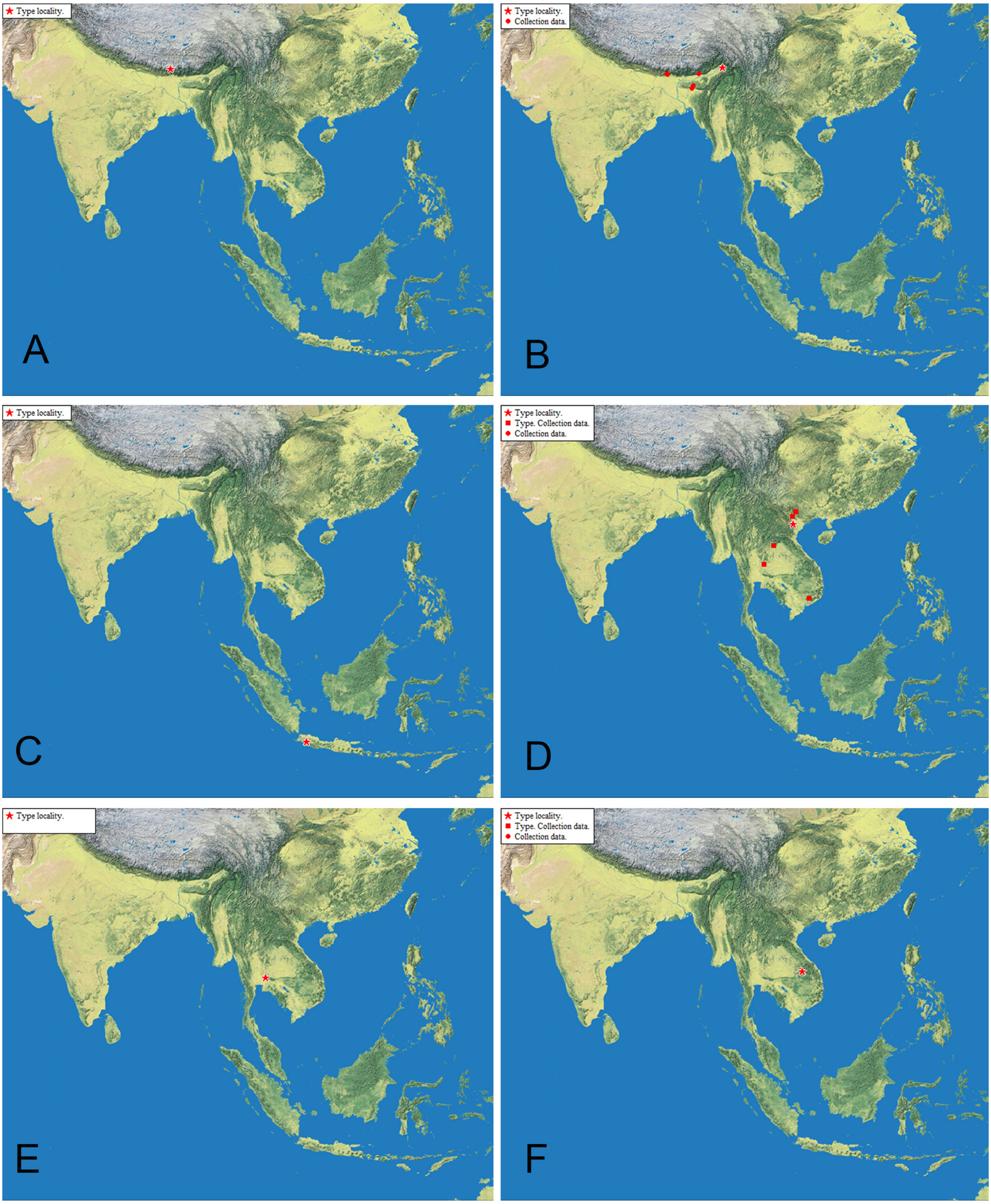

FIGURE 26. Distribution maps of *Parachorius* species. (A) *Parachorius hookeri.* (B) *Parachorius humeralis.* (C) *Parachorius javanus.* (D) *Parachorius longipenis.* (E) *Parachorius maruyamai.* (F) *Parachorius newthayerae. Type locality*—type locality of species (holotype or lectotype); *Type. Collection data*—localities of type specimens associated with species (paratypes or paralectotypes); *Collection data*—localities of other specimens examined in this study.

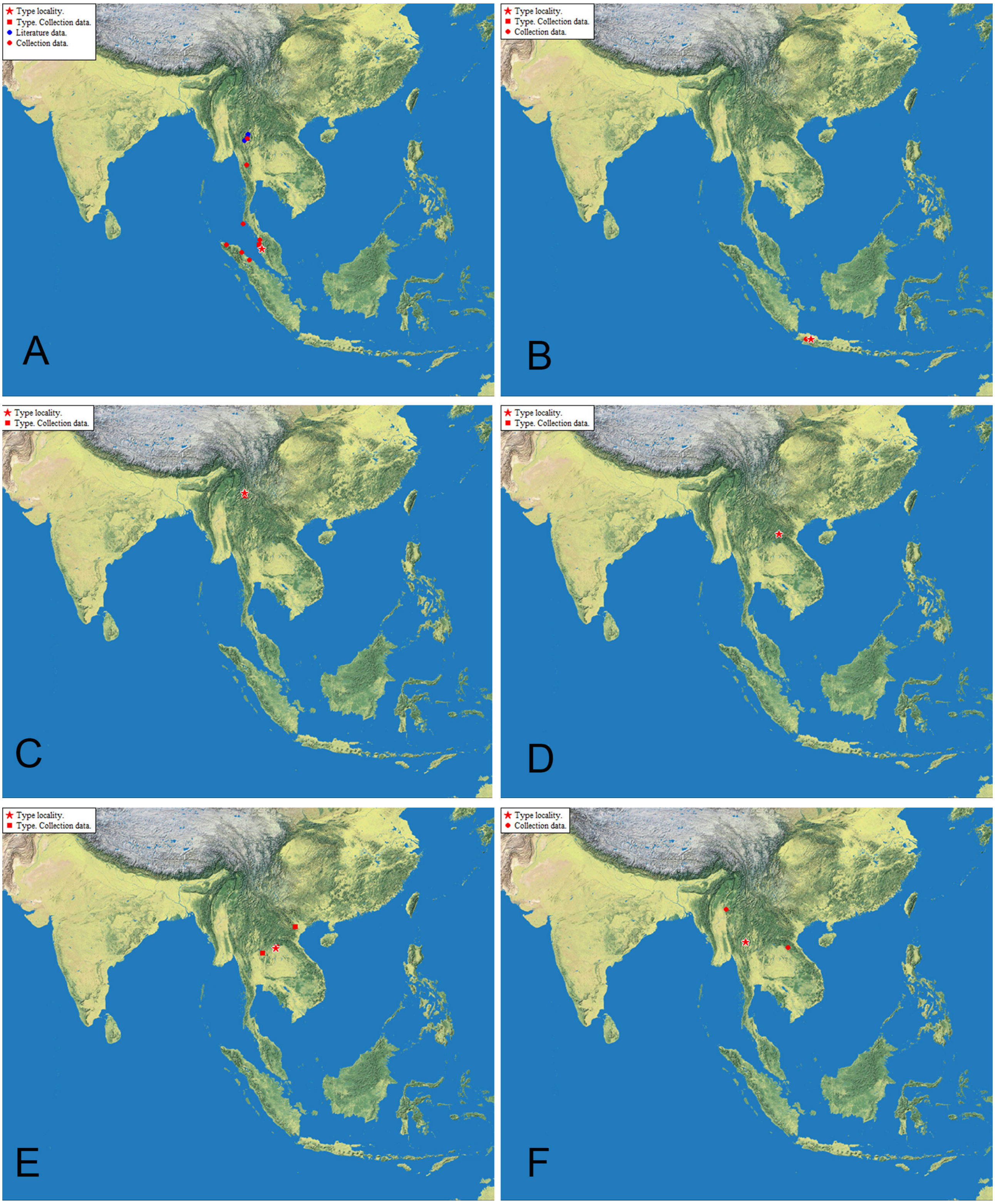

FIGURE 27. Distribution maps of *Parachorius* species. (A) *Parachorius peninsularis.* (B) *Parachorius pseudojavanus.* (C) *Parachorius schuelkei.* (D) *Parachorius semsanganus.* (E) *Parachorius solodovnikovi.* (F) *Parachorius thomsoni. Type locality*—type locality of species (holotype or lectotype); *Type. Collection data*—localities of type specimens associated with species (paratypes or paralectotypes); *Collection data*—localities of other specimens examined in this study. *Literature data*—localities retrieved from literature.

Elytra. Elytra covered with sparse punctures.

Wings. Wings normally developed.

Legs. Profemur with anterior margin medially produced in angle or with almost straight or sinuate anterior margin. Protibia with apical spur approximately reaching middle of protarsomere 3. First tooth almost not modified in males, approximately as wide as second tooth; first and second teeth distinctly separated from each other; first distinctly separated from denticles located between first and second teeth. Metafemoral posterior margin not serrate, with two distinct denticles of which apical denticle is spur-like, produced. Metatibia slightly sinuate, inner margin not denticulate, excavated apically.

Metasternum. Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length.

Aedeagus. Parameres symmetrical, simple; apex slightly rounded, forming triangle.

Material examined. Holotype of *Parachorius thomsoni*: **India**: **1 male**, "India or. Parachorius Thomsoni Typ. Harold. / Ex Musæo E.Harold / MUSEUM PARIS 1952 Coll. R. OBERTHÜR / TYPE / HOLOTYPE Parachorius thomsoni Horld, 1873 det. S. Tarasov 2010" (MNHN). **Holotype of *Parachorius lannathai*: Thailand**: **1 male**, "Maesa Valley Chiang Mai THAILAND 3-6/V/1994 K. MASUMOTO leg. / Coll Masumoto 200 / Holotype Parachorius lannathai Han. & Mas. / Parachorius thomsoni Harold, 1873 det. S. Tarasov, 2015", 18°53.988'N, 98°52.524'E (NSMT). **1 male**, collection J. Thomson 830 (ISNB). **India**: **1 male**, India orientale (BMNH). **Laos**: **1 male**, Khammouane Province, Ban Khun Kham (Nahin), 18°13.027'N, 104°30.88'E, 300 m, disturbed rainforest, on 3–5/vi/2008 (A. Solodovnikov, J. Pedersen) (ZMUC). **Myanmar**: **1 male**, Shan State, Shweudaung Wildlife Sanctuary (Moe Meik Township), Kyauk-maw village (91f), flight intercept trap, 23°5.129'N, 96°13.527'E, 360 m, on 1–15/viii/2002 (Myint Hlaing, Aung Moe) (NMW).

Character report

The morphological data matrix used in present study was constructed by adding 27 characters and 20 species to the previously developed morphological matrix (Tarasov & Génier 2015), which was subsequently extended to incorporate fossil species (Tarasov *et al.* 2016). Since character statements of the original matrix were not modified, they are not provided here as they can be found in Tarasov & Génier (2015). Here, I list only the newly added characters preserving enumeration consistent with the original study.

206. *Clypeus with two teeth, outer margin of each tooth distinctly notched basally:* (0) absent; (1) present.
207. *Clypeus with two teeth, outer margin of each tooth slightly notched basally:* (0) absent; (1) present.
208. *Clypeus with two indistinct teeth, outer margin of each tooth not notched basally:* (0) absent; (1) present.
209. *Clypeus with two distinctly produced teeth, their outer margin not notched basally:* (0) absent; (1) present.
210. *Elytra with yellow humeral spot:* (0) absent; (1) present.
211. *Elytra covered with dense contiguous and rugose punctures:* (0) absent; (1) present.
212. *Apical spur of protibia in males reaches second tarsomere:* (0) absent; (1) present.
213. *Apical spur of protibia in males approximately reaches middle of third tarsomere:* (0) absent; (1) present.
214. *Protibia with first tooth almost not modified in males, approximately as wide as second tooth:* (0) absent; (1) present.
215. *Protibia with first tooth notably modified in males:* (0) absent; (1) present.
216. *Protibia with first tooth wide, nearly merging with second tooth:* (0) absent; (1) present.
217. *Protibia with first and second teeth distinctly separated from each other:* (0) absent; (1) present.
218. *Protibia with first tooth looking bifurcated as it merging with denticles located between first and second teeth:* (0) absent; (1) present.
219. *Metatibia strongly curved and notched medially:* (0) absent; (1) present.
220. *nner margin of metatibia denticulate:* (0) absent; (1) present.
221. *Metatibial inner margin produced in small angle preapically:* (0) absent; (1) present.
222. *Metatibial inner margin excavate preapically:* (0) absent; (1) present.
223. *Pronotum angulate laterally or at least its frontal angels sharp:* (0) absent; (1) present.
224. *Parameres with dorsally horn-like upper lobes:* (0) absent; (1) present.
225. *Transverse basal ridge of metasternum present:* (0) absent; (1) present.
226. *Transverse basal ridge of metasternum reduced and extremely short:* (0) absent; (1) present.
227. *Transverse basal ridge of metasternum long, at least 1/5 of mesocoxa length:* (0) absent; (1) present.

228. *Aedeagal parameres simple, apex widely rounded and inferiorly angulate (P. fungorum groundplan):* (0) absent; (1) present.
229. *Inferior portion of axial sclerite with long fork-like process (LFP), SA reduced (small):* (0) absent; (1) present.
230. *Axial and SA sclerites simple, FLP absent, SRP small, LC absent (P. javanus ground plan of aedeagus):* (0) absent; (1) present.
231. *Axial sclerites enlarged inferiorly with moderately short filiform process extending superiorly that reaches only FLP; inferior portion of axial sclerite with LFP; SA small (P. fungorum ground plan):* (0) absent; (1) present.
232. *Axial sclerites enlarged inferiorly with long filiform process extending superiorly that reaches LC; inferior portion of axial sclerite with LFP; SA small (P. longipenis ground plan):* (0) absent; (1) present.

Conclusions

The present study attempts to apply an integrative approach to the systematics of dung beetles that is based on the elucidation of phylogenetic placement of the taxon of interest and its subsequent revision using cybertaxonomic tools. Two Oriental genera, *Parachorius* and *Cassolus*, became the focus of this study as they were left without tribal placement; they had rich but unsuccessful historical record of finding their tribal placement as well as plenty of unresolved taxonomical problems. This study used morphological and molecular data to conduct their phylogenetic assessment that recovered monophyly and phylogenetic distinctiveness of the clade embracing these genera. In turn, this led to the recognition of a new generic concept - *Parachorius* **sensu novo** (with *Cassolus* synonymized) that was revised and placed in the separate new tribe Parachoriini**.** However, further phylogenetic analysis incorporating larger gene sample would be useful to obtain higher clade support and, thereby, refine phylogenetic position of Parachoriini within Scarabaeinae.

The integrative approach, used here, despite considerable time investment, demonstrated its power as an effective tool that is capable to resolve phylogeny and taxonomy in one study. Although, identification of female specimens remains problematic due to the lack of diagnostic characters, in general this does not pose a problem since species can be reliably identified using males. I believe such synthesis of different data sources and techniques is especially important in building the new dung beetle classification that, despite long-standing attempts, is still unresolved.

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