Dung beetles as sensitive indicators of land use change and quantification of their ecosystem services in northern and central Vietnam

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SUMMARY

The conversion of tropical forests by anthropogenic land-uses has generated a large variety of fragmented habitats, leading to changes in animal diversity. Dung beetles (DB) respond sensitively to both, changes in the composition of vertebrates whose excrements provide food and nesting material, as well as changes in the physical structure of their habitats. Changes in DB communities have been often described via the taxonomic identity, but difficulties in the delineation of DB species that are taxonomically difficult to determine and highly diverse, combined with fundamental changes in the taxonomic composition of DB communities between different biogeographical regions, have posed great challenges for the taxonomic identification and therefore hindered the generalization of results. Morphological traits of beetles instead directly reflect their environmental adaptations through natural selection across species borders, and may provide a more robust means to detect patterns of community change imposed by different land uses.

The main objective of the dissertation was to examine the effects of the conversion of primary forests (1st Forests) to secondary forests (2nd Forests) and to meadows on DB communities of tropical karst ecosystems, and the consequences for key ecosystem functions, using both taxonomic identity and morphological trait-based approaches. As the tropical karst ecosystems typically harbour unique flora and fauna, it was hypothesized that these ecosystems would also host unique DB communities with high potential of endemism, and accordingly may reveal particular patterns in responses to forest conversion. Further we hypothesized that changing environmental conditions would lead to morphological adaptations of DB, eventually measurable as distinct clusters of morphological traits. Finally, changes in DB morphological traits may affect dung removal rate, being an important ecosystem function.

This dissertation started with quantification and comparison of the structure and community attributes (i.e., species richness, abundance and biomass) of DB between land-use types in two spatially separated nature reserves (NR) in north-eastern and north-central Vietnam. Surprisingly, ***species composition and community structure differed remarkably between two NR. Clear patterns of responses of DB to forest conversion were found between forests and meadows, with meadows showing a higher abundance and species richness being compared to forests*** **(Chapter 1).**

In **Chapter 2**, we successfully used the morphological trait-based approach to identify and characterize three distinct morphological trait clusters reflecting DB adaptations to changing environmental conditions resulting from the forest conversion. Our results highlight ***the potential to further the use of morphological traits in examining anthropogenic impacts on community structure***. In **Chapter 2**, we found that body length and body mass rather than abundance determined dung removal rate, but the large-bodied DB were particularly vulnerable to forest conversion. Accordingly, ***the forest conversion by human land uses resulted in a loss of DB functioning and resulting their key ecosystem service, dung removal rate***.

Since large-bodied DB play a vital role in ecosystem functions and were highly sensitive to forest conversion, it is critical to focus on the large DB species in conservation management. However, the poor understanding of the taxonomy of SE-Asian DB is hindering conservation decisions, because reliable information on species composition, distribution and diversity is lacking. Therefore, in **Chapter 3**, we focussed on the taxonomy and distribution of the dominant and large-bodied DB of the genus *Copris* by providing a species list for Vietnam with detailed illustrations and identification keys to all Vietnamese members, and with the worldwide distributions of all these species. Two new *Copris* species, one country records and rare species recorded from the karst ecosystems were also described and included in the key. In addition, the little-known subgenus *Copris* (*Paracopris*) was reviewed along with description of a new species from Java (Indonesia).

The genus *Synapsis* contains remarkably large-bodied DB reaching a length of up to 52 mm (i.e., in *S. tmolus Fischer,* 1821). Since *Synapsis* spp. mainly occur in SE-Asian tropical forests, they may be useful bio-indicators for undisturbed forests. However, the species status of particular taxa has undergone repeated changes due to poorly defined species boundaries. In **Chapter 4**, we therefore presented a thoroughly illustrated key and diagnoses of all worldwide known *Synapsis* species based on morphological examinations of a great number of type specimens housed at European natural history museums. In addition, a new species and a rare species of the genus *Synapsis* recorded from the karst ecosystems were formally described.

ZUSAMMENFASSUNG

Die Umwandlung von Tropenwäldern durch anthropogene Landnutzung hat zu einer großen Vielfalt von fragmentierten Lebensgemeinschaften geführt, die zu einer Veränderung der Tiervielfalt führen. Dungkäfer (DB) reagieren empfindlich auf Veränderungen in der Zusammensetzung von Wirbeltieren, deren Exkremente Nahrung und Nistmaterial darstellen, sowie auf Änderungen in der physischen Struktur ihrer Lebensräume. Änderungen in DungkäfergDungkäfergemeinschaften wurden oft über die taxonomische Identität beschrieben, aber dies schränkte die Verallgemeinerung der Ergebnisse ein, da es Schwierigkeiten bei der Abgrenzung von Dungkäferarten gibt, da sie taxonomisch schwer zu bestimmen sind, und sich die taxonomische Zusammensetzung von Dungkäfer gemeinschaften zwischen verschiedenen biogeographischen Regionen grundlegend unterscheiden kann. Morphologische Merkmale von Käfern spiegeln stattdessen ihre Umweltanpassungen durch natürliche Selektion über Artengrenzen hinweg direkt wider und können ein robusteres Mittel zum Erkennen von Gemeinschaftsveränderungen durch verschiedene Landnutzungen darstellen.

Das Hauptziel der Dissertation bestand darin die Auswirkungen der Umwandlung von Primärwäldern (1^{ry} Forest) in Sekundärwälder (2^{nd} Forest) und zu Weiden auf Dungkäfergemeinschaften Dungkäfergemeinschaftenin tropischen Karstökosystemen und die Auswirkungen auf Schlüssel-Ökosystemfunktionen unter Verwendung von taxonomischer morphologisch-merkmalsbezogener Ansätze zu untersuchen. Da die tropischen Karst-Ökosysteme typischerweise eine einzigartige Flora und Fauna beherbergen, wurde die Hypothese aufgestellt, dass diese Ökosysteme auch einzigartige Dungkäfergemeinschaften mit einem hohen Endemismuspotenzial beherbergen und dementsprechend bestimmte Muster in Reaktionen auf die Waldumwandlung aufdecken könnten. Des Weiteren stellten wir die Hypothese auf, dass veränderte Umweltbedingungen morphologischen Anpassungen der Dungkäfer bedingen, die über morphologischer Merkmale messbar sind. Schließlich können Änderungen in den morphologischen Merkmalen der Dungkäferdie Dungentfernungsrate beeinflussen, die eine wichtige Ökosystemfunktion darstellt.

Diese Dissertation begann mit der Quantifizierung und dem Vergleich der Struktur- und Gemeinschaftsattribute (d. H. Artenreichtum, Abundanz und Biomasse) von Dungkäfernzwischen Landnutzungsarten in zwei räumlich getrennten Naturschutzgebieten im Nordosten und Norden von Vietnam. Überraschenderweise unterschieden sich die Artenzusammensetzung und die Gemeinschaftsstruktur zwischen zwei Naturschutzgebieten

erheblich. Zwischen Wäldern und Wiesen wurden deutliche Muster der Reaktionen der Waldbrut auf Waldbestände gefunden, wobei Wiesen im Vergleich zu Wäldern eine höhere Abundanz und Artenvielfalt aufweisen (Kapitel 1).

In Kapitel 2 haben wir erfolgreich den morphologischen Merkmalsansatz verwendet, um drei verschiedene morphologische Merkmalscluster zu identifizieren und zu charakterisieren, die Anpassungen der Dungkäfer an sich ändernde Umgebungsbedingungen aufgrund der Waldumwandlung widerspiegeln. Unsere Ergebnisse unterstreichen das große Potenzialder Untersuchung morphologischer Merkmale bei der Untersuchung anthropogener Auswirkungen auf die Gemeinschaftsstruktur von Käfern. In Kapitel 2 stellten wir fest, dass nicht Abundanz, sondern Körperlänge und Körpermasse die Dungentfernungsrate bestimmten. Jedoch war die Dungkäfer mit großem Körper besonders anfällig für die Waldkonversion. Dementsprechend führte der Umbau der Wälder durch menschliche Landnutzung zu einem Verlust der Funktionsfähigkeit der Dungkäfergemeinschaften und zu ihrem wichtigsten Ökosystem-Service, der Entfernung von Dung. Da großkörperige Dungkäfergemeinschaften eine wichtige Rolle in Ökosystemfunktionen spielen und sehr empfindlich auf die Waldumwandlung reagieren, ist es wichtig, sich auf die großen Dungkäferarten im Naturschutzmanagement zu konzentrieren. Das schlechte Verständnis der Taxonomie von südost-asiatischen Dungkäfer behindert jedoch Naturschutzentscheidungen, da verlässliche Informationen über Artenzusammensetzung, Verbreitung und Vielfalt der Dungkäfer fehlen. Daher konzentrierten wir uns in Kapitel 3 auf die Taxonomie und Verteilung der großräumig dominanten Dungkäfer der Gattung *Copris*, indem wir eine Artenliste für Vietnam mit detaillierten Abbildungen und Identifikationsschlüsseln für alle vietnamesischen Arten und Informationen zur weltweiten Verbreitung aller Arten bereitstellten. Zwei neue *Copris*-Arten, ein Länderdatensatz und seltene, aus den Karstökosystemen erfasste Arten wurden ebenfalls beschrieben und in den Schlüssel aufgenommen. Darüber hinaus wurde die wenig bekannte Untergattung *Copris* (*Paracopris*) zusammen mit der Beschreibung einer neuen Art aus Java (Indonesien) überprüft.

Die Gattung *Synapsis* beinhaltet bemerkenswert große Dungkäfer die eine Körperlänge von bis zu 52 mm erreichen (z.B. *S. tmolus* Fischer, 1821). Weil *Synapsis* Arten hauptsächlich in südostasiatischen Tropenwäldern vorkommen könnten sie nützliche Bioindikatoren für ungestörte Wälder sein. Der Artenstatus bestimmter Taxa hat sich jedoch aufgrund unzureichend definierter Artengrenzen wiederholt verändert. In Kapitel 4 haben wir daher einen gründlich überarbeiteten und neu illustrierten Schlüssel mit Diagnosen aller weltweit bekannten *Synapsis*-Arten vorgestellt, die auf morphologischen Untersuchungen einer großen Anzahl von Typus-Exemplaren in europäischen Naturkundemuseen basieren. Darüber hinaus wurden eine neue Art und eine seltene Art der Gattung *Synapsis* aus den Karstökosystemen neu beschrieben.

INTRODUCTION

1. Dung beetles: Taxonomy and ecosystem functions

The term “dung beetles” used in this thesis denotes “true” dung beetle (DB) species belonging to three families: Scarabaeidae, Aphodiidae and Geotrupidae (Coleoptera: Scarabaeoidea) (Hanski & Cambefort, 2014; Scholtz et al., 2009). They typically utilize animal droppings as food and nesting material, and are among the most predominant members of dung insect communities in tropical and warm temperate regions (Hanski & Krikken, 1991; Davis, 2002; Davis et al., 2008). Dung beetles currently comprise around 7000 formally described species. They are commonly separated into three main functional groups, namely tunnelers (paracoprids), dwellers (endocoprids) and rollers (telecoprids), reflecting their distinct nesting and breeding behaviour. The tunnelers habitually dig tunnels directly below dung pats to store dung resources for their feeding and breeding activities. Taxonomically the tunnelers comprise the subfamily Geotrupinae and six tribes of the subfamily Scarabaeinae, including *Coprini*, *Dichotomiini* (=*Ateuchini*), *Oniticellini*, *Onitini*, *Onthophagini* and *Phanaeini*. The dwellers comprise the subfamily Aphodiinae that feed and reproduce either within dung pats or at the interface between the dung pat and soil surface. The rollers produce dung balls from animal dung, and then roll these balls to translocate these resources to suitable new places. Most rollers belong to the subfamily Scarabaeinae comprising various tribes: *Scarabaeini*, *Canthonini* (=*Deltochilini*), *Gymnopleurini*, *Eucraniini*, *Eurysternini* and *Sisyphini* (Hanski & Cambefort, 1991; Krell et al., 2003; Scholtz et al., 2009; Inward et al., 2011; Nervo et al., 2014). The different functional groups show patterns of predominance according to geographic region. For example, the dwellers, especially in the genus *Aphodius*, are characteristic DB species in north temperate regions, while tunnellers are dominant in tropical regions, with *Onthophagus* spp. being particularly dominant in Southeast Asia (Hanski & Krikken, 1991; Davis et al., 2001; Hayes et al., 2009; Shahabuddin et al., 2005).

In contrast to the relatively good knowledge on DB taxonomy in north and south temperate regions, there is still a lack of understanding of the taxonomy of DB in the tropics, particularly in SE-Asia. Only few identification keys and species lists exist, mostly outdated, e.g., Paulian (1945), Balthasar (1963), Ochi (1992) and Kabakov and Napolov (1999), and numerous unidentified species hinder the application of ecological studies. For example, almost 30% and 40% of the total recorded DB species in Sabah (Malaysia) and Babe

(Vietnam), respectively, were unidentified in Davis et al. (2001) and Hayes et al. (2009). This is posing major obstacles for ecological studies and conservation decisions that are mainly based on the taxonomic data of DB. Therefore there is an urgent need to establish identification keys and provide clear taxonomic diagnoses of DB species in this region.

Dung beetles are worldwide distributed and occur in various habitats such as farmlands, deserts, grasslands and forests. They contribute to key ecosystem functions such as dung removal, nutrient cycling, biological control of vertebrate parasites and secondary seed dispersal (Halfter & Matthews, 1966; Hanski & Cambefort, 2014; Nichols et al., 2008). Due to these dung-burying beetles, dung pats quickly disappear from soil surface and are incorporated into the soil. This helps to reduce harmful insects and to increase soil nutrients (Bierregaard, 2001; Brown et al., 2010; Thomas, 2001; Yamada et al., 2007). Because of the highly intense competition with other dung-feeding insects, DB reduce harmful insect outbreaks, e.g. a typical case in Australia (Bornemissza, 1970; Bornemissza, 1976), and accidentally and rapidly relocate and burry defecated seeds, leading to a reduction in seed predation and seed mortality resulting from seed-feeding animals and pathogens (Shepherd & Chapman, 1998; Andresen, 1999; Andresen & Levey, 2004). Being buried in the soil, the seeds find microclimates more suitable for germination and emergence (Andresen & Levey, 2004; Nichols et al., 2008).

Among the ecosystem functions and services of DB, dung removal is one of the most important functions (Nichols et al., 2008), and accordingly the links between this function and community attributes and structure of DB communities under land-use change have received worldwide attention, and can be generally summarized as follow:

- The effects of land-use changes on dung removal rate vary with the intensity of disturbances. For example, Gray et al. (2014) found no significant differences in dung removal rate between riparian reserves, oil palm plantation and logged forests, while Frank et al. (2017) reported a serious reduction in dung removal rate in grasslands compared to forests.
- The different functional groups of DB show different efficiencies in removing dung across spatial and temporal scales. The tunnelers were twice as efficient as dwellers in dung removal, due to their particular nesting strategies (Nervo et al., 2017).
- The body mass and/or body length of DB have been found to be positively associated with dung removal rate (Nervo et al., 2014; Tixier et al., 2015; Frank et al., 2017).

- Also the abundance of dung beetles was strongly associated with dung removal rate, with more abundant communities being more efficient in dung removal (Tixier et al., 2015; Frank et al., 2017).

Most studies on the efficiency of dung removal by DB focussed on individual traits, such as body length/body mass. Therefore there is a critical need to examine the various traits of DB as a whole in order to identify the key traits responsible for this key ecosystem function.

2. The taxonomic-based approach in examining human impacts on biodiversity

Dung beetles are highly sensitive to changes in the physical structure of habitats, such as vegetation cover (Costa et al., 2017; Salomão et al., 2018), leaf litter layer (Campos & Hernández, 2013; Nichols et al., 2013; Tixier et al., 2015) and soil characteristics (Osberg et al., 1994; Farias et al., 2015; Beiroz et al., 2017). Therefore, dung beetles are considered as good indicators of a wider range of biodiversity impacts resulting from habitat changes (Nichols et al., 2007; Audino et al., 2014; Beiroz et al., 2017). On other hand, since DB depend on vertebrate droppings as essential food and nesting resources, they may better reflect changes in the composition and structure of vertebrate communities (Estrada et al., 1999; Vulinec, 2000; Harvey et al., 2006; Andresen & Laurance, 2007; Enari et al., 2013).

The conversion of tropical forests to anthropogenic land-uses has generated a great variety of natural fragments, resulting in the loss of biodiversity, ecosystem functions and services of different groups of organisms (Heydon & Bulloh, 1997; Wells et al., 2007; Gardner et al., 2008; Bernard et al., 2009; Wood, 2017). Dung beetles are increasingly being used in the assessment of the influences of forest transformations on biodiversity (Vulinec, 2002; Quintero & Roslin, 2005; Vulinec et al., 2006; Gardner et al., 2008; Audino et al., 2014; Beiroz et al., 2017; Davis et al., 2001; Shahabuddin et al., 2005; Hayes et al., 2009; Boonrotpong et al., 2004, 2012).

Changes in DB communities have been often described at the taxonomic level, focusing on species composition and species richness (Fountain-Jones et al., 2015). However, there have been obstacles to the use of this approach. First, DB are highly diverse, posing great challenges in species identification. Secondly, the species boundaries on morphological level of DB are poorly defined, because many morphological traits have showed significant intraspecific variation across different land-uses (Raine et al., 2018). This has sometimes led to inconsistent species identification of DB. For example, the species status of particular taxa of SE-Asian members of *Synapsis* spp. and *Copris* spp. has undergone repeated changes. Finally, the fundamental differences in the taxonomic composition of DB between different biogeographic regions due to different evolutional trajectories may hinder the generalization of results. In fact, there is still little consensus on the responses of the taxonomic attributes of DB to forest degradation. For example, Boonrotpong et al. (2004), Shahabuddin et al. (2005) and Gardner et al. (2008) reported strongly species-depleted DB communities in secondary forests (2^{nd} Forests) compared to primary forests (1^{st} Forests). In contrast, Vulinec (2002), Quintero and Roslin (2005), Vulinec et al. (2006) and Nichols et al. (2007) were unable to find any differences in species richness between these two forest types. Therefore, using different approaches in evaluating human impacts on DB biodiversity is critically needed.

3. The trait-based approach in examining the human impacts on biodiversity

Functional traits reflect adaptations to environmental conditions and strongly influence organismal performance and fitness, such as foraging and nesting success, fecundity and survival (McGill et al., 2006; Violle et al., 2007). These fitness traits in turn can influence demographic characteristics of populations (Arnold, 1983; Violle et al., 2007). Thus, functional traits hold information about community structure and function, and the niche space occupied by species traits, and accordingly may exactly predict community responses to habitat transformation (Gagic et al., 2015). However, there are difficulties due to the fact that data on functional traits (e.g., activity periods, foraging and nesting behaviour) of numerous organisms is still lacking, because functional traits, in general need to directly observed from living individuals, and therefore may be difficult to obtain (Raine et al., 2018). Instead morphological traits (e.g., body length, body mass, wing loadings) are not only easily measured on individuals collected from fields or already available from reference collections, but also can reflect the interaction of organisms with environments as well as organismal functions (Raine et al., 2018). Hence, the morphological trait approach may be a more robust means in examining the impacts of habitat change on organismal communities.

Dung beetles exhibit a large variety of behavioural characteristics reflecting distinct functional traits. They can nest and reproduce within dung pats (dwellers or endocoprids) or in vertical chambers below or in close proximity to original dung pats (tunnelers or paracoprids), or they can roll dung balls horizontally away from animal droppings to suitable new places (rollers or telecoprids) (Hanski & Cambefort, 1991; Nichols et al., 2008; Scholtz et al., 2009). Dung beetles are strictly active at night (nocturnal tunnelers/rollers) or in the daytime (diurnal tunnelers/rollers) (Doube, 1990; Feer & Pincebourde, 2005). These functional traits have direct and varying influences on ecosystem functions and services performed by DB, such as bioturbation, nutrient cycling and secondary seed dispersal (Slade et al., 2007; Nichols et al., 2008; Griffiths et al., 2015). For example, the tunnelers, through their tunnelling activities, move the amount of soil in tunnels to the surface, leading to increases in soil aeration and water porosity, while the rollers play a vital role in secondary seed dispersal (Nichols et al., 2008). So far, DB behavioural traits have been mostly based on field observations (Raine et al., 2018), and are still incomplete worldwide (Buse et al., 2018). To overcome this obstacle, some studies used phylogenetic relationships to deduce the behavioural traits of a species or genus where trait information is unavailable (Barton et al., 2011; Griffiths et al., 2015). However, Raine et al. (2018) showed that using phylogeny may lead to an inaccurate prediction about DB behavioural traits, particularly in rolling traits. Further molecular information is not comprehensive for DB, particularly in the tropics (Monaghan et al., 2007). This is posing major challenges in using the functional trait-approach to assess the human impacts on biodiversity.

Dung beetles possess diverse morphological traits, strictly associated with their ecosystem functions and adaptations to environmental conditions. For example, the tunnelling species bear relatively short and thick legs for digging, and therefore their distribution is more dependent on soil texture (Hanski & Cambefort, 1991). The rollers bear elongated hind legs for rolling dung balls, and hence restricted to litter free areas because obstacles on the soil surface hinder the rolling process (Scholtz et al., 2009; Nichols et al., 2013). The morphological trait-based approaches have gained increasing attention in the assessment of the effects of LUC on DB communities (Gardner et al., 2008; Larsen et al., 2008; Nichols et al., 2013; Tixier et al. 2015; Frank et al., 2017). These studies were based on data from all functional groups that are all in an analytical framework. However, as different functional groups certainly show distinct responses to habitat change (Hayes et al., 2009), it is critical to detect the responses of individual functional groups to get insights into the questions of whether and how morphological traits of specific functional groups of DB differ across gradients of LUC.

Among morphological traits, body size (e.g., body length, body mass) has been considered as a universally important driver of the relationships between biodiversity and ecosystem functions within food web processes (Nichols et al., 2013). Additionally, this trait, together with taxonomic and functional identifies, may help to determine species interaction that shapes community structure (Elton, 1927; McGill et al., 2006, Hendriks & Mulder, 2008). Hence, DB body size has been widely used in the assessment of human impacts on communities, and the consequence for ecosystem functions, and this trait showed a high sensitively to habitat change as well as a strong correlation with dung removal capacity (Filgueiras et al., 2011; Nervo et al., 2014; Feer & Boissier, 2015; Salomão et al., 2018). Despite the undoubted effectiveness of body size, we expect that other morphological traits related to the dispersal capacity and foraging behaviour in addition to body size may be sensitive indicators of habitat change.

The community trait-based approaches have often used information available in three tables: an environmental variable table (R) containing variables measured from m sites, a species abundance table (L) recording the abundances (relative or absolute abundances, or occurrences) of the n species from m sites and a table with trait measurements for each species (Q) (Fig. 1) (Dolédec et al., 1996). The co-inertia (RLQ) analysis and the fourth-corner analysis were broadly used to summarize multivariate structures and test the significance of bivariate associations, respectively. However, Dray et al. (2014) showed problems in using each method. The RLQ method does not provide significance tests, while the fourth-corner method does not consider the covariation among environmental variables or among traits. Accordingly, Dray et al. (2014) combined these two methods in that the fourth-corner method was computed to directly test the links between RLQ axes and morphological traits and environmental variables. This combination has been used for multi-group communities or whole invertebrate communities (Ossola et al., 2015, Ding et al., 2017; Murphy et al., 2017; Kuzmanovica et al., 2017; Andrade et al., 2017; Braaker et al., 2017; Mocq & Hare, 2018; Castro et al., 2018), but yet to be applied for DB communities.

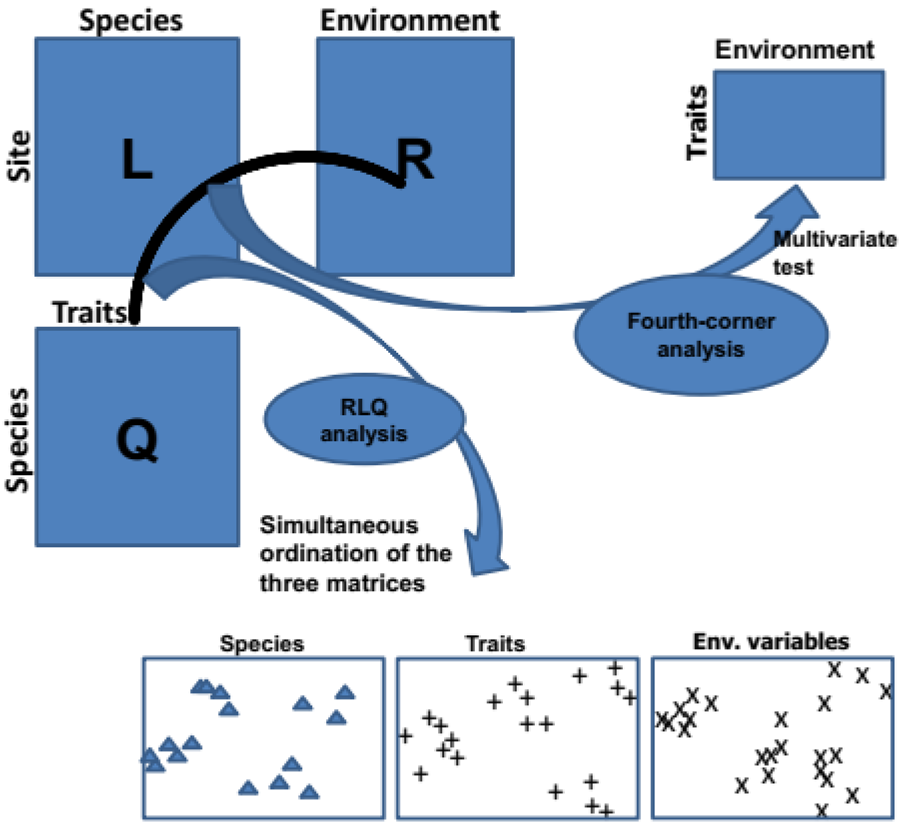

Fig. 1 Analysis of species traits-environment relationships (modified from Brind'amour et al., 2011)

4. Dung beetles in SE-Asian tropical karst ecosystems

Characteristics of SE-Asian tropical karst ecosystems

Tropical karsts are an exceptionally unique and important landscape element of SE-Asia. These karst ecosystems cover a large area of around 400,000 km^2, and contain a high number of endemic species (Day & Urich, 2000; Schilthuizen et al., 2005; Clements et al., 2006). The single limestone hill or isolated mountain of this area typically harbours unique flora and fauna, particularly in plants and invertebrates with limited dispersal capacities (Clements et al., 2006; Chung et al., 2014). For example, no single hill harbours more than 20% of the limestone flora in peninsula Malaysia (Wikramanayake et al., 2000). Such a distinct flora of isolated limestone hills or mountains may support a unique mammal fauna that strictly dependent on the karst flora. In fact, the SE-Asian karst ecosystems have recorded several endemic medium and large-bodied mammals, even though these mammals possess a high dispersal capacity, such as the serow (*Capricornis* spp.), leaf monkeys (*Trachypithecus* spp.) and macaques (*Macaca* spp.) (Clements et al., 2006; Dang, 2003; Le & Do, 1998).

Undoubtedly, the SE-Asian karst ecosystems are one of the most important “reservoirs” of biodiversity around the world with high endemism and species richness, and accordingly need to be strictly protected (Furey et al., 2010; Tuyet et al., 2001). Yet, these ecosystems have been frequently fragmented due to anthropogenic land-use changes, but also under recent enormous pressures resulting from the increasing human demand, such as coal mining, limestone quarrying and illegal logging and poaching (Clements et al., 2006). In terms of agricultural practices, because of the rugged terrain in karsts, clearing and burning have been often used to prepare flat arable land for planting, resulting in loss of not only natural forest cover, but also of topsoil (Vermeulen & Whitten, 1999). After several years of cultivation, the arable land has been abandoned and eventually overgrown with grasses, brushes, and secondary forests following decades of successful regeneration (Vermeulen & Whitten, 1999). Inevitably, this transformation process has significantly altered various organismal communities as well as their contributions to ecosystem functions.

Karst ecosystems and study areas in Vietnam

Tropical karst ecosystems are also a prominent landscape element in Vietnam with a total area of 60,000 km², and primarily situated in northern and central Vietnam. Our research was conducted in two spatially separated nature reserves (NR) in north-eastern and north-central Vietnam. Both NR, Pù Luông Nature Reserve and Pia Oắc Natural Reserve (hereafter referred to simply as Puluong and Piaoac, respectively), are influenced by a tropical monsoon climate with an average annual rainfall of 1500 to 1700 mm and average annual temperatures of 20°C–22°C. The dry season lasts from November to March, but is not severe (Nguyen et al., 2000; Sterling et al., 2006).

Puluong Nature Reserve (20°21'–20°34'N, 105°02'–105°20'E) is located in Thanhhoa Province in north-central Vietnam. The NR consists of two parallel mountain ridges. Both ridges run northwest-southeast, and are separated by a valley with human settlements as well as their arable land (Averyanov et al., 2003; Vermuellen & Maassen, 2003) (Fig. 2). The two mountains are characterized by remarkably contrasting landforms. The southwestern ridge, i.e., the smaller ridge, is mainly formed by igneous and metamorphic rocks, and characterized by wide and shallow valleys, while the larger ridge is characterized by heavily dissected karsts with elevations ranging from 60 to 1.667 m (Nguyen et al., 2000; Sterling et al., 2006).

Piaoac Natural Reserve (22°32'–22°40'N, 105°49'–105°57'E) is located in Caobang Province in north-eastern Vietnam. The NR is topographically complex, characterized by steep terrains and narrow valleys. Most area of NR are located at the elevational range of 700–1950 m above sea level, with mixed karst and non-karst ecosystems (Tordoff, 2000; Tran & Le, 1999).

The two NR have a wide variety of fragments, including areas of 1st Forests, patches of 2nd Forests, plantations, meadows and arable land, because both NR, like most NR in Vietnam, has been irreversibly destroyed by clear-cutting for shifting agriculture, selective logging and limestone quarrying. Therefore, it is critical to examine the biological value of the existing fragments in order to determine conservation priorities for these unique and important ecosystems.

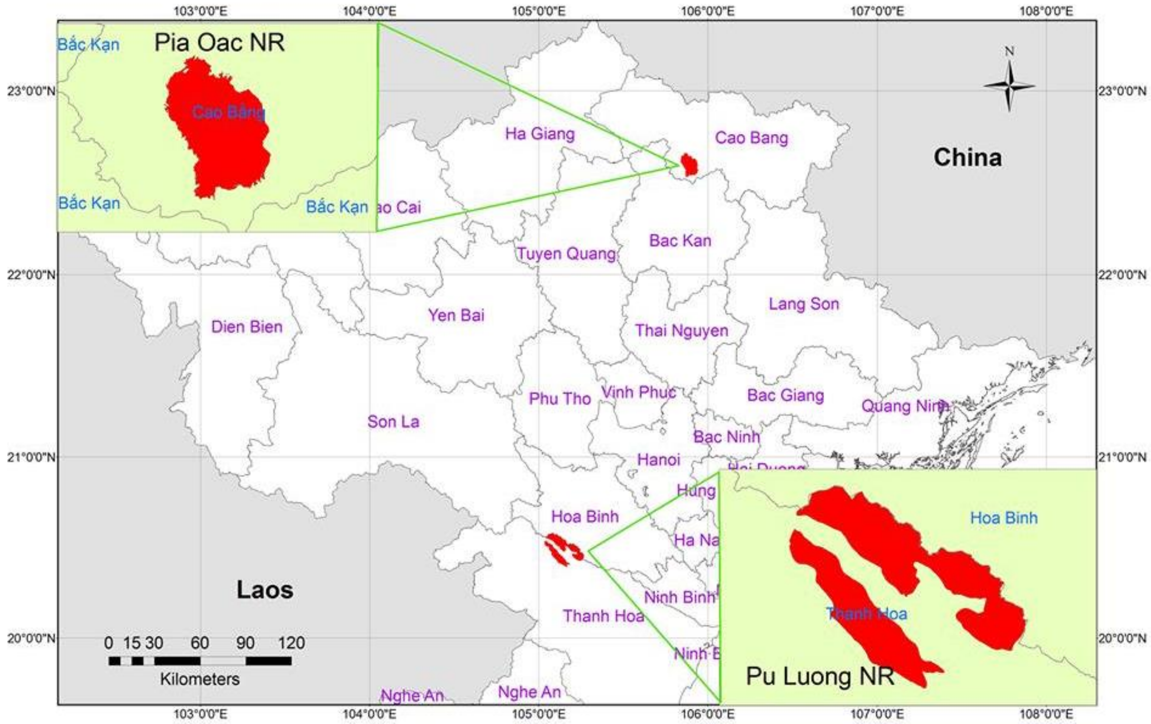

Fig. 2 Map of study areas: Piaoac and Puluong Nature Reserves

The sampling sites covered an elevation range of 780–900 m of increasing land-use intensities (LUI) from 1st Forests and 2nd Forests to meadows across two NR. Sampling sites with different LUI were separated from each other by at least 2 km. According to the classification of Vietnamese forests by Thai (1978), the 1st Forest sites were the closed and evergreen forests on limestone with a complex vertical structure of five layers, including an upper, a dominant, a lower, a bush and a ground vegetation layers. There were no signs of clear-cutting, selective logging, or other anthropogenic or natural disturbances in the surveyed 1st Forest sites (Fig. 3-A&B). The 2nd Forests could be characterized as a swidden fallow system with trees re-growing on abandoned agricultural land, following forest clearing 35- to 40 years ago (Fig. 3-C&D). The meadow sites in Puluong NR had been forests no more than 5–7 years ago. They were vegetated by grasses interspersed with bushes and few small trees (Fig 3-E&F). The meadow sites of Piaoac are part of natural succession. In contrast to the meadows in Piaoac which are intensively grazed by cows and buffalos throughout the year, the meadows in Puluong are now included in the conservation planning, hence livestock grazing is strictly forbidden.

Table 1. The characters of three main land-use types on limestone in the research areas (based on Thai (1978) and on our field surveys)

Land use types	**Characters of land-use types**
Primary forests	The surveyed 1st Forests were closed and evergreen forests on limestone with five main storeys. The upper storey was dominated by trees of more than 35 m height, mostly belonging to Dipterocarpaceae and Combretaceae. The two dominant and lower storeys encompassed tree species with a height of 15 to 25 m, belonging to the families: Lauraceae, Magnoliaceae, Meliaceae, Fagaceae, Sapindaceae, Mimosaceae, Ulmaceae and Annonaceae. The bush storey consisted of small trees and bushes below 8 m, containing species of the Rubiaceae, Acanthaceae and Apocynaceae. The ground vegetation comprised plant families of Urticaceae, Araceae and Begoniaceae.
Secondary forests	The investigated 2nd Forests were classified as swidden fallow 2nd Forests, and have experienced the following transformation processes: ***Primary forests*** (*cleared & burned*) ⟶ ***Arable land*** (*abandoned after a 2- to 3 year cultivation period*) ⟶ **Secondary forests** (after the *fallow regeneration for 35–40 years*) The 2ndForests were dominated by emergent tree species around 50 cm in diameter. Bushes and fresh vegetation are relatively dense in the 2nd Forests.
Meadows	The meadow sites in Puluong NR comprised grass interspersed with bushes and few small trees that all have been regrown from abandoned arable land,

following forest clearing 5- to 7 years ago. The investigated meadow sites are now part of the strictly protected areas.

The meadow sites of Piaoac are part of natural succession, and are intensively grazed by cows and buffalos throughout the year.

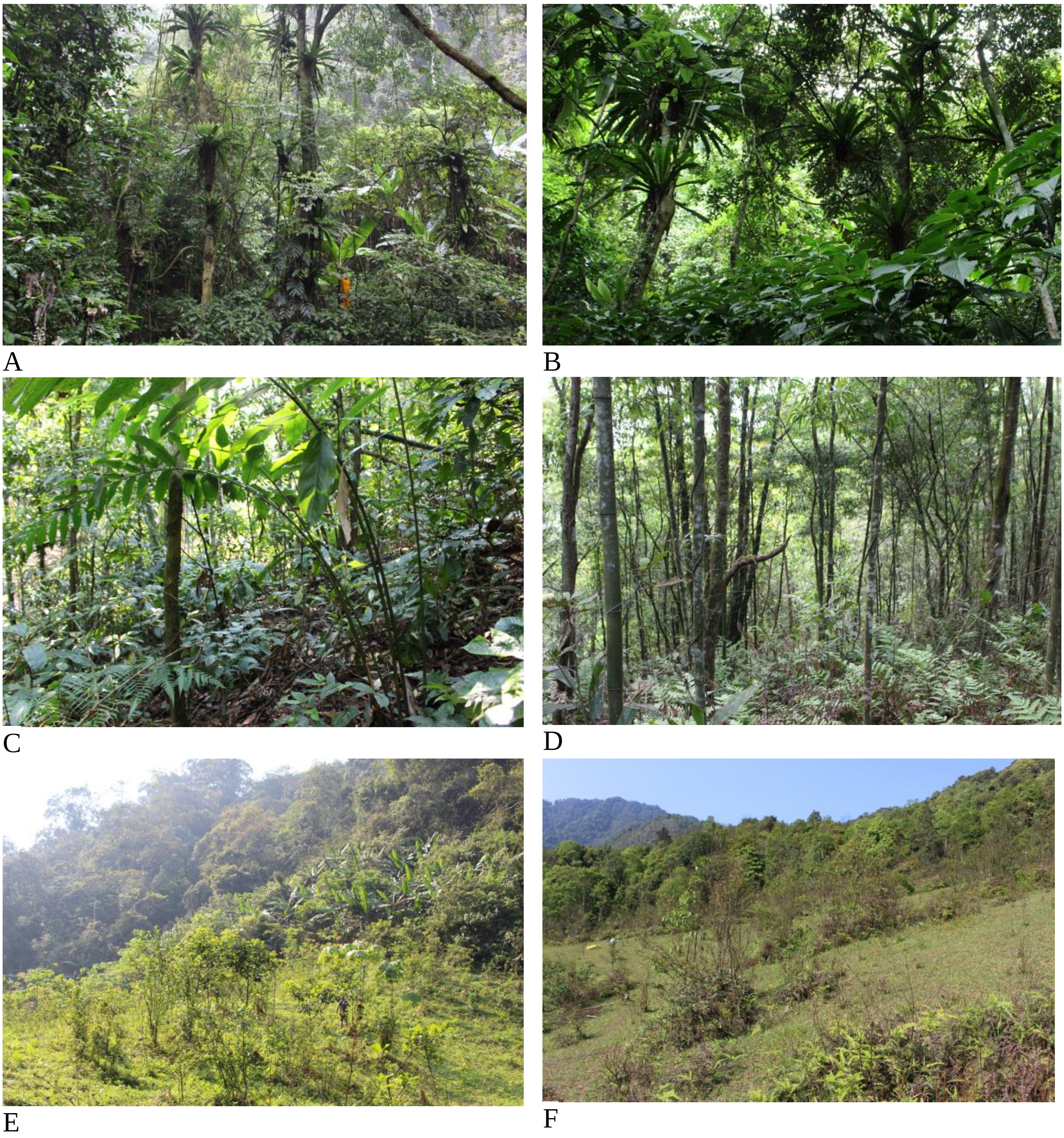

Fig. 3 Three main land-use types in Puluong (A, C, E) and Pioac (B, D, F). A & B – Primary forests. C & D – Secondary forests. E & F – Meadows

The dung beetle fauna of SE-Asian karst ecosystems

Understanding of SE-Asian DB communities inhabiting karst ecosystems is not comprehensive. The only study on DB primarily focusing on small-bodied species, being *Onthophagus* spp., in lowland limestone areas of Ton Nga Chang Wildlife Sanctuary (Thailand) indicated significant effects of anthropogenic disturbance on species composition (Boonrotpong et al., 2012). This finding confirmed a high sensitivity of small-bodied DB species to environmental changes. However, large DB (such as *Synapsis* spp., *Catharsius* spp., and *Copris* spp.) rather than small DB (such as *Onthophagus* spp. and *Aphodius* spp.) play major roles in ecosystem functions (Gardner et al., 2008; Frank et al., 2017b; Tixier et al., 2015). Accordingly, research data for conservation management should include also large-bodied DB species.

Aims:

Investigating DB communities in the three land-use types (meadows, secondary and primary forests) across the two spatially separated karst ecosystems, our specific aims were to:

1) Explore patterns of community response to the effect of land-use change (LUC).

2) Assess the endemism of DB in tropical karst ecosystems.

3) Identify morphological traits, at the community level, sensitive to LUC.

4) Identify complementary morphological traits, at the community level, related to dung removal capacity.

5) Evaluate the biological conservation value of 2nd Forests in tropical karst ecosystems for DB.

The following hypotheses were proposed:

H1. Due to the possession of unique biotic and abiotic conditions, the tropical karst ecosystems would harbour distinct DB communities, and these communities would specifically respond to LUC.

H2. The exceptionally karst abiotic characteristics of karst ecosystems may restrict gene flow between population and promote allopatric speciation. DB with generally low dispersal and small populations would exhibit high endemism.

H3. Harsh environmental conditions in karst ecosystems would act as a strong filter of DB communities with clusters of morphological traits associated to dispersal capacity, foraging behaviour, dung resource requirements and stress tolerance.

H4. The shape of pronotum and elytra and the robustness of middle and hind legs in addition to body length, hind wings and fore legs would correlate with dung removal.

H5. Old 2nd Forests can shelter many 1stForest species but could not provide a substitute for 1stForests.

CHAPTER 1 INFLUENCE OF LAND USE CHANGE ON DUNG BEETLE COMMUNITIES IN TROPICAL KARST ECOSYSTEMS OF VIETNAM

***Manuscript prepared for publication*:**

Influence of land use change on dung beetle communities in high tropical karst ecosystems of Vietnam

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Abstract

We examined variation in community composition, abundance, species richness and biomass of dung beetles from 90 trapping sites distributed in primary forests, old (35–40 years) secondary forests and meadows throughout two spatially separated high-elevation karst ecosystems of Vietnam. Our main aim was to explore patterns of community response to the effect of land-use change (LUC). Further we asked which certain species best being indicator species for these land-uses. Community composition differed strongly among the three land-uses, and was broadly separated between the two karst ecosystems. Unexpectedly species richness and abundance were consistently higher in meadows than in forests across the two karst ecosystems as a consequence of the increasing number of small-bodied species. While biomass exhibited contrasting patterns in responses to LUC, most likely reflecting shifts in the occurrence of ruminants. Although most species showed clear local land-use preferences, few species showed land-use preferences at the regional scale. Taken together, our study confirms that dung-beetle communities in high-altitude karst ecosystems specifically respond to LUC, and contain locally restricted communities of dung beetles with high potential of endemism.

Key words: forest conversion, coprophagous beetles, community composition, abundance, biomass, species richness, indicator species, biological conservation

Introduction

Dung beetles (Coleoptera: Scarabaeinae) depend on vertebrate droppings as main food and nesting resources (Hanski & Cambefort, 1991). Scarabaeine fulfill key ecosystem services through the removal of animal excrements, improving soil nutrient cycling, secondary seed dispersal and suppressing dung parasites (Doube, 2018; Vulinec, 2002; Nichols et al., 2008). Yet, dung-beetle communities have undergone massive modifications, mainly due to anthropogenic land use changes that are becoming increasingly global. Particularly in the tropics more than 80% of the new agricultural land came at the expense of forests during the 1980–2000 period (Gibbs et al., 2010). In order to better conserve dung-beetle biodiversity as well as maintaining their ecosystem functions, it is critical to understand the influences of land-use change (LUC) on dung-beetle communities. Although the consequences of forest conversion for dung beetles has received worldwide attention, from Central Europe (Frank et al. 2017b) and South America (Vulinec 2002; Quintero & Roslin, 2005; Vulinec et al., 2006; Gardner et al., 2008; Audino et al., 2014; Beiroz et al., 2017) to Southeast Asia (Davis et al., 2001; Shahabuddin et al., 2005; Hayes et al., 2009; Boonrotpong et al., 2004, 2012), there is little consensus on the responses of dung-beetle communities to forest conversion from primary forests to secondary forests and meadows. For example, while some authors reported strongly species-depleted dung-beetle communities in secondary forests (2^{nd} Forests) compared to primary forests (1^{ry} Forests) (Boonrotpong et al., 2004; Shahabuddin et al., 2005; Gardner et al. 2008), other studies could not find differences in species richness (Vulinec, 2002; Quintero & Roslin, 2005; Vulinec et al., 2006; Nichols et al. 2007). Despite comprehensive comparisons of dung-beetle composition and ecosystem services between meadows, grasslands or pasture and forests were conducted in tropical regions in Australia (Kenyon et al. 2016) and South America (Braga et al., 2013) and also in temperate regions (Frank et al., 2017; Negro et al., 2011), there is little information on dung beetle communities of tropical meadows in Southeast Asia. The lack of consensus on the biological value of 2^{nd} Forests for dung beetle conservation and the limited knowledge on the composition of dung beetle communities in meadow ecosystems have hindered progress in DB-conservation in SE-Asia.

In Vietnam karst ecosystems on limestone are particularly dominant landscape elements, covering a large area of 60.000 km². These karst ecosystems are characterized by steep and isolated mountains, separated by rivers on plateaus with intensive agriculture (Schilthuizen et al., 2005; Clements et al., 2006). Many medium and large-bodied mammals, being the main dung providers for dung beetles, are endemic to these karst ecosystems. Examples are the Chinese serow (*Capricornis milneedwardsii* David, 1869), or various primates, including Delacour's leaf monkey (*Trachypithecus delacouri)*, Francois' leaf monkey (*T. francoisi*) and macaques (Dang, 2003; Le & Do, 1998). Undoubtedly, tropical karst ecosystems are crucial for maintaining Vietnam’s biodiversity. However, these ecosystems have been increasingly fragmented by anthropogenic land-uses. More recently additional pressures from increasing human demand such as coal mining, limestone quarrying and illegal logging and poaching are threatening these ecosystems. This has been creating a wide variety of fragmented and modified natural forest areas (Wikramanayake et al., 2000; Clements et al., 2006), with concomitant negative consequences for the diversity of mammals and the vegetation structure. Dung beetles were found to respond sensitive to changes in the physical structure of the vegetation (Silva & Hernández, 2015a, b) and the composition of mammal droppings (Estrada et al., 1999; Whipple & Hoback, 2012; Frank et al., 2007a). Accordingly, they may be indirectly affected by land-use changes. However, the community composition of dung beetles inhabiting karst ecosystems of Vietnam is still vastly unknown. A recent study on dung beetles, primarily focusing on the genus *Onthophagus* in lowland karst ecosystems of Ton Nga Chang Wildlife Sanctuary (Thailand) confirmed significant effects of anthropogenic disturbance and subsequent environmental changes, such as light intensity, vegetation cover and temperature, on the composition of the Scarabaeine species (Boonrotpong et al. 2012). These findings indicated a particular sensitivity of small *Onthophagus* species to environmental changes. However, large-bodied dung beetles, such as *Synapsis* spp., *Catharsius* spp., and *Copris* spp. rather than the small *Onthophagus* play major roles in ecosystem functions (Gardner et al. 2008; Frank et al. 2017b; Tixier et al., 2015). Accordingly, research for conservation management nust include large-bodied dung-beetle species.

Investigating and quantifying dung-beetle communities in trajectories of LUC in two spatially separated karst ecosystems of northcentral and northeastern Vietnam, our aim was to evaluate the potential consequences of LUC on the diversity and community composition of dung beetles. We hypothesized that the karst ecosystems would host particular dung-beetle communities, with high potential of endemism. Also we expected clear and unique responses of dung-beetle communities from forest conversions to meadows. Finally, comparing the structure and community attributes of dung beetles between 35- to 40-year-old ^{2nd} Forests and ^{1ry} Forests gave indications on the conservation value of these old ^{2nd} Forests for dung beetle conservation.

Materials and methods

Study sites

The research was conducted in two spatially separated nature reserves (NR), the Piaoac NR (22°32'–22°40'N, 105°49'–105°57'E) located in Caobang Province in northeastern Vietnam, and the Puluong NR (20°21'–20°34'N, 105°02'–105°20'E) located in Thanhhoa Province in northcentral Vietnam. Both NR are being influenced by a tropical monsoon climate with an average annual rainfall of 1500 to 1700 mm and average annual temperatures of 20°C–22°C.

The dry season lasts from November to March and is not severe, particularly in the constantly humid forested areas (Nguyen et al., 2000; Sterling et al., 2006). Much of the natural forest area within the two NR has been irreversibly destroyed by clear-cutting for shifting agriculture, selective logging and limestone quarrying. This has led to the existence of a wide variety of fragments in the two NR, including areas of ^{1ry} Forests, patches of 2^{nd} Forests, plantations, meadows and arable land. Although the Vietnamese Government imposed a ban on logging and shifting agriculture in natural forests already in 1991 (Forest Protection and Development Law No. 58-LCT/HĐNN8), anthropogenic disturbance is still ongoing, particularly in the high mountain areas, around the settlements of ethnic minorities (Pierce Colfer et al., 2008; Do, 2001).

The sampling sites covered an elevation range of 780–900 m of increasing land use intensity (LUI) from ^{1ry} Forests and 2^{nd} Forests to meadows were sampled in both NR. Sampling sites with different LUI were separated from each other by at least 2 km. According to the Vietnamese forest classification by Thai (1978), the ^{1ry} Forest sites were the evergreen closed forests on limestone with a complex vertical structure of five storeys, including an upper, a dominant, a lower, a bush and a ground vegetation layers. There were no signs of clear-cutting, selective logging, or other anthropogenic or natural disturbance in the surveyed ^{1ry} Forest sites. The ^{2nd} Forests could be characterized as a swidden fallow system with trees re-growing on abandoned agricultural land, following forest clearing 35- to 40 years ago. The meadow sites in Puluong NR had been forests no more than 5–7 years ago. They were vegetated by grasses interspersed with bushes and few small trees. The meadow sites of Piaoac are part of natural succession. In contrast to the meadows in Piaoac, which are intensively grazed by cows and buffalos throughout the year, the meadows in Puluong are now included in the conservation planning, hence livestock grazing is strictly forbidden.

Dung beetle sampling and identification

Dung beetles were collected in a standardized manner throughout the two NR within a 25-day period from 15thApril to 10thMay 2016, using baited pitfall traps. Each trap consisted of a plastic bucket, 22 cm in diameter and 16 cm depth, buried to its rim in the soil, filled with 70% ethanol, and baited with 300 g of a fresh pig-buffalo dung (1:1 vol. ratio) mixture. We placed 15 traps in two parallel transects (100 m distant from each other) at each spatially independent LUI. In total, 90 traps were set up at three land use types in the two NR. To minimize trap interference, traps were placed at intervals of at least 150 m along a transect

(Larsen & Forsyth, 2005; Silva & Hernández, 2015a). All trapped dung beetles were removed from the traps after 72 hours of trap exposure and preserved in ethanol until examination in the laboratory.

Dung beetles were identified based on the identification keys of Balthasar (1963 a, b), Bui et al. (2018) and Bui & Bonkowski (2018), the list of Vietnamese dung beetles documented by Kabakov & Napolov (1999), and by comparison with reference collections at the National Museum of Natural History (NMNH) (Paris, France), the National Museum Prague (NMPC) (Prague, Czech Republic), the Naturalis Biodiversity Center (RMNH) in Leiden (The Netherlands) and the private collection of Dr. Jan Krikken (Leiden, The Netherlands). Reference collections containing the species from this study are now deposited in RMNH, the Zoological Collection of the Institute of Zoology, University of Cologne (Germany) and the Vietnam National University of Forestry, Hanoi (Vietnam). To obtain biomass measurements of each species, between 1 and 20 individuals of each species (i.e., 10–20 individuals of abundant species and all individuals of rare species) were dried at 65°C for 48 hours before weighting on a balance accurate to 0.0001 g. The biomass of each species per trap was calculated by multiplying the average dry weight of a species with the total number of individuals caught in the trap. The total biomass of all dung-beetle species recorded from a trap was the dung-beetle biomass per trap.

Environmental variables

Concurrently with dung-beetle sampling, we measured environmental variables at each sampling site using the quadrant-section method as described in Brower et al. (1998) and Campos & Hernández (2015). Briefly, with trap in the center, a cross was marked to divide each trapping site into four quadrants. In each quadrant, the nearest trees (diameter at breast height > 6 cm) and shrubs (DBH < 6 cm and height >1 m) to the center point were marked, and their traits comprising trunk diameter (trees), crown diameter (shrubs), height and distance to center point were measured. At the same time, from a small plot of 1x1 m in each quadrant, leaf litter thickness, percentage of leaf litter cover and the area of ground vegetation were determined, using six ranks: 0–5%, 6–25%, 26–50%, 51–75%, 76–95% and 96–100%. Forest canopy cover was estimated according to the index by Braun-Blanquet (1928): 5 (75–100%), 4 (50–75%), 3 (25–50%), 2 (5–25%), 1 (1–5%). From each quadrant around the trap, four soil samples were collected for measurement of soil texture.

Data analysis

Data obtained from the 79 trapping sites were used for statistical analyses using R v. 3.4.0 (R Core team, 2017). Although some pitfall traps were lost during the period of dung-beetle sampling, total trapping effort for each LUI was approximately equal, with 14 traps in ^{1ry} Forests of Puluong NR and 13 traps each in the remaining sites. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities using relative abundances from a species matrix was computed to characterize differences in the community structure of dung beetles between land use types and the two NR. Analysis of Permutational multivariate analysis of variance (PERMANOVA) was computed to test for differences among dung-beetle communities. All tests and ordination plots were performed using the vegan package v. 2.4–5 (Oksanen et al., 2017), and each test was based on 999 permutations. Environmental factors were fitted onto NMDS ordinations using the envfit function in vegan in order to detect environmental drivers for community dynamics. Venn diagrams were generated using the VennDiagram package v. 1.6.18 (Hanbo, 2017) to show the number of dung beetles common to both NR. An indicator value analysis (IndVal) was carried out using the indicspecies package v. 1.7.6 (Caceres & Jansen, 2016) in order to identity the species characteristic for specific sites (Dufrene & Legendre, 1997).

Results

Community structure of dung beetles in land-use types across two nature reserves

In total, 3352 dung beetles comprising 75 species were sampled and identified from the 79 trapping sites in the two nature reserves. The dung beetles were distributed across 14 genera: *Copris* (420 individuals, 6 species), *Catharsius* (52 ind., 1 spe.), *Synapsis* (21 ind., 3 spe.), *Sisyphus* (55 ind., 1 spe.) *Eodrepanus* (48 ind., 1 spe.), *Tibiodrepanus* (12 ind., 1 spe.), *Sinodrepanus* (15 ind., 1 spe.), *Paragymnopleurus* (80 ind., 2 spe.), *Liatongus* (240 ind., 3 spe.), *Onthophagus* (1158 ind., 47 spe.), *Ochicanthon* (10 ind., 2 spe), *Caccobius* (18 ind., 1 spe.), *Parachorius* (1 ind., 1 spe.) and *Aphodius* (1222 ind., 5 spe.) (Appendix 1).

Most small-bodied dung-beetle species, with a body length<10 mm, showed habitat preferences: two species of *Ochicanthon* and one species of *Sinodrepanus* (i.e., *S. similis*) were found exclusively in forests, while *Liatongus* spp., *Caccobius* spp., one species of *Sisyphus* (i.e., *S. denticrus*) and one species of *Tibiodrepanus* (i.e., *T. sinicus*) were found exclusively in meadows. Also 98% of *Eodrepanus striatulus* specimens occurred in meadows. The genus *Onthophagus*, contained specialists of meadow and forest habitats. Almost 60% of all *Onthophagus* species occurred exclusively in meadows and more than 20% only in forests. One *Onthophagus* species, *O. trituber*, was a real forest specialist with 98% of the all individuals being found in forests. The other small-bodied species in the genus *Aphodius* showed a similar distribution as *Onthophagus* spp. with 60% of all *Aphodius* species exclusively occurring in meadows and 20% occurring in forests.

Although large-bodied dung-beetle species, i.e., body length>10 mm, are known to forage over long distances, many species appeared as specialized for either forests or meadows. For example, *Synapsis* spp., *Copris caobangensis* and *C. sonensis* were only found in forests, and also *C. szechouanicus* and *C. confucius* occurred mostly in forests, while *C. magicus* was only found in meadows. The habitat preferences of one particularly large-bodied species, *Catharsius molossus,* differed between locations, with 92% individuals being trapped in meadows of Piaoac, but with 81% individuals trapped in forests of Puluong. The two large-bodied species in the genus *Paragymnopleurus* were almost identical on a morphological level, but while *P. melanarius* was exclusively restricted to meadows of Piaoac, *P. brahminus* was only found in forests of Puluong. This indicates that other factors than the habitat determined its occurrence.

The community structure of dung beetles differed significantly between the two nature reserves (PERMANOVA, $F_{1,\ 77}=35.132$, $p<0.001$), and locally between land-use types (in Piaoac, PERMANOVA, $F_{2,36}=27.078$, $p<0.001$; in Puluong, PERMANOVA, $F_{2,\ 37}=42.125$, $p<0.001$). The species ordination in NMDS clearly separated the forest dung-beetle communities from the meadow communities in both nature reserves. This difference was larger in Piaoac than in Puluong. Although there was some overlap between ^{1ry} Forests and 2nd Forests, the community structure differed significantly between the two forest types (in Piaoac, PERMANOVA, $F_{1,24}=8.0149$, $p<0.001$; in Puluong, PERMANOVA, $F_{1,25}=7.8827$, $p<0.001$)

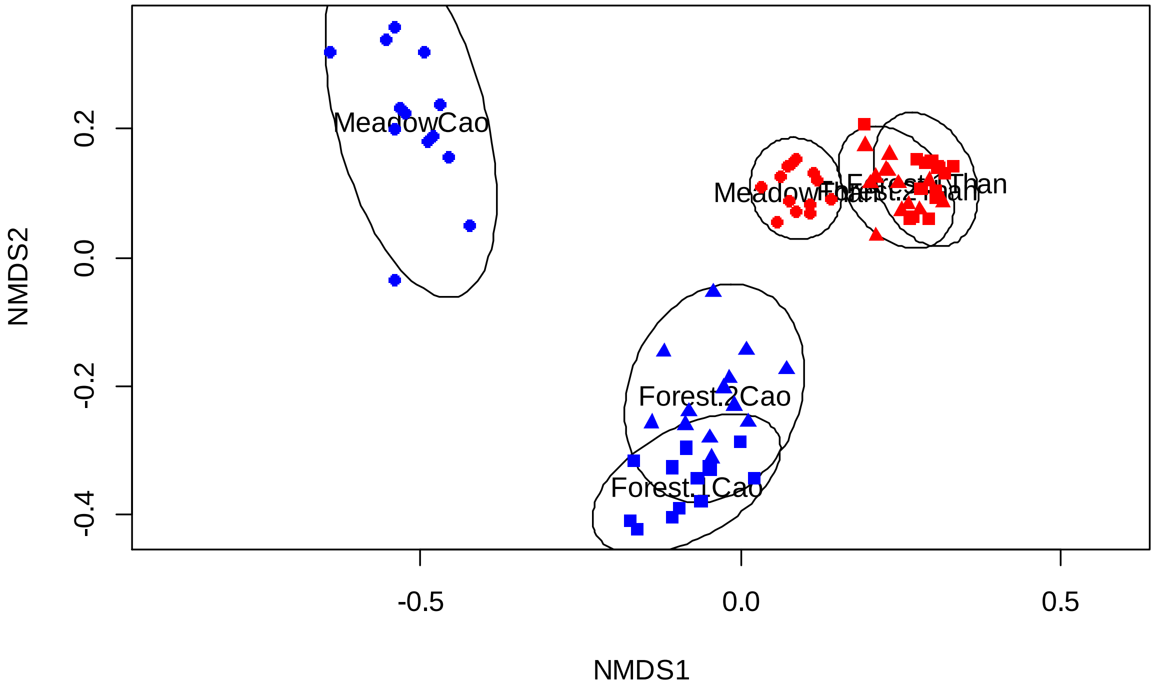


Fig. 1 NMDS ordination showing clear differences in community structures of dung beetles between the two nature reserves in northeastern Vietnam (Piaoac, blue) and in northcentral Vietnam (Puluong, red), and among land-use types. Primary forests (Fores.1, filled squares), secondary forests (Forest.2, filled triangles) and meadows (Meadow, filled circles). Ellipsoids represent 95% confidence intervals surrounding each land use types. Stress value: 0.07.

Tropical karst ecosystems harbour unique subsets of dung beetles

Species overlap was surprisingly low between the two nature reserves, with eight common species in forests and 13 common species in meadows from 75 species in total (Fig. 2), suggesting that each spatially independent nature reserve harbours unique dung-beetle species. Only three of the 13 common meadow species showed a meadow-habitat preference in both Piaoac and Puluong: *Onthophagus* (*Phanaeomorphus*) *sycophanta* (InVal in PiaOac: 0.877, $p<0.001$, InVal in Puluong: 0.961, $p<0.001$), *Onthophagus crassicollis* (InVal in PiaOac: 0.784, $p<0.001$, InVal in Puluong: 0.832, $p<0.001$) and *Onthophagus luridipennis* (InVal in PiaOac: 0.555, $p=0.029$, InVal in Puluong: 1.000, $p<0.001$). In contrast, none of the strict ^{1ry} Forest or 2^{nd} Forest species showed significant habitat preferences in both nature reserves.

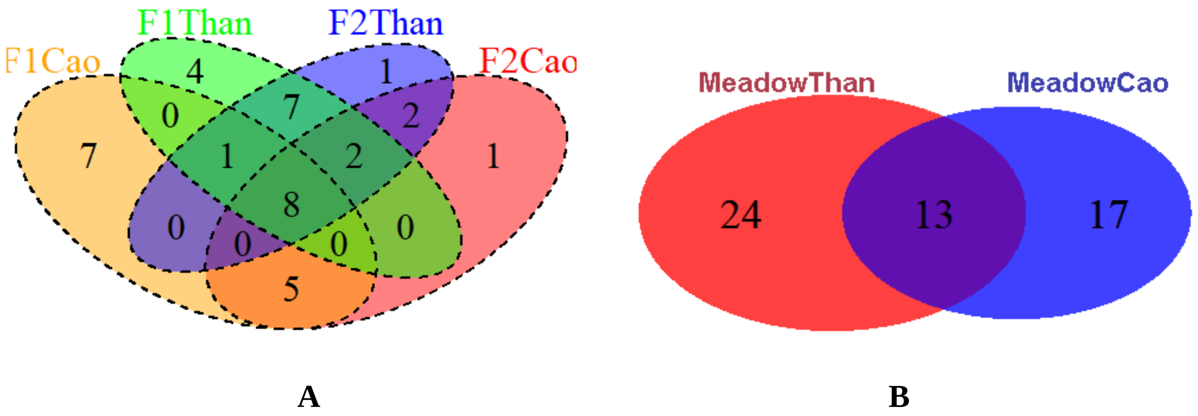


Fig. 2 Venn diagrams demonstrating the number of dung beetles common to the two spatially separated forests (A) and meadows (B). Primary forests, secondary forests and meadows in Pioac (Caobang) (F1Cao, F2Cao and MeadowCao), and in Puluong (Thanhhoa) (F1Than, F2Than and MeadowThan).

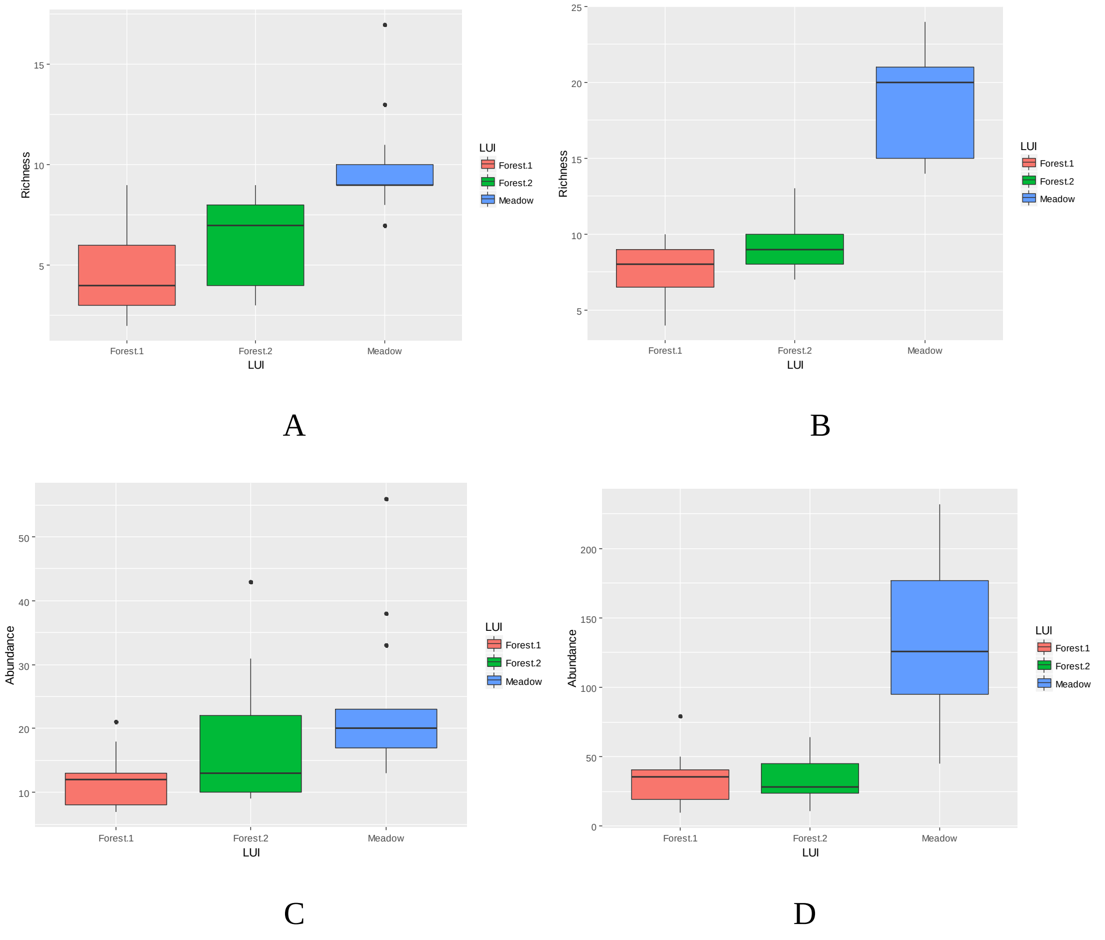
Changes in the community attributes (species richness, abundance and biomass) of dung beetles in trajectories of LUC on limestone

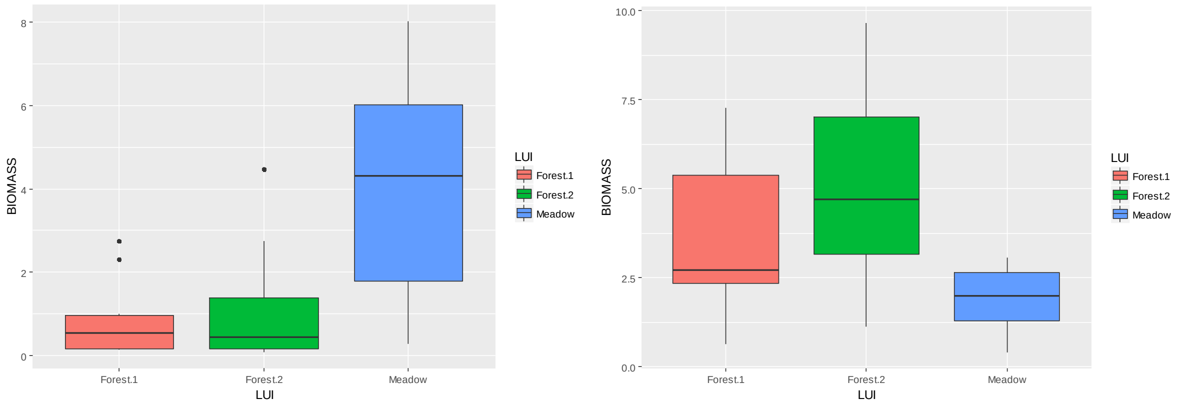
In total 48 dung-beetle species were collected in Piaoac NR with 21, 18, and 30 species being collected in 1ry Forests, 2nd Forests and meadows, respectively. Almost the same number, with 50 species in total was found in Puluong NR, of which 22, 21, and 37 species were recorded in 1ry Forests, 2nd Forests and meadows, respectively. Sampling efficiency (according to Chao1 estimator) was high in all land-use types of both NR, ranging from 74% to 94% for 1ry Forests, 96 to 100% for 2nd Forests and 76 to 93 % in meadows. The species accumulation curves indicated higher species richness in meadows than in forests. This pattern was consistent across the two NR (Appendix 2), in Piaoac (ANOVA: $F_{2,36}=16.36$, $p<0.001$, Tukey's HSD: each of $p_{Meadow\text{-}PF}$ and $p_{Meadow\text{-}SF}$ <0.001), in Puluong (ANOVA: $F_{2,37}=86.1$, $p<0.001$, Tukey's HSD: each of $p_{Meadow\text{-}PF}$ and $p_{Meadow\text{-}SF}$ <0.001) (Fig. 3-A, B).

Also the dung-beetle abundance according to the trapped individuals was significantly higher in meadows than in 1ry Forests of Piaoac (ANOVA: $F_{2,36}=5.553$ and $p=0.007$; Tukey's HSD tests: $p_{Meadow\text{-}PF} = 0.005$). In Puluong, the average number of individuals was higher in meadows than in both 1ry Forests and 2nd Forests (ANOVA: $F_{2,37}=39.67$ and $p<0.001$; Tukey's HSD: each of $p_{Meadow\text{-}PF}$ and $p_{Meadow\text{-}SF}$ <0.001) (Fig. 3-C, D).

Dung-beetle biomass however, did not reflect these clear patterns in responses to LUC across the two nature reserves. Compared to forests, dung-beetle biomass was higher in meadows of Piaoac (ANOVA: $F_{2,36}$=13.25 and p<0.001) but lower in meadows in Puluong (ANOVA: $F_{2,37}$=6.975 and p=0.002)(Fig. 3-E, F).

There was no significant difference in species richness (SR), abundance (Ab) and biomass (Bio) of dung beetles between ^{1ry} Forests and 2^{nd} Forests, and this finding was consistent throughout both nature reserves (in Piaoac, p_{PF-SF} = 0.287, 0.223 and 0.947 for SR, Ab and Bio, respectively; in Puluong, p_{PF-SF} = 0.278, 0.989 and 0.175 for SR, Ab and Bio, respectively).





E F

Fig. 3 Boxplots of species richness, abundance and biomass in trajectories of LUC, primary forests (Forest.1), secondary forests (Forest.2) and meadows (Meadow) in Piaoac (Caobang) (A, C, E) and Puluong (Thanhhoa) (B, D, F).

Effects of environmental variables on the community structure of dung beetles in forests

At the local scale, the community structures of dung beetles in ^{1ry} Forests and old (40 years) ^{2nd} Forests of Puluong appeared to be influenced by the cover of ground vegetation (GV) (R^2=0.2444, p=0.03), the diameter of trees (Di.t) (R^2=0.2164, p=0.04) and the forest canopy cover (Fc) (R^2=0.3342, p=0.007) (Fig. 4).

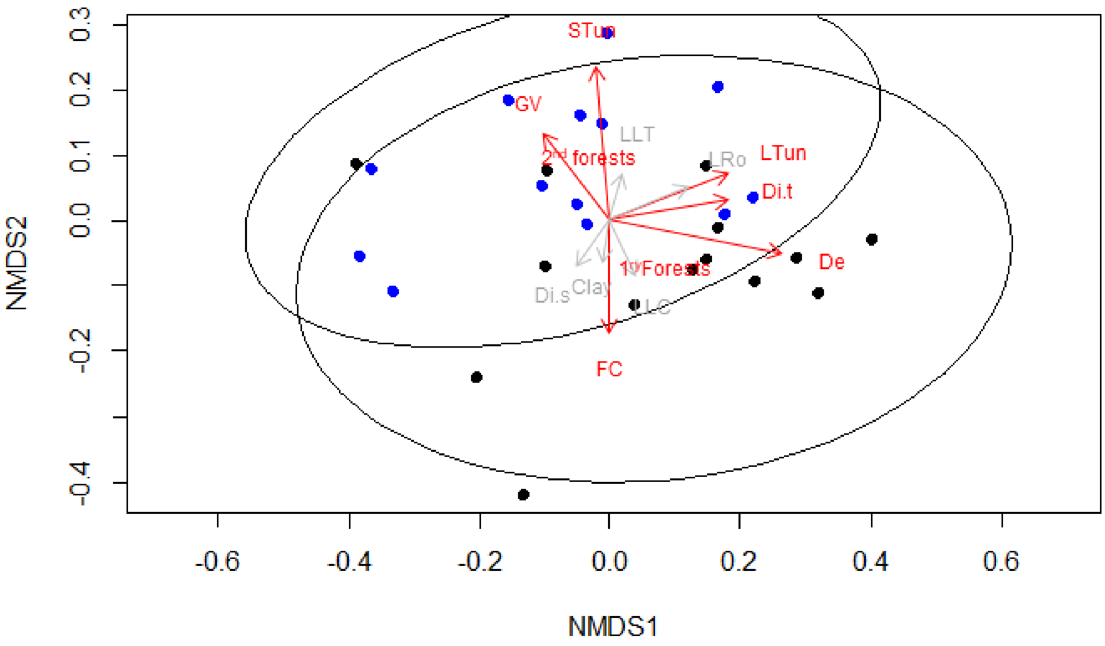


Fig. 4 NMDS ordination showing differences in the dung-beetle structure between primary and secondary forests in Puluong (stress value: 0.09). The fitted vectors of environmental

variables are displayed only for the significant variables ($p<0.05$). Secondary forests (^{2nd} Forests, blue), primary forests (^{1ry} Forests, black), cover of ground vegetation (GV), leaf litter cover (LLC), leaf litter thickness (LLT), diameter of shrub crown (Di.s), diameter of trees (Di.t), forest canopy cover (Fc) and soil clay content (Clay), large-bodied tunnelers (LTun, body length ≥10 mm), small-bodied tunnelers (Stun, body length <10 mm), large-bodied rollers (LRo, body length > 10 mm) and dwellers (De).

Discussion

The community structure of dung beetles among land-use types and between the two karst ecosystems

This study provides a first assessment of the effects of habitat transformation on dung beetles inhabiting two spatially separated tropical karst ecosystems using the same trapping protocol and equal survey times in Vietnam. It was not surprising to find significant differences in the community structures of dung beetles between different land-use types, because dung beetles are known to respond sensitive to LUC, such as conversion of forests to grasslands (Verdú et al., 2011; Frank et al., 2017b). However, dung beetles have been found to respond also to more subtle changes of their habitats, such as ambient temperature (Scholtz et al., 2009) and soil texture (Beiroz et al., 2017). An unexpected result of the current study was that the community structure of dung beetles varied greatly between the two nature reserves (Fig. 1). The karst ecosystems of Vietnam are famous for their high numbers of endemic vertebrates (Wikramanayake et al. 2000; Schilthuizen et al. 2005; Clements et al., 2006). Our study indicates that this may also apply for dung beetles, whose diversity and species turnover between the two spatially separated nature reserves was by far larger than expected.

The fact that the large-bodied *Catharsius molossus* was preferentially trapped in meadows of Piaoac, but in forests of Puluong indicates only a weak binding to particular habitats for this species. Large-bodied dung beetles depend on dung pats of large mammals as nesting sites (Doube, 1990). The distribution of *C. molossus* most likely reflects shifts in the abundance, identity or community structure of mammal dung providers between both nature reserves. The strictly protected forests of both nature reserves contain large and medium mammals such as the Sumatran serow, and a number of wild boars, and monkey species, while grasslands of Piaoac are mainly grazed by buffalos and cows. In contrast, livestock grazing is strictly forbidden in the meadow areas of Puluong, because these areas are included in the conservation planning (FFI, 2006, 2009), leading an overall impoverished availability of ruminant dung. More detailed studies are needed to clarify the ecological factors determining the occurrence of rare and large-bodied dung beetles, such as *C. molossus*.

The patterns of dung-beetle attributes in trajectories of land-use change

When comparing species richness, abundance and biomass of dung-beetles between land-use types of both nature reserves, we found consistent patterns in species richness and abundance. Most dung-beetle species of our study showed clear preferences for either forests or meadows as seen in other studies (Frank et al., 2017b). However, the species richness and abundance of dung beetles was significantly higher in meadows than in forests of the investigated karst ecosystems. This finding is contrary to those found in Europe (Numa et al., 2009) and in South America (Braga et al., 2013). Apparently, responses of dung beetles to habitat changes cannot be easily generalized between continents. Communities of SE-Asian dung beetles considerably differ by their high numbers of *Onthophagus* species (Davis et al. 2001, Shahabuddin et al. 2005, Hayes et al. 2009). Also in our study *Onthophagus* species dominated the dung-beetle communities, with more than 60% of both the total species richness and numbers of individuals in Piaoac and Puluong, respectively. Also the other abundant genus, *Liatongus* spp. was found exclusively in meadows throughout both nature reserves. Small dung beetles (body length<10 mm), e.g., *Onthophagus* spp., *Liatongus* spp., *Caccobius* spp. perch on the leaves of the ground vegetation to locate food resources (Howden & Nealis, 1978; Peck & Forsyth, 1982; Hanski & Cambefort, 1991; Larsen et al., 2008; Silva & Hernández, 2015a), and meadows offer these structures in abundance in contrast to forests. The advantage of small body size in meadows may turn into a disadvantage in the shades of high-elevation forests of 800 – 1000 m, as the lower ambient temperature for flight may limit the dispersal of small-bodied dung beetles, particularly in tunneler groups as shown by Verdú et al. (2006).

Similar to species richness and abundance, we found a higher dung-beetle biomass in the intensively cattle-grazed meadows of Pioac compared to forests, but the strictly protected meadows of Puluong had a lower dung-beetle biomass compared to forests, despite having a higher dung-beetle species richness and abundance. Apparently, the dung-beetle communities are strongly dependent on the resource basis provided by large mammals. The high dung-beetle biomass in Puluong forests was due to the dominance of large-bodied dung-beetle species in Puluong forests such as *Synapsis tridens* and *Catharsius molossus* with a body mass of 2.20 g and 1.25 g, respectively, while the average individual body mass of dung beetles was 0.21 g (Fig. 5). As discussed above, large-bodied dung-beetle species are constrained to utilize the dung of large mammals (Howden & Nealis, 1978; Hanski & Cambefort, 2014), and apparently these were more abundant in Puluong forests than in meadows.

The conservation value of secondary forests for dung beetles

Although many studies have examined the biological conservation value of 2^{nd} Forests, there are still uncertainties about their value for the conservation of dung beetles. Our results were consistent with Vulinec (2002), Quintero & Roslin (2005), Vulinec et al. (2006) and Nichols et al. (2007) showing no differences in species richness, abundance and biomass between 2^{nd} Forests and 1^{ry} Forests, but differed to the studies of Boonrotpong et al. (2004), Shahabuddin et al. (2005) and Gardner et al. (2008) who found significant differences in DB communities between both forest types. If 2^{nd} Forests are sufficiently old, they may have a high potential conservation value for dung beetles due to the similarity of refuges to 1^{ry} Forests (the current study, Vulinec, 2002; Quintero & Roslin, 2005), whereas young 2^{nd} Forests may lack these attributes (Boonrotpong et al., 2004; Shahabuddin et al., 2005). Despite this, the distinct separation between 2^{nd} and 1^{ry} Forest communities observed in the current study, seems to reflect irreversible shifts in functional groups, particularly in the tunnelers group (Fig.4). The NMDS analysis highlighted a significant correlation between the cover of ground vegetation (GV) and the abundance of small tunnelers (STun) (Fig. 4). It is very likely that the higher abundance of small tunnelers in 2^{nd} Forests reflects their preferences for a high cover of ground vegetation that, as above discussed, provides perches for small tunnelling beetles during the foraging process for food. Large-bodied tunnelers (LTun) were correlated to the diameter of trees (Di.t) (Fig. 4), because trees may provide shelter and food for many mammals such as primates, civets and boars, and thus indirectly drive mammalian associations with large tunnelling DB.

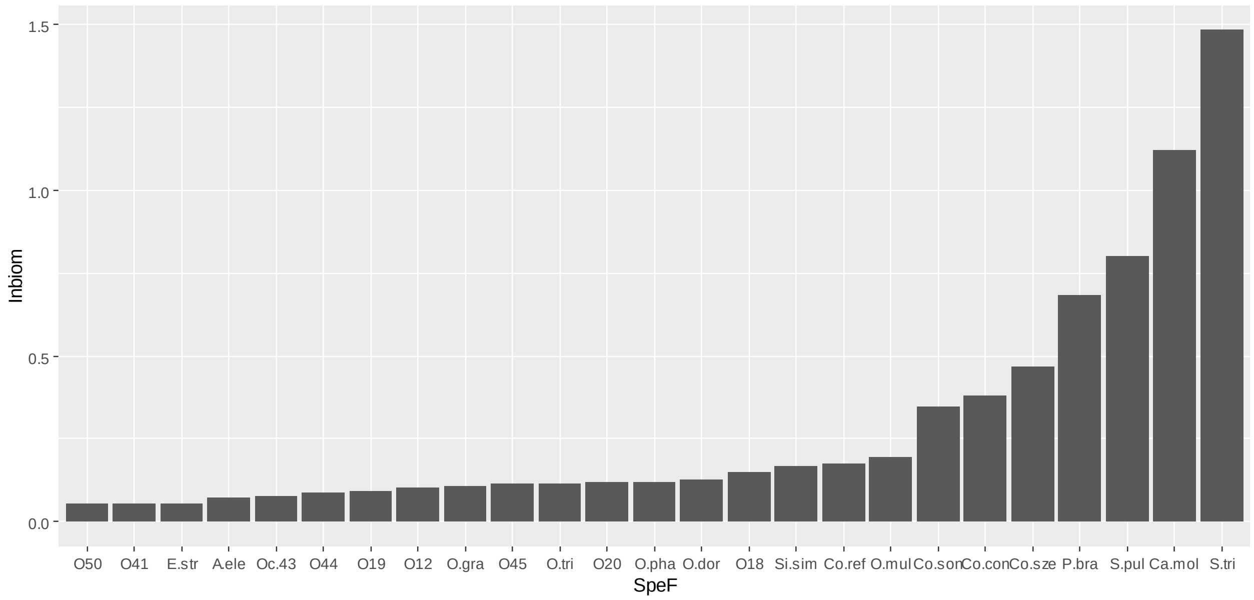


Fig. 5 Differences of average individual body mass (sqrt scale) of dung-beetle species collected in forests of Puluong, Inbiom: individual biomass (g dry weight).

Conclusion

Dung-beetle communities inhabiting high-elevation karst ecosystems of Vietnam showed shifts in community composition, abundance, richness and biomass between land-use types. However, the discrepancy in the patterns of species richness and abundance between the current study and earlier studies emphasizes the importance to study the context of biogeography and landscape in structuring dung-beetle communities. The generalization of results based on the species identity is biogeographically restricted, since species composition strongly differed between the nature reserves in Piaoac and Puluong. A high species turnover with only a few common species was characteristic for the two spatially separated karst-communities. Based on these results, the diversity of dung beetles in Vietnam appears highly underestimated. Likely also containing endemic species, but more data on the distribution of species are required. The high regional diversity of DB limits their use as indicator species. In contrast, the biomass of communities and of individual large-bodied DB appears to indicate shifts in mammal communities.

Although the old (35–40 years) 2^{nd} Forests showed similarities in DB species richness, abundance and biomass to 1^{ry} Forests, the community structure of functional groups still differed across the two forest types, indicating that differences in ecosystem functions of dung beetles might still persist between 1^{ry} Forests and 2^{nd} Forests.

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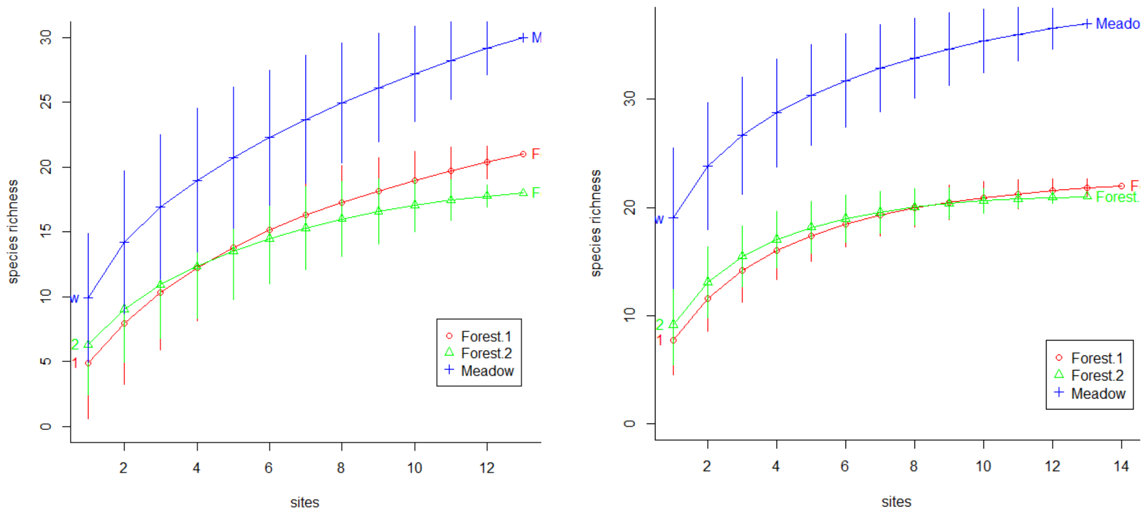
Appendix 1 Numbers of dung beetles of each species recorded at each land use type: meadows in Cao Bang (M.Cao), secondary forests in Cao Bang (F.2Cao) and primary forests in Cao Bang (F.1.Cao); meadows, secondary forests and primary forests in Thanh Hoa corresponding to M.Than, F.2Than and F.1Than, respectively.

Species	M.Cao 13 sites	F.2Cao 13 sites	F.1Cao 13 sites	M.Than 13 sites	F.2Than 13 sites	F.1Than 14 sites
Aphodius elegans Allibert	0	10	3	80	113	261
Aphodius mirificus Balthasar	0	0	0	568	0	0
Aphodius sp. 01	0	0	0	125	0	0
Aphodius sp. 02	0	0	0	9	0	0
Aphodius sp. 03	3	40	10	0	0	0
Caccobius unicornis (Fabricius)	3	0	0	15	0	0
Catharsius molossus (Linnaeus)	24	1	1	5	17	4
Copris caobangensis Bui, Dumack & Bonkowski	0	0	3	0	0	0
Copris confucius Harold	0	0	0	5	4	15
Copris magicus Harold	16	0	1	0	0	0
Copris reflexus Fabricius	0	7	1	27	65	11
Copris sonensis Bui, Dumack & Bonkowski	0	0	0	0	9	3
Copris szechouanicus Balthasar	1	10	8	26	115	93
Eodrepanus striatulus Paulian	0	0	0	47	0	1
Liatongus gagatinus (Hope)	23	0	0	0	0	0
Liatongus sp. 01	0	0	0	6	0	0
Liatongus vertagus (Fabricius)	0	0	0	211	0	0
Ochicanthon obscurum (Boucomont)	0	0	0	0	8	0
Ochicanthon sp. 01	0	0	2	0	0	0
Onthophagus aloysiellus Zunino	0	0	0	12	0	0
Onthophagus crassicollis Boucomont	16	0	0	30	0	0
Onthophagus dorsofasciatus Fairmaire	12	100	90	105	4	1
Onthophagus gracilipes Boucomont	0	0	0	0	0	4
Onthophagus jeannelianus Paulian	52	14	1	0	0	0
Onthophagus luridipennis Boheman	13	0	0	200	0	0
Onthophagus mulleri Lansberge	0	0	0	0	0	6
Onthophagus muticifrons Endrödi	2	0	0	0	0	0
Onthophagus orientalis Harold	9	2	2	0	0	0
Onthophagus papulatus Boucomont	1	0	0	2	0	0
Onthophagus phanaeiformis Boucomont	0	0	1	0	4	3
Onthophagus proletarius Harold	2	0	0	40	0	0
Onthophagus rectecornutus Lansberge	0	0	0	10	0	0
Onthophagus rudis Sharp	2	0	0	0	0	0
Onthophagus saigonensis Boucomont	0	0	0	3	0	0
Onthophagus sp. 01	1	0	0	7	0	0

Onthophagus sp. 02	0	0	0	1	0	0
Onthophagus sp. 03	3	0	0	0	0	0
Onthophagus sp. 04	14	0	0	2	0	0
Onthophagus sp. 05	0	6	4	0	6	3
Onthophagus sp. 06	0	0	0	1	0	0
Onthophagus sp. 07	0	0	0	1	1	1
Onthophagus sp. 08	0	2	0	0	10	2
Onthophagus sp. 09	0	0	0	2	5	11
Onthophagus sp. 10	0	0	1	0	0	0
Onthophagus sp. 11	0	2	7	0	0	0
Onthophagus sp. 12	0	0	2	0	0	0
Onthophagus sp. 13	11	1	0	0	0	0
Onthophagus sp. 14	1	0	0	0	0	0
Onthophagus sp. 15	1	0	0	0	0	0
Onthophagus sp. 16	2	0	0	0	0	0
Onthophagus sp. 17	1	0	0	0	0	0
Onthophagus sp. 18	1	0	0	0	0	0
Onthophagus sp. 19	1	0	0	0	0	0
Onthophagus sp. 20	0	0	0	5	0	0
Onthophagus sp. 21	0	0	0	2	0	0
Onthophagus sp. 22	0	0	0	5	0	0
Onthophagus sp. 23	0	5	6	0	0	0
Onthophagus sp. 24	0	0	0	1	0	0
Onthophagus sp. 25	0	2	0	1	2	0
Onthophagus sp. 26	1	0	0	0	0	0
Onthophagus sp. 27	0	0	0	0	6	2
Onthophagus sycophanta Fairmaire	33	0	0	55	0	0
Onthophagus taurinus White	0	0	0	57	3	6
Onthophagus thanwaakhomus Masumoto	0	2	0	0	2	0
Onthophagus trituber (Wiedemann)	0	24	3	1	18	13
Onthophagus vaulogeri Boucomont	0	0	0	46	0	0
Parachorius sp. 01	0	0	1	0	0	0
Paragymnopleurus brahminus (Waterhouse)	0	0	0	0	15	8
Paragymnopleurus melanarius (Harold)	57	0	0	0	0	0
Sinodrepanus similis Simonis	0	1	0	0	3	11
Sisyphus neglectus Gory	4	0	0	51	0	0
Synapsis horaki Zidek & Pokorny	0	0	3	0	0	0
Synapsis puluongensis Bui & Bonkowski	0	0	0	0	0	6
Synapsis tridens Sharp	0	3	1	0	3	5
Tibiodrepanus sinicus (Harold)	1	0	0	11	0	0
Total	**311**	**232**	**151**	**1775**	**413**	**470**

Appendix 2 Species accumulation curves for three land use types in Piaoac (A) and in Puluong (B)



A

B

CHAPTER 2 INFLUENCE OF LAND USE CHANGE ON MORPHOLOGICAL TRAITS AND KEY ECOSYSTEM FUNCTIONS OF DUNG BEETLES IN TROPICAL KARST ECOSYSTEMS

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Morphological traits reflect dung beetle response to land use changes in tropical karst ecosystems

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Abstract

Dung beetles respond sensitive to changes of their environment, in particular to land use change following the conversion of primary forests. Changes in dung beetle communities have been often described on a taxonomic level, but the high diversity of dung beetles and difficulties in the delineation of species have hindered the generalization of results. Morphological traits of beetles instead reflect their environmental adaptations through natural selection across species borders, and may provide a more robust means to detect patterns of community change imposed by different land uses.

We investigated changes in morphological traits of 41 tunnelling dung beetle species in a sequence of land use change from primary forests, to secondary forests and meadows in tropical karst mountain ecosystems in Vietnam (South East Asia). Tunnelers were by far the dominant functional group of dung beetles in these ecosystems. In addition, we measured dung removal rate as a key ecosystem service of these beetles. By combining RLQ and fourth-corner methods to characterize shifts in morphological species traits, we identified three distinct morphological trait clusters of dung beetles, reflecting distinct community adaptations to land use changes. Meadows, despite harbouring highest dung beetle abundance and species richness were severely impoverished in large-bodied dung beetles. The large-bodied dung beetles however, turned out to play crucial roles for dung removal. These data indicate that land use change led to significant changes of species traits in dung beetle communities which in turn fed back on critical ecosystem services. Since trait-based approaches directly reflect species adaptations to their current environment, species traits contain more relevant information of environmental change compared to taxonomic approaches which, in comparison, reflect more past phylogenetic evolution. Trait-based approaches may be better suited to understand the functional implications of environmental changes on species-rich arthropod communities and may better allow generalizations of adaptive responses between ecosystems.

Key words

Forest conversion, tunnelers; biomass, body length; trait-based approach, co-inertia analysis (RLQ); fourth-corner method; ecosystem services, dung removal, functional diversity

Introduction

Dung beetles (DB) (Coleoptera, Scarabaeidae) are highly sensitive to changes in the physical structure of terrestrial habitats, and have been widely used as indicators in the assessment of habitat disturbances (Audino et al., 2014; Beiroz et al., 2017; Davis et al., 2001; Nichols et al., 2007). Because DB typically utilize vertebrate droppings and carcasses as essential food and nesting resources, they may further reflect changes in the composition and structure of vertebrate communities (Andresen and Laurance, 2007; Enari et al., 2013; Estrada et al., 1999; Harvey et al., 2006; Vulinec, 2000). Land use change (LUC) may thus directly feed back on vital ecosystem functions that DB provide through their feeding and nesting processes, such as dung removal, nutrient cycling, secondary seed dispersal and biological control of vertebrate parasites (Doube, 2018; Hanski and Krikken, 1991; Nichols et al., 2008; Vulinec, 2002).

Research on the influence of LUC on DB communities has been conducted worldwide, from Europe (Frank et al., 2017; Hutton and Giller, 2003) to South America (Audino et al., 2014; Beiroz et al., 2017) and Southeast Asia (Boonrotpong et al., 2004; Davis et al., 2001; Hayes et al., 2009; Shahabuddin et al., 2005). These studies were traditionally based on taxonomic information of the community composition. However, the intricate taxonomy and high diversity of DB pose problems because many taxa possess similar external morphological characters, separated only by minute morphological differences, such as *Onthophagus* spp.. In addition, morphological boundaries are sometimes poorly defined in DB taxonomy (Hanski and Krikken, 1991; Philips, 2016). Therefore, it is not clear if inconsistent responses of DB communities to LUC, can be partly attributed to taxonomic resolution, to different phylogenetic trajectories in DB evolution between continents, or to differences in functional responses. For example, Quintero and Roslin (2005) and Vulinec (2002) were unable to detect differences in species richness between primary forests (1^{st}Forests) and secondary forests (2^{nd}Forests) DB communities in South America, whereas, Gardner et al. (2007) reported severely impoverished DB communities in 2^{nd}Forests compared to 1^{st}Forests. Similarly, changes within individual functional groups, such as dung rollers, were inconsistent across biogeographical regions in responses to LUC (Favila and Halffter, 1997; Hayes et al., 2009; Vulinec, 2002).

Trait analyses provide a reliable means to investigate functional changes, as traits directly reflect adaptations to the environment and have consequences for performance and fitness, such as foraging and nesting success, fecundity and survival (McGill et al., 2006). These fitness traits in turn can influence demographic characteristics of populations, such as immigration, emigration, birth and death (Arnold, 1983; Violle et al., 2007). Thus, traits hold information about community structure and functioning, and the niche space occupied by species traits may better predict community responses to anthropogenic disturbances than species diversity (Gagic et al., 2015). Dung beetles exhibit a large variety of morphological traits, strictly associated with their ecosystem functions and adaptations to environmental conditions. For example, the rollers possess elongated hind legs for moving dung balls away from manure patches, and they are restricted to litter free areas because obstacles on the soil surface hinder the rolling process (Nichols et al., 2013; Scholtz et al., 2009). The tunnelers bear relatively short and thick legs for digging; hence their distribution is stronger dependent on soil texture (Hanski and Cambefort, 2014). Body size and/or mass of DB have been related to habitat disturbance, indicating that large-bodied DB are more vulnerable to habitat change (Larsen et al., 2005; Senior et al., 2013). Wing loading (wing area/ (body length × thorax width)) has been related to flight ability, showing significant intraspecific differences between old-growth and logged forests (Raine et al., 2018). Therefore, approaches focusing DB traits, such as shifts in body size, body mass and wing loading, have gained increasing attention (Frank et al., 2017; Gardner et al., 2007; Larsen et al., 2008; Nichols et al., 2013; Tixier et al., 2015). Such studies hold promise to show more consistent shifts in trait patterns of DB communities in responses to disturbance than taxonomic identity. As different functional groups typically show contrasting responses to habitat change, it is important to separately analyze the responses of individual functional groups (Hayes et al., 2009). Yet, there is still a lack of understanding of whether and how specific morphological traits of specific functional groups of DB differ across gradients of LUC.

Dung beetles have been broadly classified into three functional groups according their feeding and nesting behaviour, as tunnelers, rollers and dwellers. The tunnelers group in SE Asia is species-rich and abundant, and predominantly responsible for dung removal in these tropical ecosystems, representing around 90% of the captured DB species in SE Asia (Boonrotpong et al., 2004; Davis et al., 2001; Hayes et al., 2009). Focusing on the dominant tunnelers, our aim was to evaluate the influence of LUC on the diversity and functional traits of DB in SE Asian tropical ecosystems on limestone. We hypothesized to identify specific community traits associated with LUC and with the ecosystem function “dung removal rate”. Additionally, we hypothesized that comparing community-level attributes (such as species richness, abundance, and evenness of 40-year-old-2ndForests to those of 1stForests) would allow us to better assess the conservation values of these 2ndForests for DB in the tropics.

Materials and methods

Study sites

The study was conducted in the Pu Luong Nature Reserve (NR) (20^{o}21'–20^{o}34'N, 105^{o}02'–105^{o}20'E), Thanhhoa Province, North Central Vietnam, in Cao Son district, on the Pha He–Pha Chien mountain ridge. The NR is a forest ecosystem on limestone of the Cuc Phuong–Pu Luong range (Averyanov et al., 2003) and is influenced by a tropical monsoon climate with an average annual precipitation of 1500 to 1700 mm, with a dry and cool season from November to March and a mean annual temperature of 20–22^{o}C (Nguyen et al., 2000; Sterling et al., 2006). Like most NR in Vietnam, much of the natural forest area within the reserve has experienced strong disturbances, primarily related to clear-cutting for shifting agriculture and to selective logging. As a result, the NR contains a wide variety of land use types: areas of 1stForests, patches of 2ndForests, meadows, plantations or agricultural land. Although a ban on logging and shifting agriculture in natural forests has been imposed since 1991 in Vietnam (Forest Protection and Development Law No. 58-LCT/HĐNN8), anthropogenic LUC, especially around settlements of ethnic minority communities is still ongoing, sometimes expansively and intensive in high mountain areas (Colfer et al., 2012; Tuyet, 2001).

Classes of LUC are including 1stForests, 2ndForests and meadows, and thus reflecting a gradient of land use intensification, were chosen as sampling sites. Individual LUC sites were situated at an elevational range of 780–900 m, and were separated by at least 2 km. Following the forest classification in Vietnam by Thai (1978), the 1stForests were evergreen closed forests on limestone, characterized by a complex vertical structure with five main storeys. The upper storey was dominated by trees of more than 35 m height, mostly belonging to Dipterocarpaceae and Combretaceae. The two dominant, lower storeys encompassed tree species with a height of 15 to 25 m, belonging to the families Lauraceae, Magnoliaceae, Meliaceae, Fagaceae, Sapindaceae, Mimosaceae, Ulmaceae and Annonaceae. The bush storey consisted of small trees and bushes below 8 m, containing species of the Rubiaceae, Acanthaceae and Apocynaceae. The ground vegetation comprised plant families of

Urticaceae, Araceae and Begoniaceae. The 2ndForests were classified as swidden fallow 2ndForests, with trees re-growing on abandoned agricultural land, following forest clearing 40 years ago. The meadow sites had a fallow time of five years, and were vegetated by bushes, grasses and few small trees.

Dung beetle sampling, identification and categorization

Sampling was conducted within a 10-day period from 15th to 25th April 2016, using baited pitfall traps. We set up 15 baited pitfall traps in two parallel transects (100 m distant from each other) at each spatially independent land use type. Traps were placed at intervals of at least 150 m along a transect to minimize trap interference (da Silva and Hernández, 2015). In total, 45 traps were set up in the study. Each pitfall trap consisted of a plastic bucket (22 cm in diameter, 16 cm depth) buried to its rim in the soil, filled with 70% ethanol, and baited with 300 grams of a fresh pig: buffalo dung (50: 50 ratio) mixture in order to collect a wide variety of DB species. All captured beetles were removed from the traps after 72 hours of trap exposure and preserved in ethanol until examination in the laboratory.

DB species were identified according to the keys and species lists of Bui et al. (2018), Bui and Bonkowski (2018), Kabakov and Napolov (1999), and by comparison with reference collections at the French National Museum of Natural History (MNHN) (Paris, France), the National Museum Prague (NMPC) (Prague, Czech Republic), the Naturalis Biodiversity Center (RMNH) (Leiden, the Netherlands) and the private collection of Dr. Jan Krikken (Leiden, the Netherlands). Reference collections containing the species from this study are now kept in the Naturalis Biodiversity Center (RMNH) (the Netherlands), the Zoological collection of the Institute of Zoology, the University of Cologne (UoC) (Cologne, Germany) and the Vietnam National University of Forestry (VNUF) (Hanoi, Vietnam).

The tunnelers were defined according to Hanski and Cambefort (2014), Scholtz et al. (2009) and Hayes et al. (2009). Morphological traits were measured mostly based on calibrated photographs taken using a digital microscope (Keyence VHX-500F). Only the body length of one large-bodied species, *Synapsis tridens* Sharp 1881 was measured by a digital caliper. The following morphometric traits were measured: BoL – body length;; HeadL – head length; HeadW – head width; ProL – pronotum length; ProW – pronotum width; ElyL – elytra length; ElyW – elytra width; MesoTiL – mesotibia length; MesoTiW – mesotibia width; MetaTiL – metatibia length; MetaTiW – metatibia width; MetaTaL – metatarsus length. Dry biomass (BioM) of DB was determined after drying at 65°C for 48 hours. The BioM and morphological traits of each species were determined as mean values of 10–20 individuals of abundant species and by measuring all individuals of rare species. We used nine response trait variables obtained from the measured morphological traits for statistical analyses, comprising body length (BoL), head length-width ratio (Head L/W), pronotal length-width ratio (Pro. L/W), elytral length-width ratio (Ely. L/W), mesotibial length-width ratio (MesoTi. L/W), metatibial length-width ratio (MetaTi. L/W), distance from the elytral widest part to elytral posterior apex in relation to elytral length (Dis.(Ely.W–Ely.apex)/ElyL), metatarsal length-elytral length ratio (MetaTaL/ElyL) and biomass (BioM). See Table S1, S2 and Figures S3-S6 for species and trait data of beetles.

Environmental variables

Environmental data were measured and soil samples collected concurrently with dung beetle sampling. We used the quadrant-section method modified from Brower and Zar (1998) and Campos and Hernández (2013) to measure environmental variables at each research site. With the trap in the center, a cross was generated to divide each sampling site into four quadrants. In each quadrant, the nearest shrubs (DBH < 6 cm and height >1 m) to the center point were marked, and their traits measured (crown diameter, height, distance to center point). Additionally, a small plot of 1x1 m in each quadrant was used to measure leaf litter thickness, percentage of leaf litter cover and area of ground vegetation using six ranks: 0–5%, 6–25%, 26–50%, 51–75%, 76–95% and 96–100%. Four soil samples were collected in each quadrant near the trap, mixed, and transferred to the lab to measure soil texture.

Dung removal rate

Dung removal plots were located at the trapping sites, and were set up with six plots for each land use type. In each plot, two plastic plates, each containing 300 g fresh cow dung were placed on the soil surface, one was covered with a net (mesh size of 25 x 25 mm) to prevent access of small vertebrates, the other was covered with a net (mesh size of 1.2 mm) to prevent access of DB, as control. After 72 hours of dung exposure, the remaining dung of both plates was weighted to calculate the dung removal rate. The quantification of the dung removal rate was performed 15 days before DB sampling to avoid changes in the structure of DB communities related to trapping. The sampling time did not coincide with the activity period of flesh flies in the area study (i.e., from June to July) to ensure that dung removal was due to DB and changes in moisture only.

Data analysis

Statistical analyses were carried out in R software v. 3.4.0 (R Core Team, 2014). Species accumulation curves were used to assess the completeness of dung-beetle sampling across three land uses. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities from a species relative abundance matrix was used to characterize the structure of DB communities inhabiting land use types. Although some of the pitfall traps were lost during the sampling period, total trapping effort for each land use type was approximately equal (14 traps in 1stForests and 13 traps each in meadows and 2ndForests), and in addition all species accumulation curves for three land uses appear to reach asymptotes (Fig. S 1). Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences among DB communities. All tests and ordination plots were performed using the vegan package v. 2.4–5 (Oksanen et al., 2015), and each computed test was based on 999 permutations. To get insights into environment-community pattern relations, we fitted environmental factors onto NMDS ordinations using the envfit function in the vegan package, goodness of fit and *p*-value were permuted 999 times. In addition, species richness, evenness and abundance were fitted to NMDS ordinations to test whether these individual variables were associated with community patterns. To compare species richness and abundance on meadow and forest sites we performed generalized linear models (GLM) using Poisson distribution.

Co-inertia (RLQ) analysis (Dolédec et al., 1996) was used to characterize the relationship between environmental variables (R), species abundance (L), and trait values for each species (Q). A cluster analysis was computed based on the species scores of the two first RLQ axes and the Calinsky-Harabasz criterion. The relationship between multiple morphological traits and multiple environmental variables was assessed using a combination of the RLQ and the fourth-corner method according to Dray et al. (2014). The fourth-corner method was computed to directly test the links between RLQ axes and trait variables and environmental variables using the fourthcorner.rlq function in the ade4 package (Dray et al., 2014). This method has been used for multi-group communities or whole invertebrate communities (Braaker et al., 2017; de Castro et al., 2018; Ding et al., 2017; Kuzmanovic et al., 2017; Luiza-Andrade et al., 2017; Mocq and Hare, 2018; Murphy et al., 2017; Ossola et al., 2015). Here we applied this method to test for relationships between community morphological traits of a single group of DB (i.e. the tunnelers group) and environmental variables.

We used the Rao's index of quadratic entropy (Zoltán, 2005) to examine the effect of LUC on functional diversity, because this index was independent of species richness (Mouchet et al., 2010). The Rao's index was computed from a species-by-traits matrix using the dbFD function in the "FD" package (Laliberté et al., 2014). GLM was performed using Gaussian distribution to test the effect of LUC on functional diversity.

Traits were used in statistical analyses (RLQ and fourth-corner methods, the Rao's index) comprising BoL, Head L/W, Pro. L/W, Ely. L/W, MesoTi. L/W, MetaTi. L/W, Dis.(Ely.W–Ely.apex)/ElyL, MetaTaL/ElyL and BioM.

Results

Community structure of the tunnelers along the land use gradient

In total 1417 beetles of 41 tunneling DB species were recorded, 30 species were found in meadows while 18 and 20 species were collected in 2ndForests and 1stForests, respectively (Table S1). The community structure of tunnelers differed significantly between LUC (PERMANOVA, F=27.13, R^2=0.59453, p<0.001), clearly separating meadow communities from forest communities (Fig. 1). Although there was high overlap in Bray-Curtis diversity between the 1stForests and 2ndForests, DB communities statistically differed between these two forest types (PERMANOVA, F=3.46, R^2=0.12161, p=0.005). Fitting environmental vectors to the NMDS plot demonstrated that cover of ground vegetation (GV) (R^2 = 0.78, p<0.001), distance to shrubs (Dst) (R^2= 0.27, p=0.004) and soil clay content (Clay) (R^2=0.17, p=0.031) significantly correlated with the community structure of tunneling DB, while shrub height (SH) and crown diameter of shrubs (Sdia) had no influence.

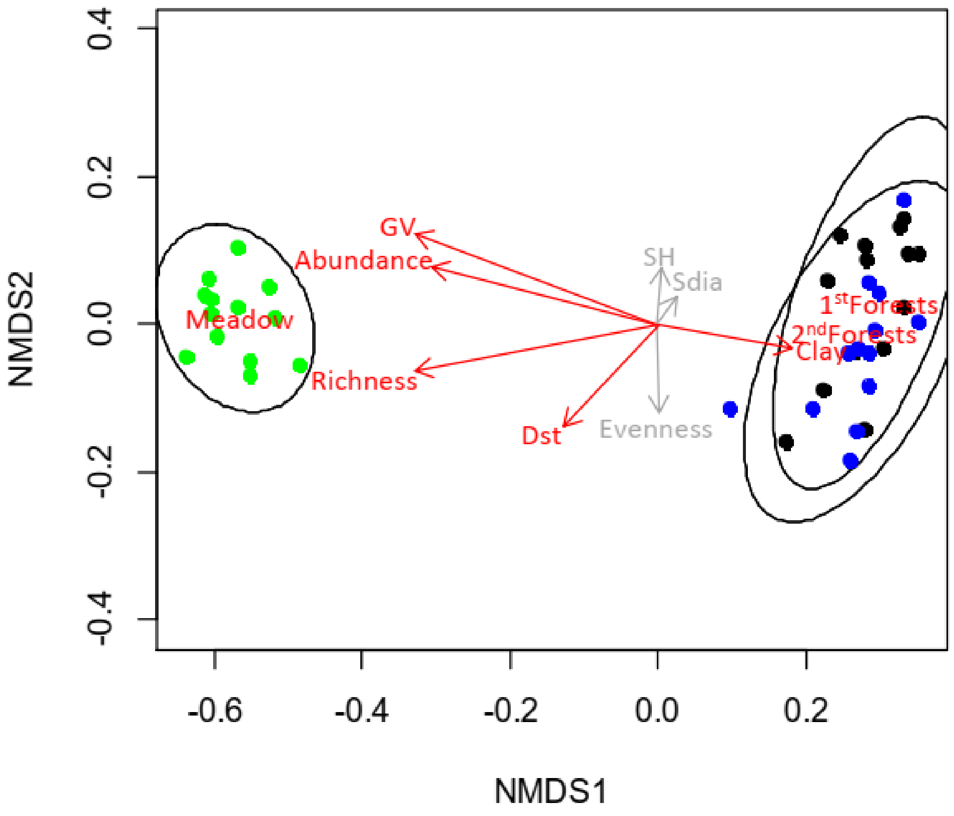

Fig. 1 NMDS ordination showing differences of the dung beetle communities between meadows and forests (stress value: 0.06). The fitted vectors of environmental variables and community attributes (species richness, evenness and abundance) are displayed for significant ($p<0.05$, red arrows) and non-significant (grey arrows) variables. Meadows (green), secondary forests (blue), primary forests (black), cover of ground vegetation (GV), distance to shrubs (Dst), crown diameter of shrub (Sdia), shrub height (SH) and soil clay content (Clay).

The generalized linear models (GLM) for abundance and species richness showed significant differences between meadows and forests (Table 1), with abundance and species richness (per trap) being more than 3.2-fold and 2-fold higher, respectively, in meadows compared to forests. Also GLM for functional diversity (Rao's quadratic entropy) revealed significant differences between meadows and forests. However, there was no difference in species richness and functional diversity between 2ndForests and 1stForests, despite abundance differing between these forest types (Table 2).

Table 1. GLM for species richness, abundance and Rao's quadratic entropy between meadows and forests. Estimates (β), standard errors (SE), test statistics (z, t-value) and *p*-values are presented.

	β	±SE	z-value	*p*-value
Abundance	1.40609	0.05619	25.02	**0.0000**
Species richness	0.78989	0.10360	7.624	**0.0000**

	β	±SE	t-value	*p*-value
Functional diversity	-3.0398	0.7171	-4.239	**0.0001**

Table 2. GLM for species richness, abundance and Rao's quadratic entropy between primary and secondary forests. Estimates (β), standard errors (SE), test statistics (z, t-value) and *p*-values are presented.

	β	±SE	z-value	*p*-value
Abundance	0.39482	0.09266	4.261	**0.0000**
Species richness	0.08516	0.14866	0.573	0.567

	β	±SE	t-value	*p*-value
Functional diversity	-1.3179	0.9523	-1.384	0.179

Trait-Environment relationships

RLQ analysis revealed that the groups of land use types including 1stForests and 2ndForests and environmental variables including leaf litter thickness (LLT) and soil clay content (Clay) could be linked to the morphological traits representing biomass (BioM), body length (BoL) and elytral aspect ratio (i.e. elytral length-width ratio (Ely. L/W)). Meadows and cover of ground vegetation (GV) correlated with pronotal aspect ratio (i.e. pronotal length-width ratio (Pro. L/W)), metatarsus relative to elytral length (i.e. metatarsal-elytral length ratio (MetaTa/ElyL)), the position of the elytral widest part (i.e. distance from the elytral widest part to elytral posterior apex-elytral length ratio (Dist.(Ely.W - Ely.apex)/ElyL)), robustness of mesotibia (i.e. mesotibial length-width ratio (MesoTi. L/W)) and robustness of metatibia (i.e. metatibial length-width ratio (MetaTi. L/W)).

Head shape (i.e. head length-width ratio (Head L/W)) could be related to distance to shrubs (Dst). The two environmental variables, shrub height (SH) and crown diameter of shrub (Sdia), did not correlate with morphological traits (Fig. 2).

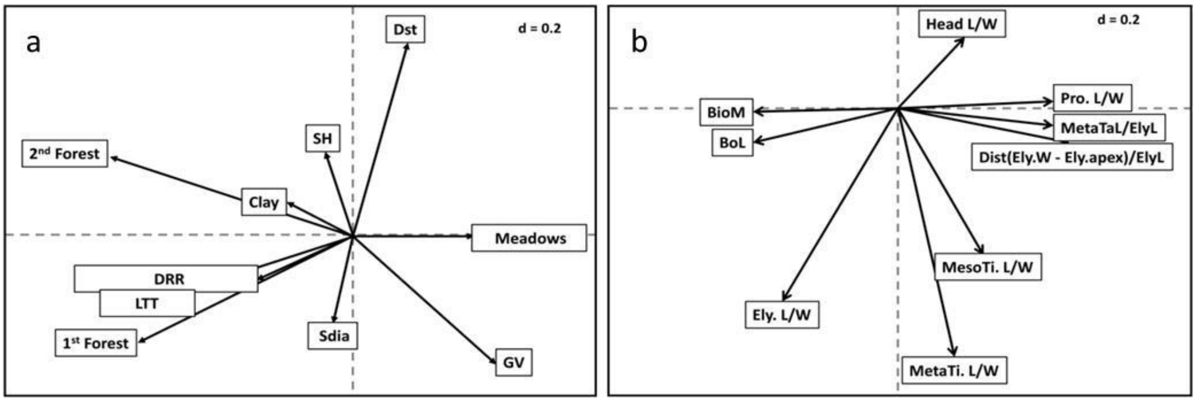

Fig. 2 Ordination of environmental variables (a) and morphological traits (b) in RLQ. Environmental variables: primary forests (1stForests), secondary forests (2ndForests), leaf litter thickness (LLT), dung removal rate (DRR), shrub height (SH), distance to shrubs (Dst), ground vegetation cover (GV), crown diameter of shrubs (Sdia). Morphological traits: biomass (BioM), body length (BoL), elytral length-width ratio (Ely. L/W), metatibial length-width ratio (MetaTi. L/W), mesotibial length-width ratio (MesoTi. L/W), distance from the elytral widest part to elytral posterior apex in relation to elytral length (Dis.(Ely.W–Ely.apex)/ElyL), metatarsal length-elytral length ratio (MetaTaL/ElyL), pronotal length-width ratio (Pro. L/W) and head length-width ratio (Head L/W).

The first axis of RLQ separated meadow and forest communities and was positively associated with cover of ground vegetation (GV), pronotal length-width ratio (Pro. L/W), metatarsal-elytral length ratio (MetaTaL/ElyL), and distance from the elytral widest part to elytral posterior apex in relation to elytral length (Dist(Ely.W - Ely.apex)/ElyL) (Table 3). Two environmental variables: leaf litter thickness (LLT) and soil clay content (Clay), and three morphological traits: biomass (BioM), body length (BoL) and elytral length-width ratio (Ely. L/W) together with the ecosystem function “dung removal rate (DRR)”, were negatively associated with the first axis. The second axis showed no correlation with any environmental variables or traits (Table 3).

Table 3. P-values of fourth-corner analyses between the two first RLQ axes and environmental variables and traits. Bold p-values indicate significantly positive or negative (with minus) associations (see Fig. 2 for variable names).

Variable	Axis 1	Axis 2
Environmental factors		
Forest.1	0.527	0.079
Forest.2	0.412	0.069
Meadows	**0.023**	1
DRR	**-0.002**	0.873
GV	**0.001**	0.857
LLT	**-0.001**	0.914
Dst	0.051	0.472
SH	0.345	0.618
Sdia	0.525	0.62
Clay	**-0.007**	0.934
Community traits		
BioM	**-0.001**	0.941
BoL	**-0.001**	0.892
Dist(Ely.W - Ely. apex)/ElyL	**0.001**	0.969
Ely. L/W	**-0.001**	0.505
Head L/W	0.175	0.815
MesoTi. L/W	0.06	0.516
MetaTaL/ElyL	**0.001**	0.997
MetaTi. L/W	0.215	0.375
Pro. L/W	**0.001**	0.989

Cluster analysis and morphological groups

The cluster analysis identified three distinct trait clusters containing 3 to 31 out of the 41 species for which morphological traits were defined (Figs. 3, 4 and S 2). Trait cluster A comprised seven species of large body size and biomass (large BoL and BioM), with broad pronotum (small Pro. L/W), elongated elytra (great Ely. L/W and small Dist (Ely.W - Ely.apex/ElyL)) and short metatarsi (very small MetaTaL/ElyL), being rare in meadows. Dung beetles representing trait cluster B had slender mesotibia and metatibia (i.e. great MesoTi. L/W and MetaTi.L/W), an elongated pronotum (i.e. large Pro. L/W), the elytral widest part in the front (i.e. large Dist (Ely.W - Ely.apex/ElyL) and small body size and biomass, occurring mainly in meadows. Dung beetles of trait cluster C comprised 31 species of small body size and biomass, nearly semicircular elytra (i.e. small Ely. L/W and large Dist (Ely.W - Ely.apex/ElyL)) and long metatarsi (i.e. large MetaTaL/ElyL), dominating in meadows with a high cover of ground vegetation.

Among the morphological traits that correlated with the RLQ axes, BioM, BoL and Ely.L/W peaked in trait cluster A, while Dist(Ely.W - Ely.apex)/ElyL and Pro. L/W peaked in trait cluster B, and MetaTaL/ElyL peaked in trait cluster C. Head aspect ratio (Head L/W) did not differ significantly among trait clusters. Head aspect ratio together with MesoTi. L/W and MetaTi. L/W remained unchanged across the LUC gradient.

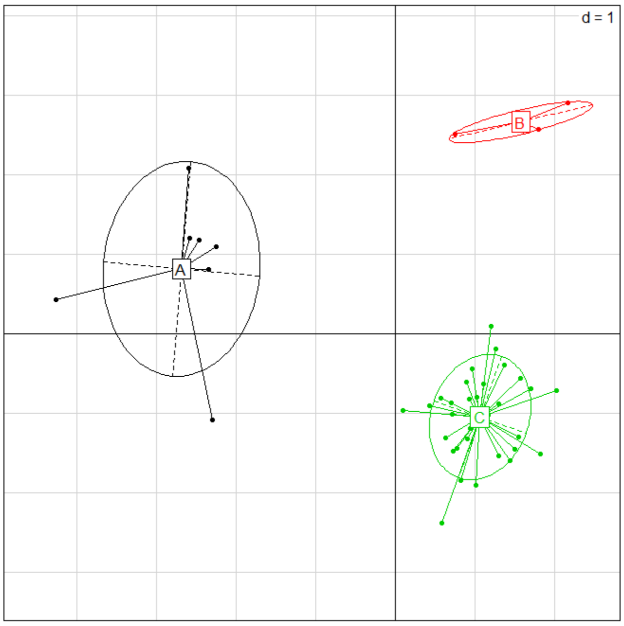

Fig. 3 Three distinct functional trait groups of dung beetles defined from cluster analysis: cluster A (seven species), cluster B (three species) and cluster C (31 species)

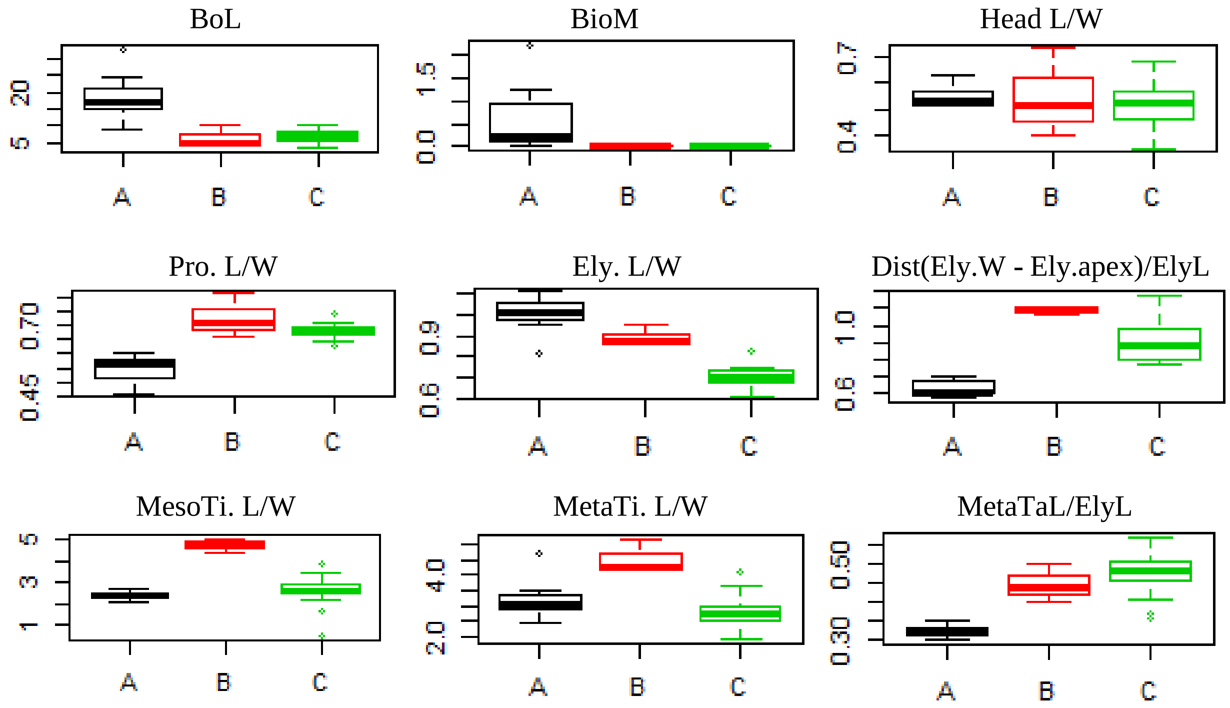

Fig. 4 Box plots showing quantitative morphological traits of three distinct trait clusters A, B and C of tunneling dung beetles.

Discussion

Differences in DB communities between forests and grasslands have been previously confirmed (Braga et al., 2013; Frank et al., 2017; Negro et al., 2011; Numa et al., 2009). However, these studies did not take functional aspects of species morphological traits into account. Our data show that the conversion of forests to meadows has resulted in significant shifts of morphological traits of SE Asian tunneling DB, as well as dung removal rate, being one of the most important ecosystem functions.

In contrast to Numa et al. (2009) and Braga et al. (2013), our results show an increase of tunneling DB species in meadows as a result of an increasing number of small-bodied DB. These tunneling DB were dominated by *Onthophagus* spp., accounting nearly 50% and 70% of the total recorded individuals and species, respectively in Puluong. This is a typical structure for SE Asian DB (Davis et al., 2001; Hayes et al., 2009; Shahabuddin et al., 2005) but never observed in Europe and South America (Braga et al., 2013; Campos and Hernández, 2013; Campos and Hernández, 2015; Costa et al., 2017; Frank et al., 2017; Harvey et al., 2006). In agreement with Frank et al. (2017), most *Onthophagus* spp., together with the abundant genus *Liatongus* were exclusively found in meadows, leading to the overall high abundance and species richness of tunneling DB in meadows compared to forests in Puluong. According to our results, it seems likely that the similarity of specific morphological traits between *Onthophagus* spp. and *Liatongus* spp. reflects convergent adaptations to the environmental conditions in meadows. Given that the morphological traits of DB will influence their contribution to ecosystem functions and services (Raine et al., 2018; Slade et al., 2007), it is important to identify the specific morphological traits of DB communities associated with LUC. We found significant changes in specific traits associated with dispersal and perching capacity of DB across land use types, reflected by an increase of tunneling DB species of small body length and biomass, nearly semicircular elytra and long metatarsi in meadows, and a severe decrease of large-bodied DB in this habitat. Morphological traits of DB in forests likely reflect adaptations to the thickness of the leaf litter layer and of increasing soil clay content by increased DB biomass, associated with an elongation of the body (BoL) and an increase of elytral length relative to width (Ely. L/W). In particular the ecosystem function “dung removal rate” appeared to be strongly associated with pronotal aspect ratio (i.e. pronotal length-width ratio), but it was not associated with the robustness of the mesotibia and metatibia (i.e. mesotibial length-width ratio and metatibial length-width ratio).

The meadow sampling sites in the current study, unlike those documented in Braga et al. (2013), are located in a protected area. Hence, the tunneling DB communities were not affected by grassland management, such as manure or pesticide applications and mechanical disturbances like the removal of herbs and mowing, that could reduce DB numbers and diversity (Braga et al., 2013; Harvey et al., 2006; Hutton and Giller, 2003). A high cover of ground vegetation in meadows offers a wide outlook over dung resources for small DB (body length<10 mm) that typically perch on the leaves of the ground vegetation to locate food resources (Howden and Nealis, 1978; Larsen et al., 2008; Peck and Forsyth, 1982). Accordingly, it seems likely that the convergence of small body sized and/or biomass, together with elongated metatarsi for climbing and nearly semicircular elytra reflect those morphological traits that confer a competitive advantage for DB to locate food from perches in the vegetation. Given that wingless DB in South Africa possess a more rounded body than equivalent-sized and winged species, as indicated in Chown et al. (1998), the nearly semicircular elytra of SE Asian DB could also reflect DB species of poor dispersal. Large-bodied DB in contrast cover much larger territories, because they tend to fly rather than perch to forage for food. Hence, large DB are not strictly dependent on ground vegetation. A higher sun exposure in meadows due to decreased canopy cover may be even detrimental to large-bodied DB, as their bodies could heat up within the hot weather period (i.e. from May to July) above the maximum tolerated temperature of 42°C (Verdú et al., 2006). Additionally, large-bodied DB are constrained to utilize the dung of large herbivores due to larger food requirements for their brood masses during the breeding season (Hanski and Cambefort, 2014). However, large herbivores are relatively rare on the non-managed meadows of Puluong NR. The scarcity of mammalian dung resources, and their temporal restricted availability due to fast drying up of the sun-exposed resources many further reduce the competitiveness of large-bodied DB. Small-bodied DB species are less dependent on large mammalian dung patches by using dung resources from small animals such as lizards and rodents in meadows (Howden and Nealis, 1978). Additionally, small-bodied DB find more easily shelter from the sun heat in meadows than large DB.

The advantage of small body size in meadows may turn into a disadvantage in the shades of forests at an altitudinal range of 800 – 1000 m where the lower ambient temperature for flight may limit the dispersal of small-bodied DB (Verdú et al., 2006). Beiroz et al. (2017) recently identified soil texture as one of the most important environmental variables for the spatial separation of DB communities in lowland tropical rainforests in the Brazilian Amazon. The positive correlation between clay content of soil and body length and biomass of DB in Puluong may indicate that soil penetration resistance, characterized by high clay content, favors larger over smaller tunneling DB during the nesting process (Table 3). A leaf litter layer is a typical physical barrier on the forest floor that hinders the dung removal process of DB (da Silva and Hernández, 2016; Nichols et al., 2013). A thick leaf litter layer in forests may exert a high resistance to dung burial for small-bodied DB species (da Silva and Hernández, 2015), but not for large DB who are favored in addition by the higher availability of mammalian dung resources.

Consistent with Nervo et al. (2014), Tixier et al. (2015) and Frank et al. (2017), our results confirmed positive correlations of the body length and body mass of tunneling DB communities with dung removal rate, even though the abundance of tunneling DB showed no correlation with dung removal rate in the current study. Thus, the size rather than the overall abundance of tunneling DB turned out to be a key morphological trait maintaining the ecosystem service of dung removal. Dung removal rate positively correlated with pronotal aspect ratio and elytral aspect ratio, while mesotibial length-width ratio, metatibial length-width ratio and head aspect ratio did not correlate with this ecosystem function. These results are best explained by the fact that the tunneling DB typically push dung balls from dung piles to their nesting sites in which the pronotal aspect ratio rather than head shape and the robustness of mesotibia and metatibia play a predominant role in the dung removal process. Tunneling DB species possessing a broader pronotum (i.e. small pronotal L/W ratio) can collect a larger amount of dung, hence have a competitive advantage over those species with a relatively longer pronotum (i.e. large pronotal L/W ratio). In the limestone karst ecosystems where unevenly distributed and scare dung resources are common, elytral aspect ratio being associated with the dispersal capacity of DB appears crucial. The DB species with high dispersal capacity, characterized by elongated elytra (i.e. large elytral L/W ratio), may be favored in locating and occupying food resources. In addition to pronotal aspect ratio and elytral aspect ratio, other morphological traits of pronotum and elytra, such as pronotal prominences, anterior declivity and excavation, or wing loading are also expected to affect the dung removal rate under LUC, requiring further studies.

Conclusion

Anthropogenic land use change profoundly affected the community structure, taxonomic diversity, functional diversity and functional morphological traits of tunneling dung beetle communities of tropical karst ecosystems in Vietnam. We characterized three distinct morphological trait clusters adapted to the altered environmental conditions. Tropical limestone meadows were severely impoverished by large tunneling DB species, although this land use type contained a higher abundance and more species-rich dung beetle communities compared to forest habitats. Because body size and body mass rather than abundance determined dung removal rate, the conversion from forests to meadows may result in a reduction in the functioning of tunneling dung beetles providing this key ecosystem service. The cover of ground vegetation in meadows appeared crucial for small-bodied dung beetles who typically employ a leaf-perching strategy in search of food. Therefore, the maintenance of ground vegetation in meadows appears important to maintain functional diversity of dung beetles. The secondary forests, after 40 years of regrowth showed similarities in species richness and functional diversity (Rao’s quadratic entropy) of tunnellers to 1stForests. This gives hope for the recovery of tunneling dung-beetle communities during forest succession.

Despite this, irreversible changes in the community composition (NMDS analyses) following forest clearing can lead to unpredictable changes in ecosystem services that need to be further studied.

The successful combination of RLQ and fourth-corner methods provides a new means to identify shifts in morphological species traits in response to land use change in South East Asian tropical ecosystems. In agreement with previous studies, we confirmed changes in body size and body mass of dung beetles in responses to land use changes, but in addition, we identified a number of new and potentially important functional traits, such as elytral aspect ratio and the length of metatarsi in tunneling dung beetle communities. Our results support recent calls for the increased use of trait-based approaches to assess the influence of land use change on invertebrate communities.

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Supplementary Information

Figure S1. Species accumulation curves of dung beetle communities in three land use types (primary forests: Forest.1; secondary forests: Forest.2; meadows: Meadow) in Puluong Nature Reserve.

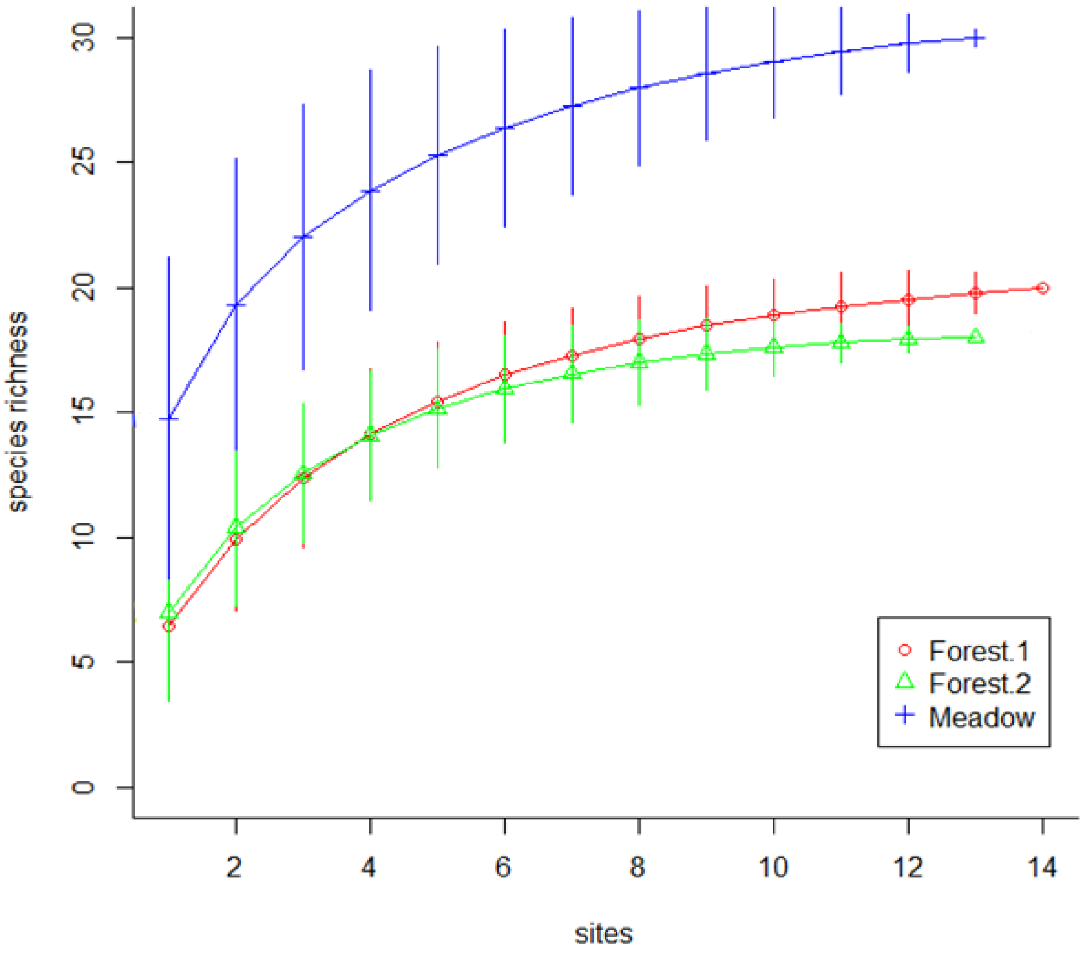

Figure S2. Three functional trait groups defined from cluster analysis: Group A (seven species), group B (three species) and group C (31 species); (see Table S1 for species names).

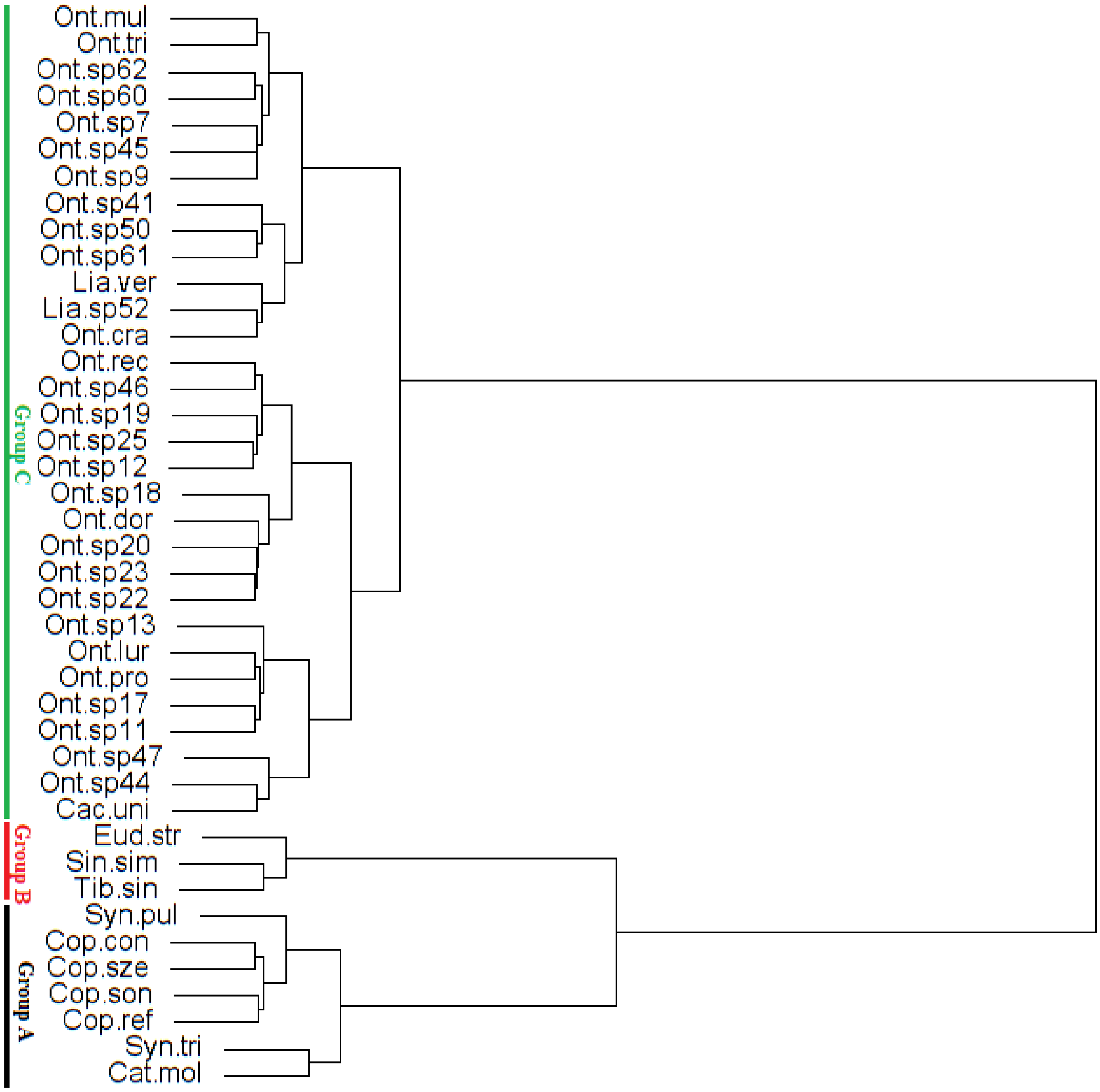

Figure S3. Species in trait group A: 1-*Catharsius molossus*, 2-*Synapsis tridens*, 3-*Copris reflexus*, 4-*Copris confucius*, 5-*Copris szechouanicus*, 6-*Copris sonensis*, 7-*Synapsis puluongensis*.

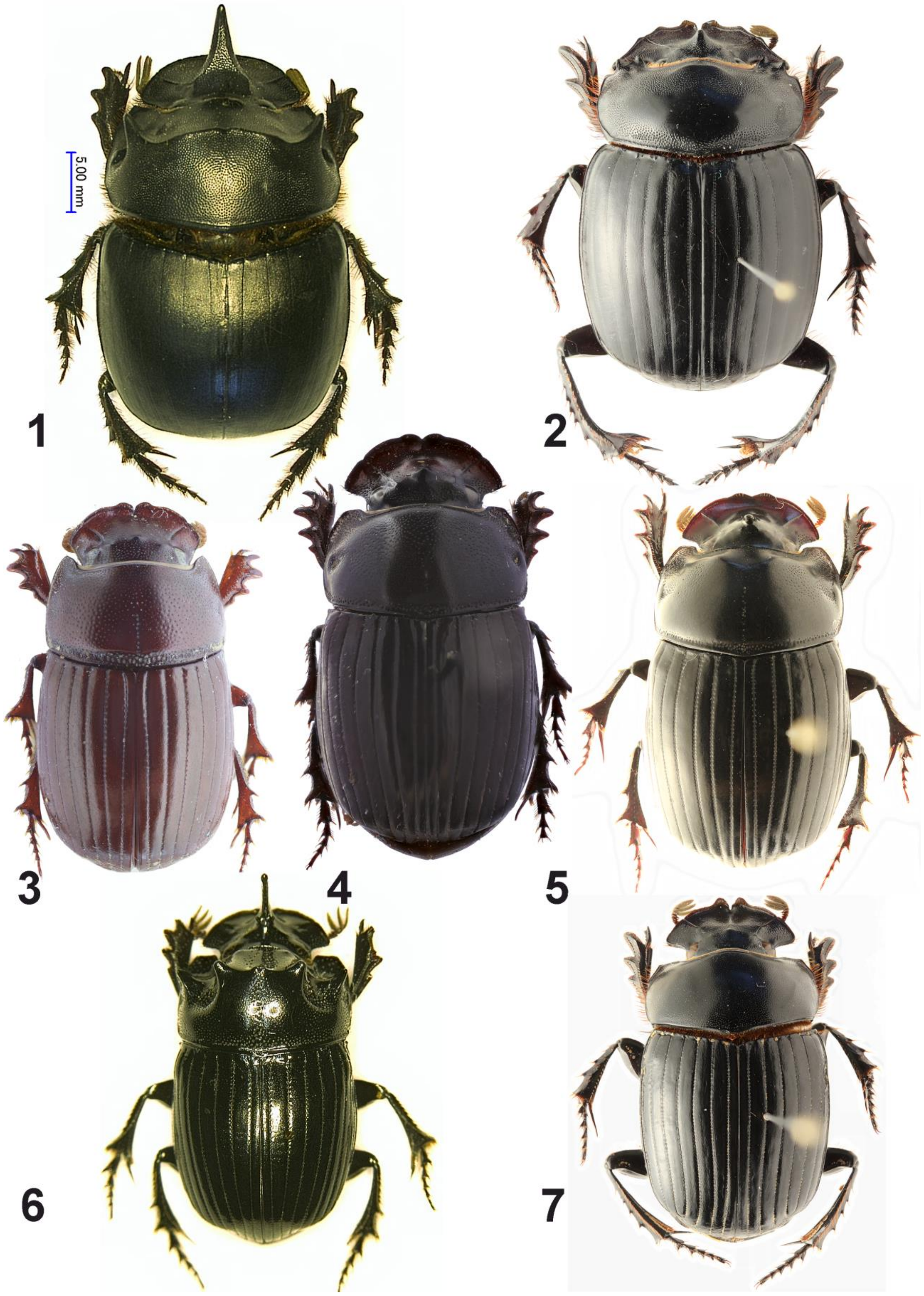

Figure S4. Species in trait group B: 1-*Tibiodrepanus sinicus*, 2-*Sinodrepanus similis*, 3-*Eodrepanus striatulus*

Figure S5. Dominant species in trait group C: 1-*Onthophagus dorsofasciatus*, 2-*O. sycophanta*, 3-*O. proletarius*, 4-*O. trituber*, 5-*O. cognatus*, 6-*O. luridipennis,* 7-*Caccobius unicornis,* 8-*O. crassicollis*, 9-*Liatongus vertagus*

Figure S6. Measurements of morphological traits used in the study

(1) BoL	Body length measured from clypeal apex to elytral posterior apex
(2a) HeadL	Head length measured from the middle of anterior clypeal margin to posterior margin of head
(2b) HeadW	Maximum head width
(3a) ProL	Maximum pronotum length
(3b) ProW	Maximum pronotum width
(4a) ElyL	Elytral suture
(4b) ElyW	Maximum elytra width
(5) Dist Ely.W-Ely.apex)	Distance from the elytral widest part to elytral posterior apex
(6a) MesoTiL	Mesotibia length
(6b) MesoTiW	Maximum mesotibia width
(7a) MetaTiL	Metatibia length
(7b) MetaTiW	Maximum metatibia width
(8) MetaTaL	Metatarsus length

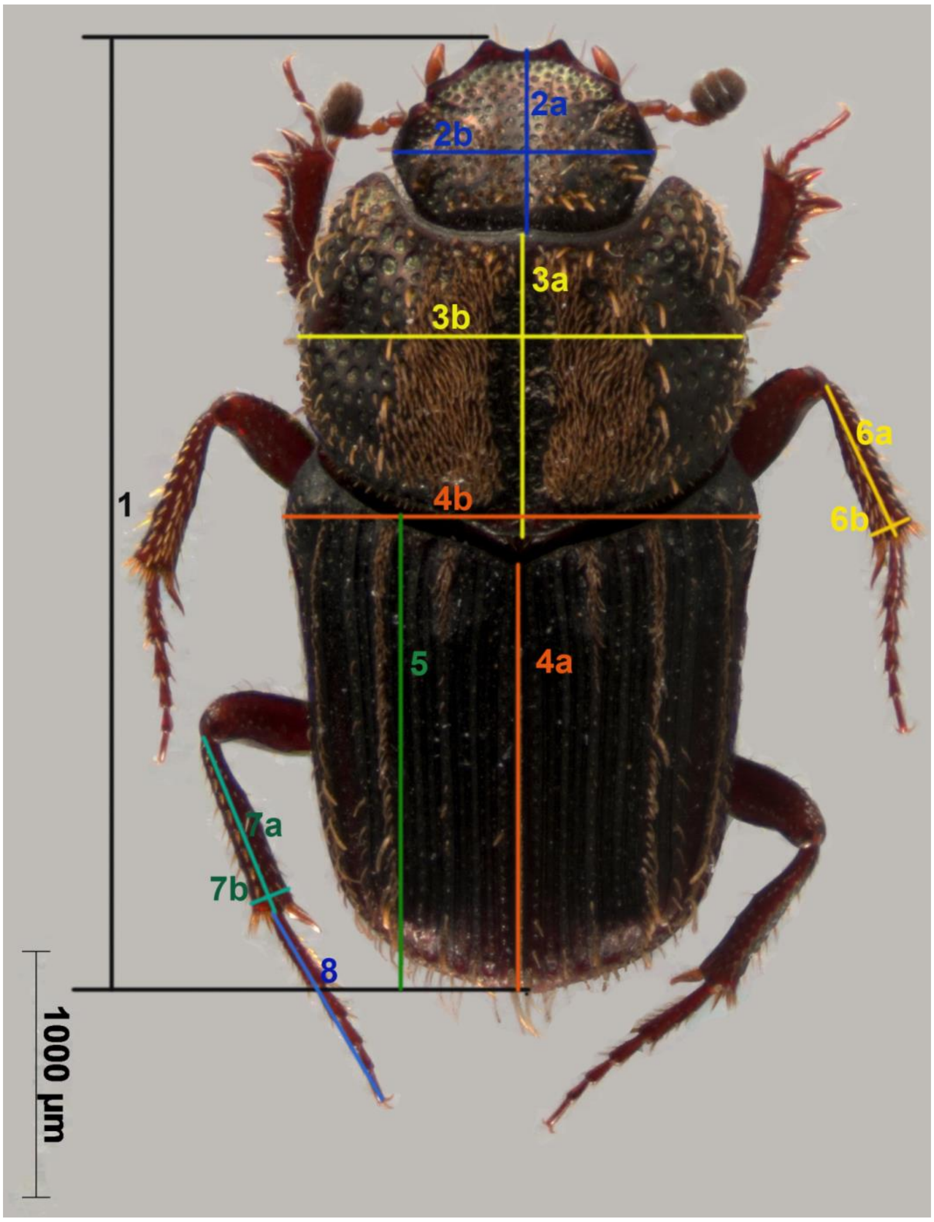
1
2a
2b
3a
3b
4a
4b
5
6a
6b
7a
7b
8
1000 µm

Table S1. Total numbers of tunneling dung beetle species in three land use types (Meadows, 2nd Forests, 1ry Forests) in Puluong Nature Reserve.

Code	Species	Meadows (13 sites)	2ndForests (13 sites)	1ryForests (14 sites)
Cac.uni	*Caccobius unicornis* (Fabricius)	15	0	0
Cat.mol	*Catharsius molossus* (Linnaeus)	5	17	4
Cop.con	*Copris confucius* Harold	5	4	15
Cop.ref	*Copris reflexus* Fabricius	27	65	11
Cop.son	*Copris sonensis* Bui, Dumack & Bonkowski	0	9	3
Cop.sze	*Copris szechouanicus* Balthasar	26	115	93
Eud.str	*Eodrepanus striatulus* Paulian	47	0	1
Lia.sp52	*Liatongus* sp. 01	6	0	0
Lia.ver	*Liatongus vertagus* (Fabricius)	211	0	0
Ont.sp7	*Onthophagus aloysiellus* Zunino	12	0	0
Ont.mul	*Onthophagus cognatus* Lansberge	0	0	6
Ont.cra	*Onthophagus crassicollis* Boucomont	30	0	0
Ont.dor	*Onthophagus dorsofasciatus* Fairmaire	105	4	1
Ont.sp22	*Onthophagus gracilipes* Boucomont	0	0	4
Ont.lur	*Onthophagus luridipennis* Boheman	200	0	0
Ont.sp9	*Onthophagus papulatus* Boucomont	2	0	0
Ont.sp23	*Onthophagus phanaeiformis* Boucomont	0	4	3
Ont.pro	*Onthophagus proletarius* Harold	16	0	0
Ont.rec	*Onthophagus rectecornutus* Lansberge	10	0	0
Ont.sp61	*Onthophagus saigonensis* Boucomont	3	0	0
Ont.sp11	*Onthophagus* sp.01	24	0	0
Ont.sp45	*Onthophagus* sp.02	0	6	3
Ont.sp19	*Onthophagus* sp.03	0	10	2
Ont.sp25	*Onthophagus* sp.04	2	0	0
Ont.sp46	*Onthophagus* sp.05	7	0	0
Ont.sp50	*Onthophagus* sp.06	1	2	0
Ont.sp20	*Onthophagus* sp.07	2	5	11
Ont.sp18	*Onthophagus* sp.08	0	6	2
Ont.sp60	*Onthophagus* sp.09	5	0	0
Ont.sp47	*Onthophagus* sp.10	5	0	0
Ont.sp62	*Onthophagus* sp.11	2	0	0
Ont.sp12	*Onthophagus* sp.12	1	1	1
Ont.sp17	*Onthophagus sycophanta* Fairmaire	55	0	0
Ont.sp44	*Onthophagus taurinus* White	57	3	6
Ont.sp41	*Onthophagus thanwaakhomus* Masumoto	0	2	0
Ont.tri	*Onthophagus trituber* (Wiedemann)	1	18	13
Ont.sp13	*Onthophagus vaulogeri* Boucomont	46	0	0
Sin.sim	*Sinodrepanus similis* Simonis	0	3	11

Syn.pul	*Synapsis puluongensis* Bui & Bonkowski	0	0	6
Syn.tri	*Synapsis tridens* Sharp	0	3	5
Tib.sin	*Tibiodrepanus sinicus* (Harold)	11	0	0

Table S2 Morphological traits of all dung beetle species recorded in Puluong Nature Reserve: BoL – body length (mm); BioM – biomass (g dry weight); HeadL/W – head length /width ratio; Pro.L/W – pronotum length/width ratio; ElyL/W – elytra length/width ratio; Dist.(Ely.W - Ely.apex)/Ely.L –distance from the elytral widest part to elytral posterior apex in relation to elytral length; MesoTiL/W – mesotibia length/width ratio; MetaTiL/W – metatibia length/ width ratio; MetaTaL/ElyL – metatarsus length/elytra length ratio

I	BoL (mm)	IV	ProL/W	VII	MesoTiL/W
II	BioM (g)	V	ElyL/W	VIII	MetaTiL/W
III	HeadL/W	VI	Dist.(Ely.W - Ely.apex)/Ely.L	IX	MetaTaL/ElyL

Code	Species	I	II	III	IV	V	VI	VII	VIII	IX
Cac.uni	*Caccobius unicornis* (Fabricius)	3.15	0.00193	0.51	0.69	0.67	0.98	1.7	2.35	0.41
Cat.mol	*Catharsius molossus* (Linnaeus)	24.63	1.25129	0.63	0.52	0.81	0.68	2.11	2.74	0.34
Cop.con	*Copris confucius* Harold	15.25	0.14555	0.55	0.56	1.03	0.58	2.45	3.5	0.32
Cop.ref	*Copris reflexus* Fabricius	9.1	0.0315	0.53	0.57	1.11	0.67	2.22	3.04	0.33
Cop.son	*Copris sonensis* Bui, Dumack & Bonkowski	14.31	0.11961	0.51	0.6	1.01	0.61	2.4	3.02	0.31
Cop.sze	*Copris szechouanicus* Balthasar	17.33	0.22057	0.58	0.58	1.09	0.61	2.34	3.26	0.32
Eud.str	*Eodrepanus striatulus* Paulian	3.99	0.00306	0.51	0.66	0.95	1.09	4.4	4.25	0.4
Lia.sp52	*Liatongus* sp. 01	6.97	0.00345	0.56	0.71	0.83	1.11	2.48	2.76	0.51
Lia.ver	*Liatongus vertagus* (Fabricius)	9.41	0.00912	0.55	0.74	0.71	1.18	2.48	3.05	0.5
Ont.sp7	*Onthophagus aloysiellus* Zunino	4.85	0.00378	0.48	0.67	0.72	0.92	3.04	3.1	0.46
Ont.mul	*Onthophagus cognatus* Lansberge	9.92	0.03767	0.59	0.68	0.7	0.89	2.9	2.75	0.48
Ont.cra	*Onthophagus crassicollis* Boucomont	6.22	0.00639	0.5	0.68	0.67	0.94	2.91	3.3	0.53
Ont.dor	*Onthophagus dorsofasciatus* Fairmaire	8.92	0.01603	0.57	0.69	0.75	0.9	3.03	2.63	0.36
Ont.sp22	*Onthophagus gracilipes* Boucomont	7.93	0.01158	0.43	0.64	0.74	0.97	2.62	2.72	0.47
Ont.lur	*Onthophagus luridipennis* Boheman	6.33	0.00685	0.56	0.67	0.61	1	2.25	2.67	0.47
Ont.sp9	*Onthophagus papulatus* Boucomont	5.22	0.00635	0.54	0.67	0.65	0.87	2.48	2.74	0.5
Ont.sp23	*Onthophagus phanaeiformis* Boucomont	7.34	0.01458	0.35	0.65	0.73	0.8	2.78	2.87	0.51
Ont.pro	*Onthophagus proletarius* Harold	6.13	0.00663	0.68	0.65	0.67	0.92	2.44	2.53	0.47

Ont.rec	*Onthophagus rectecornutus* Lansberge	8.94	0.00724	0.52	0.67	0.73	1	2.58	2.34	0.46
Ont.sp61	*Onthophagus saigonensis* Boucomont	4.36	0.00243	0.52	0.67	0.73	0.82	3.41	3.65	0.48
Ont.sp11	*Onthophagus* sp.01	5.97	0.00762	0.62	0.69	0.69	0.99	2.81	2.17	0.47
Ont.sp45	*Onthophagus* sp.02	8.06	0.01325	0.46	0.63	0.75	0.8	3.09	2.95	0.54
Ont.sp19	*Onthophagus* sp.03	7.18	0.00866	0.47	0.7	0.69	0.78	2.8	2.49	0.44
Ont.sp25	*Onthophagus* sp.04	7.67	0.01374	0.46	0.69	0.73	0.87	2.15	2.26	0.49
Ont.sp46	*Onthophagus* sp.05	7.07	0.008	0.6	0.67	0.7	0.79	2.59	2.65	0.47
Ont.sp50	*Onthophagus* sp.06	4.78	0.00292	0.52	0.66	0.75	0.81	3.9	2.88	0.52
Ont.sp20	*Onthophagus* sp.07	6.77	0.01412	0.36	0.68	0.71	0.98	2.45	2.71	0.45
Ont.sp18	*Onthophagus* sp.08	10.31	0.02177	0.46	0.64	0.72	0.95	2.6	2.77	0.37
Ont.sp60	*Onthophagus* sp.09	5.17	0.00354	0.54	0.67	0.72	0.84	3.07	2.97	0.46
Ont.sp47	*Onthophagus* sp.10	7	0.00674	0.6	0.69	0.7	0.79	0.54	2.29	0.5
Ont.sp62	*Onthophagus* sp.11	5.85	0.00239	0.38	0.71	0.68	0.89	2.62	3.2	0.45
Ont.sp12	*Onthophagus* sp.12	7.86	0.01074	0.63	0.65	0.69	0.77	2.71	2.51	0.46
Ont.sp17	*Onthophagus sycophanta* Fairmaire	8.89	0.01991	0.59	0.7	0.66	1	2.62	2.61	0.48
Ont.sp44	*Onthophagus taurinus* White	7.1	0.00788	0.57	0.7	0.67	0.81	2.51	1.9	0.48
Ont.sp41	*Onthophagus thanwaakhomus* Masumoto	5.63	0.00305	0.4	0.7	0.75	0.8	2.94	4.14	0.52
Ont.tri	*Onthophagus trituber* (Wiedemann)	7.94	0.01332	0.5	0.69	0.7	0.79	2.53	3.22	0.55
Ont.sp13	*Onthophagus vaulogeri* Boucomont	5.02	0.01069	0.54	0.71	0.67	0.87	2.59	2.34	0.57
Sin.sim	*Sinodrepanus similis* Simonis	10.16	0.02884	0.73	0.71	0.86	1.07	4.8	5.21	0.5
Syn.pul	*Synapsis puluongensis* Bui & Bonkowski	17.96	0.6433	0.52	0.51	1	0.7	2.72	4.71	0.3
Syn.tri	*Synapsis tridens* Sharp	32.62	2.1976	0.51	0.46	0.95	0.61	2.47	2.44	0.35
Tib.sin	*Tibiodrepanus sinicus* (Harold)	4.88	0.00439	0.4	0.81	0.87	1.11	5.05	4.2	0.44

CHAPTER 3 A REVIEW OF THE GENUS *COPRIS* GEOFFROY (COLEOPTERA: SCARABAEIDAE)

Publication:

Two new species and one new record for the genus *Copris* (Coleoptera: Scarabaeidae: Scarabaeinae) from Vietnam with a key to Vietnamese species

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ORIGINAL ARTICLE

Two new species and one new record for the genus *Copris* (Coleoptera: Scarabaeidae: Scarabaeinae) from Vietnam with a key to Vietnamese species

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Key words. Coleoptera, Scarabaeidae, *Copris*, taxonomy, new species, key, distribution, Oriental region, Vietnam, Caobang, Thanhhoa

Abstract. Two new species of *Copris* Geoffroy, 1762 are described and illustrated: *Copris* (subgenus incertae sedis) *caobangensis* sp. n. from Caobang Province (northern Vietnam) and *Copris* (*Copris*) *sonensis* sp. n. from Thanhhoa Province (central Vietnam). *Copris* (*Copris*) *szechouanicus* Balthasar, 1958 is recorded in Vietnam for the first time and data on the morphology, distribution and ecology of this species are given. An updated species list and an identification key for the *Copris* species so far known from Vietnam are presented along with detailed photographs of the poorly known species.

ZooBank Article LSID: 6DF5C431-52C2-45F6-8DF1-72BABC998336

INTRODUCTION

Copris Geoffroy, 1762 is placed in the group "tunnelers" of true dung beetles, comprising species of different body sizes and with various nesting strategies. Small tunnelers (less than 13 mm) make shallow nests with many brood masses, while large species make deep nests, containing fewer brood masses (Hanski & Cambefort, 1991). The genus is widely distributed in Africa, North and Central America, as well as in the Palaearctic and Oriental regions, and currently includes over 230 described species (Davis et al., 2008). Although species of *Copris* have been investigated for a long time, some groups, especially the Southeast Asian species are still poorly known. As only a few Vietnamese *Copris* species are described by Gillet (1911), Arrow (1931), Kabakov (1994), Hanboonsong et al. (2003) and Ochi & Kon (2004) there is still a poor understanding of the taxa involved. This is partly due to its somewhat intricate taxonomy as species of *Copris* are separated by minor differences, such as the morphology of the pronotum and cephalic horn, or the structure of the elytra and tibia, etc. In order to avoid taxonomic confusion between *Copris* species, an integrated taxonomic approach, combining morphological and molecular data, as well as a detailed species determination key are needed. During the course of our examination of dung beetles that were collected in limestone ecosystems in two spatially separated nature reserves (NR) in Vietnam, we discovered two new species and established a new country record, increasing the number of known species of *Copris* from Vietnam to 21. Here we describe these two new species, provide a first species identification key and an updated list of *Copris* species from Vietnam, and provide data on the new record for this country.

MATERIALS AND METHODS

Study area and sampling protocol

The field research was conducted in limestone karst ecosystems in high mountain areas at Pu Luong (Thanhhoa Province) and Pia Oac NR (Caobang Province) between March and May over a two year period (2015–2016). We used in total 90 baited pitfall traps to collect dung beetles. The traps were placed in habitats with increasing land use intensity, comprising primary forests, secondary forests and meadows in both reserves. Each trap consisted of a 5-liter plastic bucket buried to its rim in the soil, filled with 2 l of 70% ethanol, and baited with 300 g of fresh pig dung. Specimens were removed from the traps after 48 h of trap exposure and preserved in 70% ethanol until examined in the lab.

Material examined

Specimens examined for this study are deposited in the following institutions (curators in parentheses): VNUF – Vietnam National University of Forestry, Hanoi, Vietnam (Bùi Văn Bắc); PLNR – Pu Luong Nature Reserve, Quanhoa and Bathuoc districts, Thanhhoa Province, Vietnam (Nguyễn Bá Tâm);

NMPC – National Museum, Prague, Czech Republic (Jiří Hájek); RMNH – Naturalis Biodiversity Center, Leiden, Netherlands (Hans Huijbregts).

Morphometrics

Measurements were taken with a digital caliper and from photographs taken through a digital microscope (Keyence VHX-500F). The following morphometric traits were measured: BoL – body length from anterior margin of clypeus to posterior margin of elytra; BoW – maximum body width; HeadL – head length from anterior most point of clypeus to posterior margin of head; HeadW – maximum head width; PronL – maximum pronotum length; PronW – maximum pronotum width; ElyL – elytra length from apex to base; MWoI123 – maximum width of first three interstriae from elytral suture; DP10–15 – distance from puncture 10 (from base of elytra) to puncture 15 on first elytral stria; HoL – horn length from base to tip; PyL – maximum pygidium length; PyW – maximum pygidium width; ProTiL – protibia length; ProTiW – maximum protibia width; ProTiSL – protibial spur length; MesoTiL – mesotibia length; MesoTiW – maximum mesotibia width; 1st MesoTiSL – 1st mesotibial spur length (longest spur); 2nd MesoTiSL – 2nd mesotibial spur length (shortest spur); MetaTiL – metatibia length from proximal constriction to apex; MetaTiW – maximum metatibia width; MetaTiSL – metatibial spur length; MetaTaL – metatarsus length; MetaTa1L – metatarsomere 1 length; MetaTa1W – metatarsomere 1 width; MetaTa5W – metatarsomere 5 width; DDC – distance between apices of clypeal denticles (teeth).

Male genital morphology

We used forceps and needles to open the pygidium for removing the aedeagus. The extracted aedeagus was cleaned and softened in 5% KOH at 65°C for one hour before being placed in glycerin and photographed using a digital microscope (Medina et al., 2013).

DNA extraction and sequencing

Material for molecular analysis was obtained from *Copris* (*Copris*) *sonensis* sp. n. Genomic DNA was extracted from legs of two paratype specimens (1 male and 1 female), using DNeasy Blood & Tissue Kit (Qiagen). PCR amplification of the cytochrome oxidase I gene was performed in a volume of 26 µl that consisted of 14.85 µl of sterile water, 2.5 µl Green Buffer (10× ThermoFisher Scientific), 2.5 µl of 2µM dNTPs, 2.5 µl of each primer, 0.15 µl DreamTaq polymerase (ThermoFisher Scientific) and 1 µl extracted DNA. The primers used for amplification were Cox1 (5'-CAACATTTATTTTGATTTTTTGG-3') and Cox2 (5'-TCCAATGCACTAATCTGCCATATTA-3') (Wirta et al., 2008; Mlambo et al., 2015). Thermal cycling parameters had a denaturation phase of 95°C for 32 s, extension at 72°C for 2 min and an annealing temperature of 50°C for 36 s. The conditions were cycled 35 times. Amplification products were purified with Exo-SAP PCR cleanup, containing 8 µl PCR product, 1.95 µl sterile water, 0.9 µl FastAP and 0.15 µl Exonuclease (ThermoFisher Scientific). The mixture was incubated at 37°C for 30 minutes, followed by heating up to 85°C for 20 min. The purified solution was diluted by adding 99 µl sterile water before sequencing. Sequencing was conducted with the BigDye Terminator v3.1 Cycle Sequencing Kit (ThermoFisher Scientific). The sequencing was performed at Cologne Center for Genomics (CCG), University of Cologne, Germany. The new sequences were submitted to the NCBI database under the accession numbers MG642090 and MG642091.

Molecular analysis

COXI sequences of *Copris* (*Copris*) *sonensis* sp. n. and several other taxa of *Copris, Catharsius* Hope, 1837 (classified in Coprini) and *Onthophagus* Latreille, 1802 (formally used as outgroup, although this does not agree with the results of Monaghan et al., 2007) of Eurasian or African origin (Table 1) were manually aligned in SeaView (V4.5.3; Gouy et al., 2010). 837 sites were used for the alignment, of which 67.03% were invariant.

Trees were calculated in PhyML 3.1 (Maximum Likelihood; model GTR+I+G, starting tree NJ, 100 bootstrap replicates; Guindon & Gascuel, 2003) and MrBayes (settings: mcmc ngen = 1 M, sample freq = 100, print freq = 100, diagn freq = 500; burnin of 25% and final split frequencies of less than 0.01; Altekar et al., 2004; Ronquist & Huelsenbeck, 2003).

TAXONOMY

Genus *Copris* Geoffroy, 1762

Type species: *Scarabaeus lunaris* Linnaeus, 1758 (designated by Latreille, 1810).

Copris (subg. incertae sedis) *caobangensis* sp. n.

Figs 1–13, 25

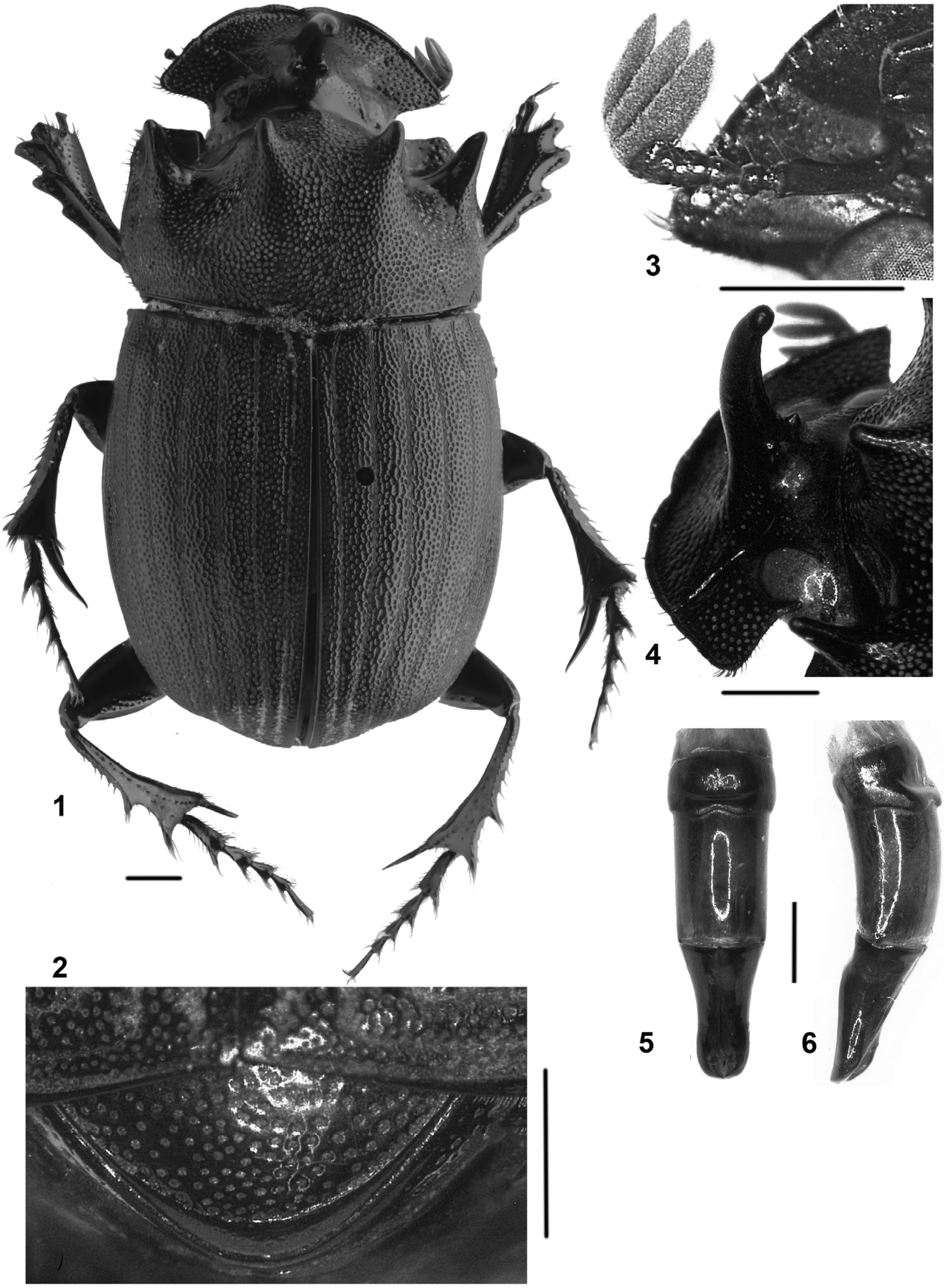
ZooBank taxon LSID:
3A4B3342-251B-471E-B9EC-56BDB94E26F4

Description of holotype male. Total body length 12 mm, maximum body width 6.5 mm. Colour: Dorsal sur-

Table 1. Species, localities, museum numbers and numbers of the GenBank accession used in the phylogenetic analysis.

Species	Locality	Museum No.	GenBank Accession No. / COXI	Reference
Copris sonensis sp. n. (♂)	Vietnam	VNUF, paratype	MG642090	This study
Copris sonensis sp. n. (♀)	Vietnam	VNUF, paratype	MG642091	This study
Copris sinicus Hope, 1842	Hong Kong	BMNH 679781	AY131862	Monaghan et al. (2007)
Copris agnus Sharp, 1875	Indonesia	BMNH 679776	AY131857	Monaghan et al. (2007)
Copris amyntor Klug, 1855	South Africa	BMNH 679777	AY131858	Monaghan et al. (2007)
Copris lugubris Boheman, 1858	Costa Rica	BMNH 679779	AY131860	Monaghan et al. (2007)
"*Copris aeneus*" *	South Africa	BMNH 679775	AY131856	Monaghan et al. (2007)
Catharsius molossus (Linnaeus, 1758)	Indonesia	BMNH 679772	AY131853	Monaghan et al. (2007)
Catharsius sesostris Waterhouse, 1888	South Africa	BMNH 679774	AY131855	Monaghan et al. (2007)
Catharsius calaharicus Kolbe, 1893	South Africa	BMNH 679771	AY131852	Monaghan et al. (2007)
Catharsius philus Kolbe, 1893	South Africa	BMNH 679773	AY131854	Monaghan et al. (2007)
Onthophagus similis (Scriba, 1790)	Spain	BMNH 679871	AY131933	Monaghan et al. (2007)
Copris confucius Harold, 1877	Laos	MNHN	EF188135	Wirta et al. (2008)
Onthophagus nuchicornis (Linnaeus, 1758)	—	—	GQ889396	Ahrens & Roessner (unpubl.)

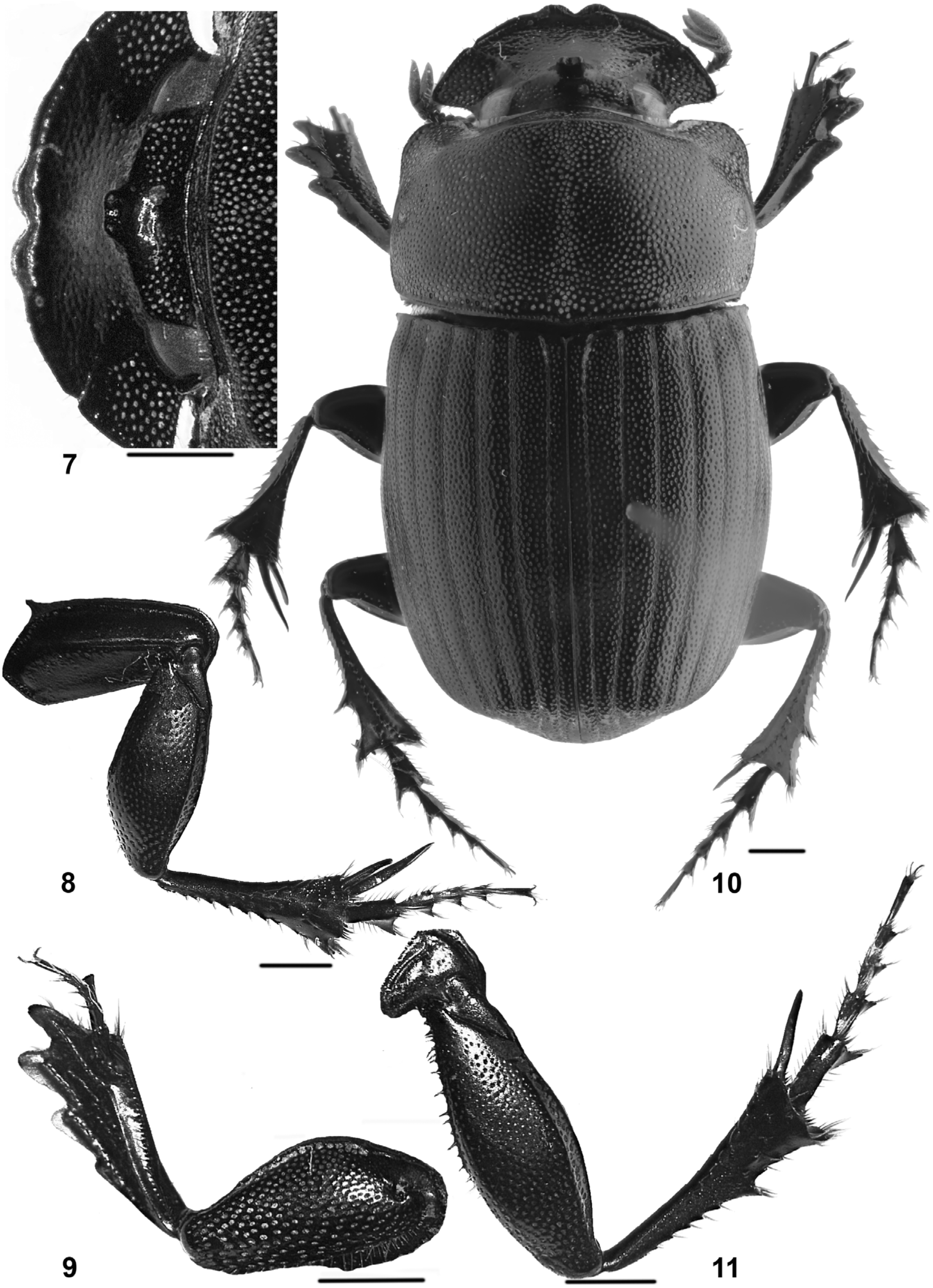
BMNH – Natural History Museum, London, UK; MNHN – Muséum national d'Histoire naturelle, Paris, France; * – not a valid name, perhaps Monaghan et al.'s error for *Copris anceus* (Olivier, 1789), a South African species.



Figs 1–6. *Copris cabangensis* sp. n., male holotype. 1 – dorsal habitus; 2 – pygidium; 3 – right antenna ventral; 4 – horn; 5 – genitalia dorsal; 6 – genitalia lateral. Scale bars 1 mm.

face chocolate brown. Ventral surface dark brown on head, shiny dark brown on thorax, abdomen and pygidium. Mouthparts, maxillary palpi, tarsi and antennomeres 1–6 reddish brown. Antennal club, setae on legs and sides of meso-metaventer yellow (Figs 1–6).

Head nearly semicircular, 2.5 mm long and 4.7 mm wide. Clypeal surface rugose and strongly punctate; clypeal apex weakly emarginated. Genae strongly and coarsely punctate. Vertex surface between eyes smooth, except for small areas near eyes sparsely punctate. Antenna with 9 anten-



Figs 7–11. *Copris caobangensis* sp. n., female paratype. 7 – horn; 8 – right mesothoracic leg ventral; 9 – right prothoracic leg ventral; 10 – dorsal habitus; 11 – right metathoracic leg ventral. Scale bars 1 mm.

nomeres; length of antennomere 1 0.9 mm, equal in length to antennomeres 2–6 combined and also antennal club. Cephalic horn long and curved backwards (length 3 mm); base of horn with two small but distinct teeth. Maxilla length 1.4 mm, bearing slender palpi. Mentum with thick and yellow setae, obscuring its surface.

Pronotum with sharp anterior declivity, nearly vertical and each side deeply excavated. Anterior angles of pronotum armed with two strong, upward and forward directed prominences on dorsum. Each side with one sharp, upward directed prominence. Pronotal disc with slight longitudinal sulcus; sulcus with chain of deep and dense punctures. Vertical anterior surface with strongly punctate carina running through its middle. Anterolateral angles of pronotum nearly square; anterior margins behind genae almost straight. Pronotal surface almost strongly, densely and equally punctate, except for quite small smooth areas of pronotal excavation. Pronotal prominences indistinctly punctate.

Elytra distinctly striate, with 10 complete striae. Each stria strongly and closely punctate (DP10–15 0.7 mm). Elytral interstriae convex, matt and strongly, equally, densely but separately punctate (Fig. 25).

Mesepimeron and metepisternum flat, rugose, and covered by yellow setae.

Meso-metaventral plate smooth; posterior part with median groove; anterior part with deep pit. Sides strongly punctate and sparsely setaceous.

Legs. Ventral surface of profemora, mesofemora and metafemora strongly, closely and equally punctate. Protibia (ProTiL 2.2 mm, ProTiW 1.3 mm) with four lateral teeth. Protibial spurs truncate and distinctly curved inwards near apex. Protibial spur length 0.8 mm, equal in length to protarsomeres 1–3 combined. Protarsomere 5 and protarsomeres 3–4 combined equal in length (0.5 mm). Mesotibia (MesoTiL 2.3 mm, MesoTiW 1.0 mm, 1st MesoTiSL 1.4 mm, 2nd MesoTiSL 0.7 mm) and metatibia (MetaTiL 2.5 mm, MetaTiW 0.9 mm, MetaTiSL 0.8 mm) broadly dilated at posterior end. Metatibia with strong transverse outer carina. Both mesotarsi and metatarsi short, bearing sparse yellow setae.

Abdomen. Pygidium length 0.9 mm, width 2.2 mm. Surface slightly convex, strongly, coarsely but not closely punctate. Abdominal ventrites sparsely punctate, becoming narrower at middle.

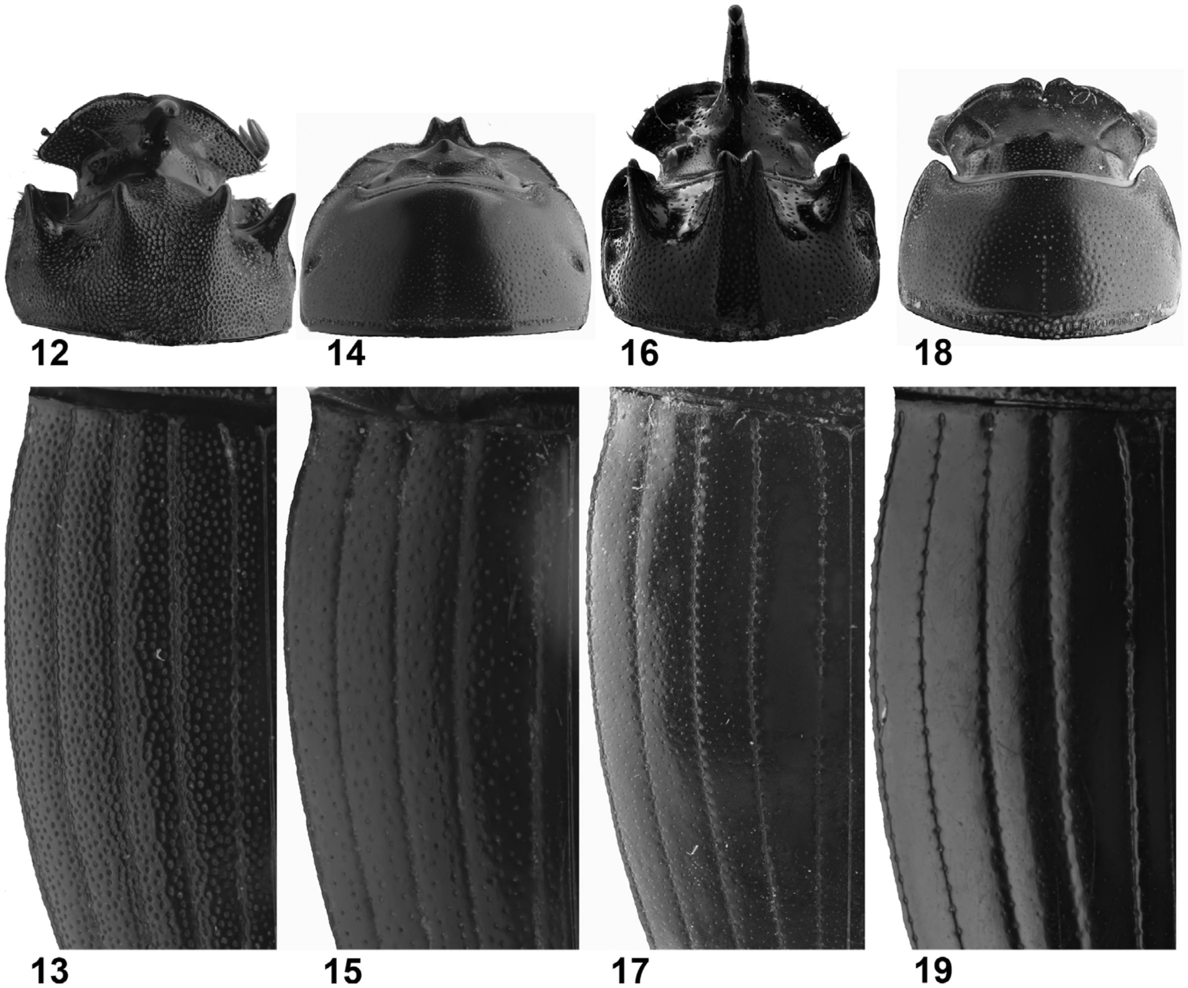
Aedeagus. Phallobase 1.8 mm in length with strong dorsal lobes. Parameres shorter than phallobase, approximately 1.3 mm in length. Broad angle of 146° formed by phallobase and parameres.

Sexual dimorphism. Females differ from the male holotype in the following characters: Cephalic horn straight, short, 0.8 mm in length; horn apex excavated. Clypeal apex more strongly emarginated. Genae and vertex between eyes with more punctures. Pronotum with a deeper median sulcus on dorsal surface. Each side of pronotum unarmed and not excavated (Figs 7–11).

Differential diagnosis. *Copris caobangensis* sp. n. is similar to species of the subgenus *Paracopris* Balthasar, 1939 in their strongly punctate elytral interstriae, but differs in its pronotal structures and the structure of the horn in males. Pronotum with sharp anterior declivity, armed and excavated in the male, transversely carinate on the upper part of the anterior declivity in the female in *C. caobangensis* sp. n. while indistinct or slight declivity occurs in species of the subgenus *Paracopris*. In addition, males of *C. caobangensis* sp. n. have a longer cephalic horn. For these reasons, we leave this new species without a subgeneric classification and consider it as "subgenus incertae sedis". Almost all species of the nominotypical subgenus bear smooth, indistinctly punctate interstriae, which distinguishes them from the new species. Two species of the nominotypical subgenus, *C.* (*Copris*) *punctatus* Gillet, 1910 and *C.* (*C.*) *saperdon* Harold, 1868 have distinctly but not closely and strongly punctate interstriae. The new species can be easily distinguished from species of the subgenus *Microcopris* Balthasar, 1958 as the front angles of prothorax are deeply excavated in all species of the

Table 2. Morphometrics of *Copris caobangensis* sp. n., *C.* (*Copris*) *sonensis* sp. n. and *C.* (*C.*) *szechouanicus* (measurements in mm).

	Character	*C. caobangensis* sp. n.		*C. sonensis* sp. n.		*C. szechouanicus*	
		Male (n =1)	Female (n = 2)	Male (n = 6)	Female (n = 3)	Male (n = 8)	Female (n = 10)
1	BoL	12	11.8–12.0	14–15.2	13.3–14.9	14.5–18.6	16.7–18.1
2	BoW	6.5	6.3–6.6	7.8–8.4	7.3–8.0	8.4–10.0	9.4–10.3
3	HeadL	2.5	2.4–2.7	2.5–3.0	2.8–3.1	3.4–3.7	3.4–4.9
4	HeadW	4.7	4.6–4.8	5.2–5.5	5.4–5.7	6.1–6.6	6.6–7.1
5	PronL	3.6	3.6	4.2–4.8	4.1–4.7	4.4–5.2	5.1–6.0
6	PronW	6.2	5.9–6.1	7.0–7.7	6.8–7.4	8.0–9.1	8.9–9.6
7	ElyL	6.6	6.5–6.7	7.7–8.4	7.2–8.2	8.6–10.1	10.3–11.5
8	MWoI123	1.5	1.5	1.8–2.1	1.9–2.0	2.0–2.3	1.6–2.5
9	DP10–15	0.7	0.8–0.9	0.8–1.1	0.8–0.9	1.1–1.4	1.2–1.5
10	HoL	3	0.5	2.8–3.3	0.8–0.9	0.4–1.0	0.7–1.1
11	PyL	0.9	0.9–1.1	1.6–1.7	1.6–1.7	1.5–1.7	1.5–2.0
12	PyW	2.2	2.3–2.5	3.1–3.3	3.3	3.3–3.8	3.1–4.7
13	ProTiL	2.2	2.1–2.2	2.0–2.8	1.8–1.9	2.9–3.2	3.1–3.5
14	ProTiW	1.3	1.3–1.4	1.0–1.6	1.0–1.1	1.5–1.8	1.7–2.0
15	ProTiSL	0.8	0.6–0.7	0.8–1.1	0.6–0.7	1.2–1.6	1.0–1.1
16	MesoTiL	2.3	2.3–2.4	2.5–2.8	2.6–2.9	2.9–3.1	3.1–3.5
17	MesoTiW	1	1.0–1.1	1.1–1.2	1.1–1.6	1.2–1.3	1.4–1.5
18	1st MesoTiSL	1.4	1.4–1.5	1.3–1.6	1.1–1.3	1.6–2.3	2.0–2.2
19	2nd MesoTiSL	0.7	0.7–0.8	0.8–0.9	0.6–0.8	0.7–1.0	1.0–1.1
20	MetaTiL	2.5	2.4–2.8	2.8–3.3	2.5–3.3	3.6–4.0	3.8–4.4
21	MetaTiW	0.9	1.0–1.1	1.1	1.0–1.2	1.1–1.2	1.3–1.4
22	MetaTiSL	0.8	1.0–1.1	1.0–1.1	1.0–1.2	1.1–1.3	1.2–1.7
23	MetaTaL	2.9	2.9	2.8–3.2	2.8–3.1	3.2–3.6	3.0–3.9
24	MetaTa1L	0.9	0.9	0.9–1.0	0.9–1.0	1.0–1.3	1.0–1.3
25	MetaTa1W	0.3	0.5	0.3–0.5	0.5–0.6	0.5–0.6	0.4–0.7
26	MetaTa5W	0.1	0.1	0.1	0.2	0.1–0.2	0.1
27	DDC	0.8	0.9	0.7	0.9–1.0	1.3–1.6	1.5–1.7



Figs 12–19. Pronotal and elytral structures. 12, 13 – *Copris caobangensis* sp. n., male, pronotum and elytra, showing the armed and excavated pronotum and deeply and densely punctured elytra; 14, 15 – *C.* (*Paracopris*) *punctulatus*, male, pronotum and elytra, showing the unarmed pronotum and deeply and sparsely punctured elytra; 16 – *C.* (*Copris*) *angusticornis,* male, showing the armed and excavated pronotum; 17 – *C.* (*C.*) *punctatus* showing the shallowly punctured elytra; 18 – *C.* (*Microcopris*) *reflexus* showing the unarmed pronotum; 19 – *C.* (*M.*) *propinquus* showing the elytra without punctures.

subgenus *Microcopris* but flat in the new species (Figs 12–19).

Copris caobangensis sp. n. morphologically resembles *C.* (*Copris*) *vietnamicus* Kabakov, 1994 that was described based on a single male specimen collected in Vinhphuc Province. Both species have a similar body shape, in particular, the head and pronotum, and both have dense and deep punctures on the pronotum and interstriae. However, both species differ in the following characters: male cephalic horn is nearly straight in *C.* (*C.*) *vietnamicus* but curved backwards in the new species. Punctures on interstriae are smaller than pronotal punctures in *C.* (*C.*) *vietnamicus*, whereas those on interstriae and pronotum are of equal size in the new species. The clypeal apex is more strongly emarginated in *C.* (*C.*) *vietnamicus*. In addition, *C.* (*C.*) *vietnamicus*, with a BoL 14.5 mm and BoW 7.8 mm, is larger than the new species, with BoL 11.8–12 mm and BoW 6.3–6.6 mm. The pronotal median sulcus is smooth in *C.* (*C.*) *vietnamicus* but strongly punctate in the new species. For differentiation see also the key below.

Type material. Holotype male and 2 female paratypes. Holotype male at VNUF labelled: "VIETNAM, Caobang Prov., Pia Oac NR, 22°34′3″N; 105°53′5″E, 1222 m a.s.l., primary forest, v.20,2016, Van Bac Bui leg." Two female paratypes (one at NMPC, one at VNUF) labelled: "VIETNAM, Caobang Prov., Pia Oac NR, 22°34′3″N; 105°53′5″E, 1214 m a.s.l., primary forest, v.20,2016, Van Bac Bui leg."

Type locality. Northern Vietnam, Caobang Province, Pia Oac Nature Reserve, 22°34′3″N; 105°53′5″E, 1214–1222 m.

Etymology. The specific epithet *caobangensis* refers to the name of the type locality, Caobang Province, North Vietnam.

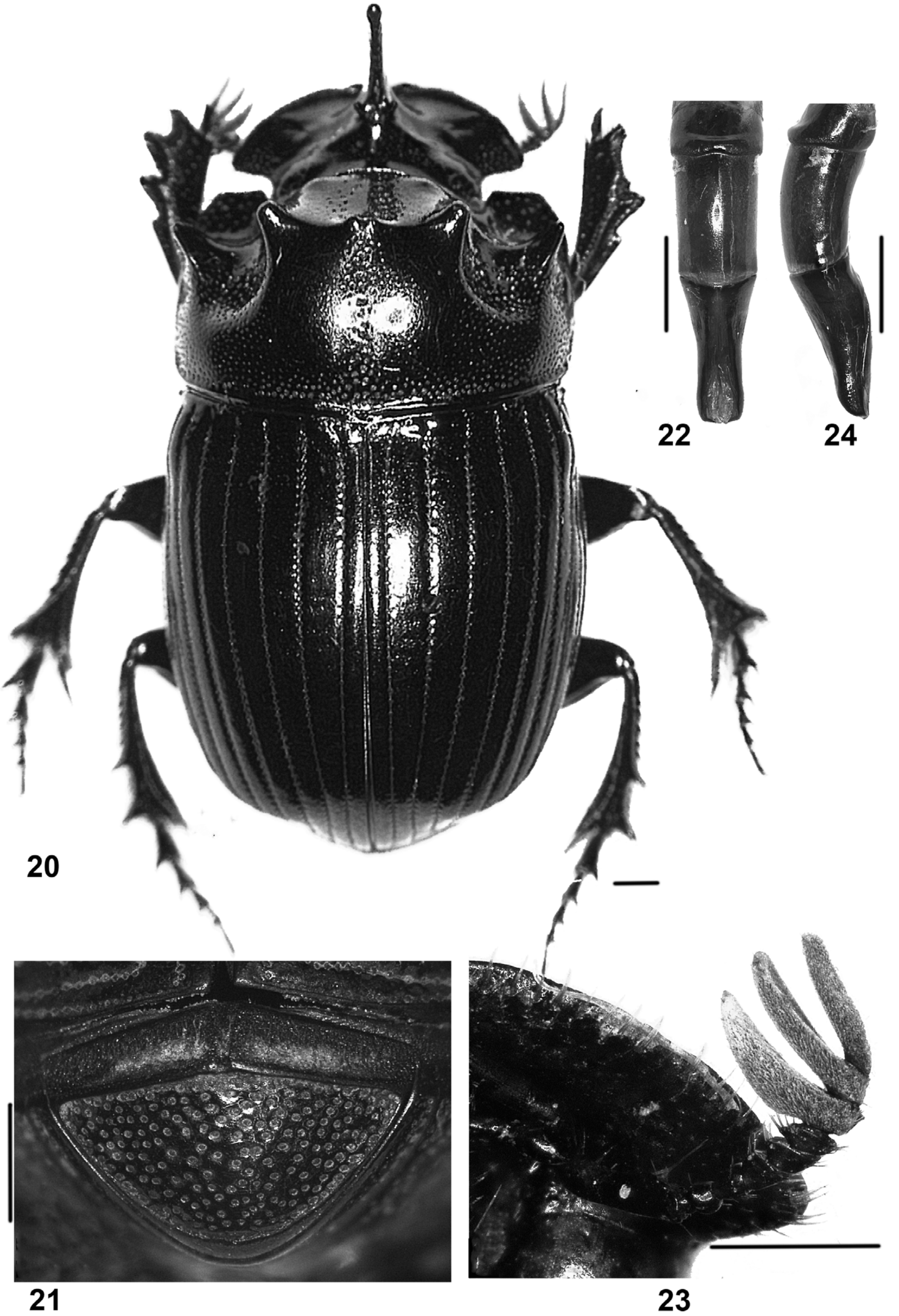
Collecting details. All specimens of *Copris caobangensis* sp. n. were collected in Pia Oac Nature Reserve, Caobang Province, North Vietnam using pitfall traps baited with fresh pig dung. The habitat sampled was primary forest that dominated at an altitude range of 1210–1230 m. Both forest canopy cover and cover of leaf litter layer were > 95%.

***Copris* (*Copris*) *sonensis* sp. n.**

Figs 20–24, 26–32, 35

ZooBank taxon LSID:
BB4A6A84-2F6C-4E28-AE36-BD947F4A3602

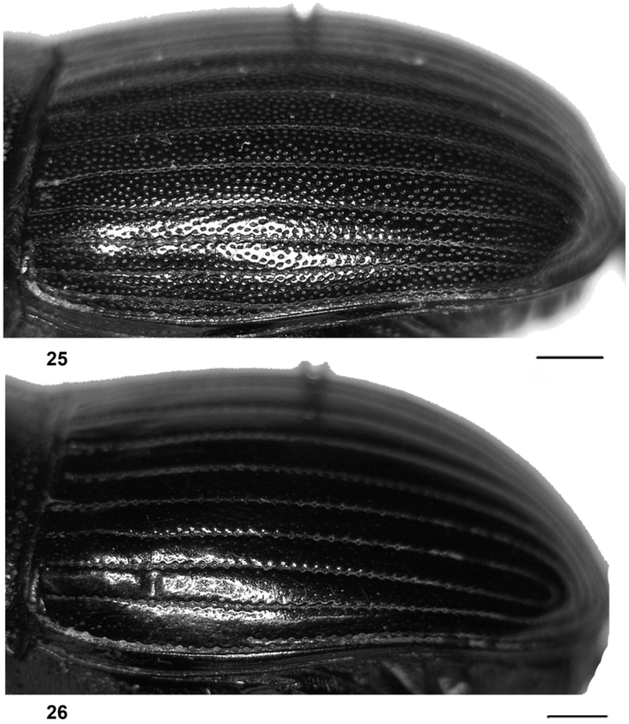
Description of holotype male. Total body length 14.7 mm, maximum body width 7.8 mm. Head, pronotum and elytra black and shiny. Mouthparts, maxillary palpi, antennomeres 1–6 reddish brown. Antennal club and setae on legs yellow (Figs 20–24).



Figs 20–24. *Copris* (*Copris*) *sonensis* sp. n., male holotype. 20 – dorsal habitus; 21 – pygidium; 22 – genitalia dorsal; 23 – left antenna ventral; 24 – genitalia lateral. Scale bars 1 mm.

Head nearly semicircular. Length 2.6 mm, width 5.5 mm. Surface of clypeus relatively smooth; clypeal apex weakly emarginated. Vertex between eyes smooth. Genae sparsely but distinctly punctate. Antenna with 9 antennomeres; antennomere 1 equal in length (approximately 1 mm) to antennomeres 2–6 combined and also antennal club. Cephalic horn long (3.1 mm), curved backwards and with two small but distinct teeth at base; surface of horn quite smooth.

Pronotum length 4.2 mm, width 7.3 mm**.** Pronotum with sharp anterior declivity. Pronotal disc deeply excavated on each side. Two forward directed prominences present on



Figs 25, 26. Form of elytra, lateral. 25 – *Copris caobangensis* sp. n. showing the stria 9 complete; 26 – *C.* (*C.*) *sonensis* sp. n. showing the stria 9 incomplete.

dorsal side on anterior part of pronotum. Each lateral angle armed with one sharp and upward directed prominence. Pronotal prominences smooth and impunctate. Pronotal anterolateral angles obtuse; lateral margin slightly curved in front while anterior margin behind genae nearly straight. Almost whole surface of pronotum punctate, except for small areas near prominences smooth; punctures deep, coarse and regular on sides of pronotum, gradually smaller and more irregular on basal half of pronotum and excavations. Vertical anterior surface of prothorax also minutely and irregularly punctate. Pronotum with weak median longitudinal sulcus; sulcus with deep, coarse but irregular punctures.

Elytra with 10 striae; striae 1–8 complete; stria 9 arise on anterior third of elytron; stria 10 complete. All striae deeply, evenly, circularly punctate; distance between two strial punctures twice as large as their diameters. Interstriae slightly convex, shiny and impunctate (Fig. 26).

Mesepimeron and metepisternum flat, rugose, covered by yellow, long and scanty setae.

Meso-metaventral plate smooth, with median distinct groove. Sides strongly, coarsely punctate and sparsely hairy.

Legs. Ventral surface of profemora strongly, coarsely, closely and unequally punctate; punctures becoming denser on anterior half of profemora near base; anterior margin of profemora with yellow, dense and long setae. Protibia (ProTiL 2.8 mm, ProTiW 1.4 mm) with four lateral teeth. Protibial spurs (ProTiSL 0.8 mm) truncate, distinctly curved inwards near apex, equal in length to protarsomeres 2–4 combined. Protarsomere 1 and 5 equal in length. Mesofemora deeply, coarsely punctate on ventral side; punctures becoming sparser and shallower toward anterior half of mesofemoral near base. Mesotibia (MesoTiL 2.8 mm, MesoTiW 1.1 mm, 1st MesoTiSL 1.3 mm, 2nd MesoTiSL 0.9 mm) broadly dilated at posterior end. Deep, coarse and distinct punctures also present on metafemora, becoming denser on third anterior part of metafemora. Metatibia (MetaTiL 3.1 mm, MetaTiW 1.1 mm, MetaTiSL 1.0 mm) with strongly transverse outer carina. Mesotarsi and metatarsi short, and both with yellow scanty setae.

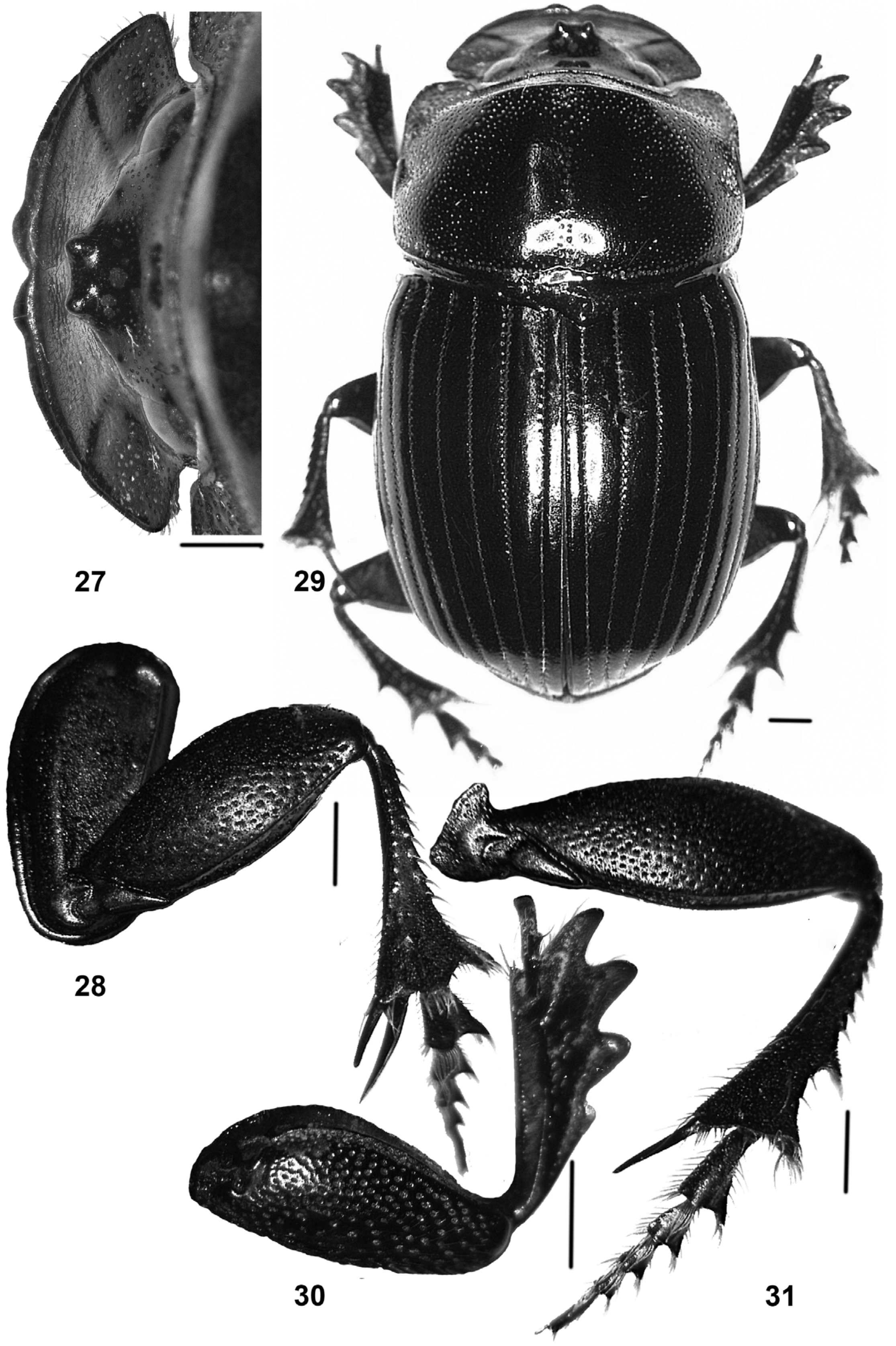
Abdomen. Pygidium length 1.7 mm, width 3.2 mm, with complete margin. Surface slightly convex, and deeply, equally punctate. Punctures on pygidium circular and very close, their distance apart equals their diameter. Abdominal ventrites deeply and closely punctate; ventrites becoming extremely narrow in middle.

Aedeagus. Phallobase 1.8 mm in length with large dorsal lobes. Parameres shorter than phallobase, approximately 1.7 mm in length. Broad angle more than 140° formed by phallobase and parameres.

Sexual dimorphism. Females differ from the male holotype in the following characters: Head armed with one straight, short horn; horn apex strongly excavated. Clypeal apex more strongly emarginated. Pronotum unarmed and not excavated on each side. Pronotal disc and frons more densely punctate (Figs 27–31).

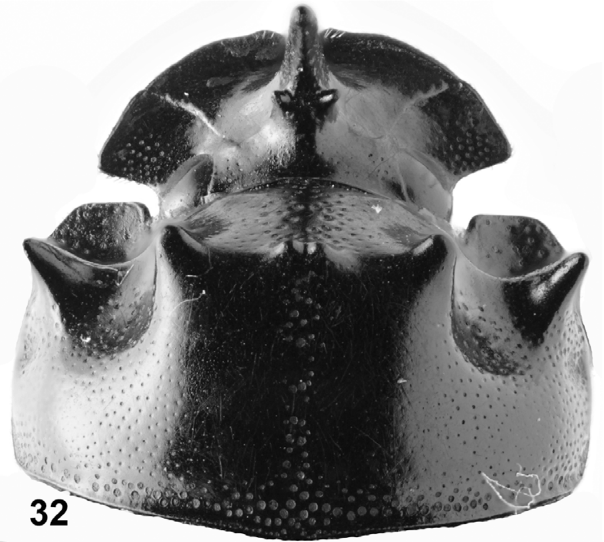
Variation. Body length 13.3–15.2 mm, body width 7.3–8.4 mm (n = 9). The four male paratypes are smaller, compared to the holotype, have smaller prominences and excavations on the pronotum but similar in the remaining characters. A large male paratype in the material examined is morphologically similar to the holotype. There are no significant differences in pronotal structures in females. Other characters of females are consistent within populations.

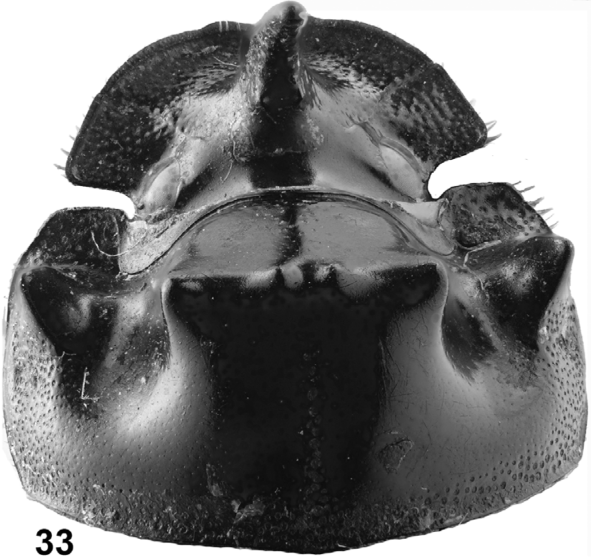
Differential diagnosis. *Copris sonensis* sp. n. can be placed in the nominotypical subgenus with the following characters: Pronotum with sharp anterior declivity, armed; interstriae sparsely and minutely punctate; front angles of pronotum not excavated on ventral side. The new species, compared to species within the subgenus *Copris* from Vietnam and adjacent countries, has many similarities to *C.* (*C.*) *zhangi* Ochi, Kon & Bai, 2009 from China, *C.* (*C.*) *tripartitus* Waterhouse, 1875 from China, Taiwan, Korea and Japan and *C.* (*C.*) *sarpedon* Harold, 1868 from Thailand, Kashmir, Assam, Nepal, but has a different clypeal surface, cephalic horn structure and pronotum. The clypeus is smooth in the new species but deeply punctate in *C. zhangi, C. tripartitus* and *C. sarpedon*. In addition, *C. sonensis* sp. n. typically bears two distinct teeth at the base of the male cephalic horn while *C. tripartitus* and *C. sarpedon* have two minute, indistinct teeth at the base. Pronotal punctures are deeper, denser and more evenly distributed in *C. sarpedon* (Figs 32–34). Characters on the male pronotal structures clearly differentiate *C. sonensis* sp. n. from *C. zhangi.* In *C. sonensis* sp. n., pronotal disc with six prominences, the median two are small and noticeably contiguous, whereas in *C. zhangi*, the median two prominences not touching or noticeably contiguous.

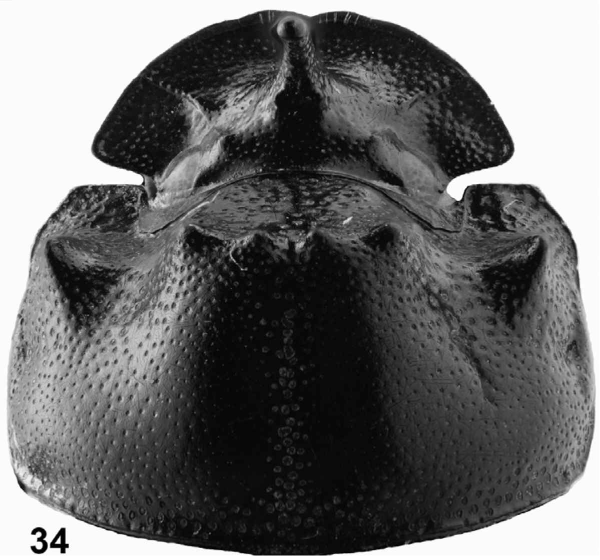


Figs 27–31. *Copris* (*Copris*) *sonensis* sp. n., female paratype. 27 – horn, 28 – left mesothoracic leg ventral; 29 – dorsal habitus, 30 – left prothoracic leg ventral; 31 – left metathoracic leg ventral. Scale bars 1 mm.

Copris sonensis sp. n. is also similar to *C.* (*C.*) *cambodiensis* Ochi, Kon & Kawahara, 2008 from Phumi Kalai Thum (Cambodia) in terms of body shape, especially the structure of the head, pronotum and legs. However, it can be distinguished from *C. cambodiensis* by the structure of the elytral striae. The new species has an incomplete stria







Figs 32–34. Form of horns and pronotal structures of males. 32 – *Copris* (*Copris*) *sonensis* sp. n.; 33 – *C.* (*C.*) *tripartitus*; 34 – *C.* (*C.*) *sarpedon.*

9 and two separate striae 9 and 10 (Fig. 26), while *C. cambodiensis* has an incomplete stria 8 and the basal halves of striae 9 and 10 merge. In addition, the new species with BoL 13.3–15.2 mm, BoW 7.3–8.4 mm is smaller than *C. cambodiensis* with BoL 17.0–18.1 mm, BoW 9.0–9.6 mm.

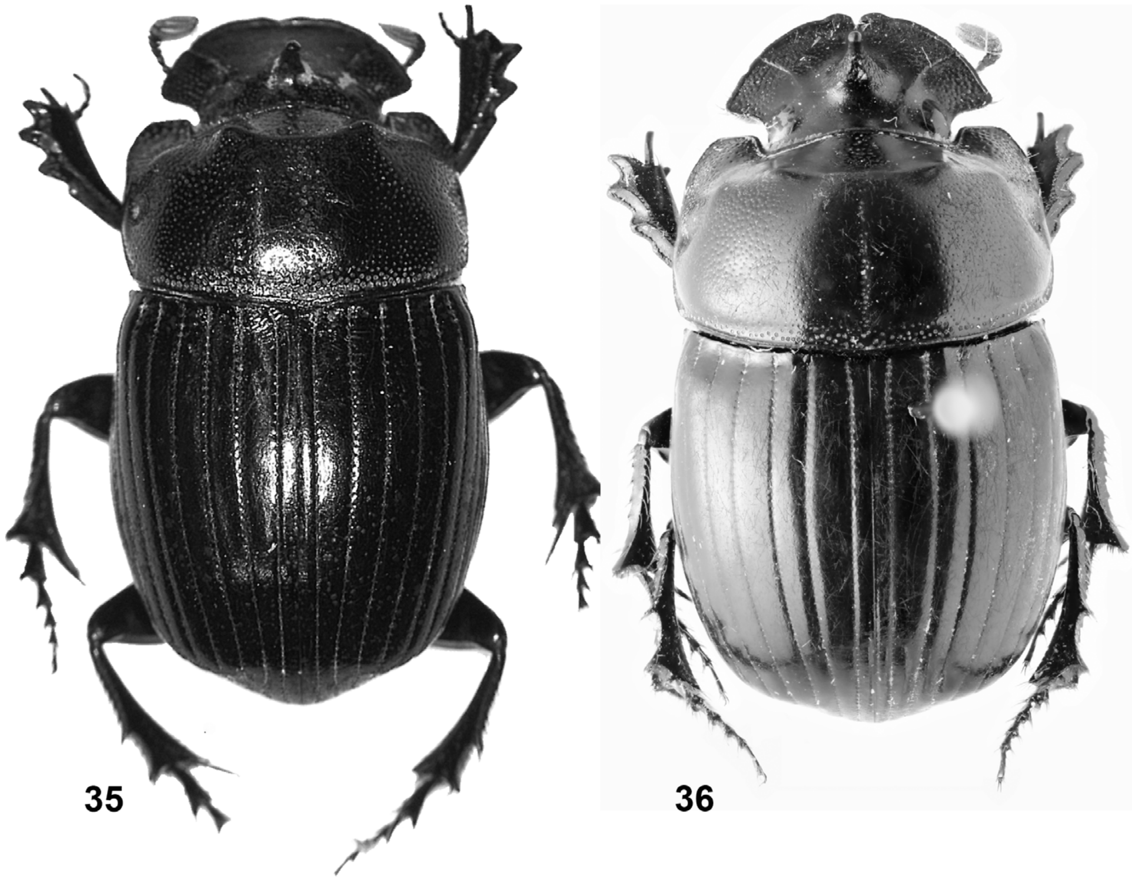
Small males of the new species are similar to *C.* (*C.*) *sinicus* Hope, 1842 but can be distinguished by the clypeal apex. All small males of the new species examined have a widely and shallowly emarginated clypeal apex while *C. sinicus* has a narrowly and deeply emarginated clypeal apex (Figs 35, 36). The clypeus is more deeply punctate in *C. sinicus.* The molecular analysis indicated a divergence between *C. sonensis* sp. n. and *C. sinicus* of 8.9–9 % in the COXI sequence.

Type material. Holotype male, 5 male paratypes, and 2 female paratypes. Holotype male at VNUF labelled: "VIETNAM, Thanhhoa Prov., Pu Luong NR, Son village, 20°28′53″N; 105°14′42″E, 853 m a.s.l., secondary forest, 10–25.iv.2016, Van Bac Bui leg." Paratypes: Male at VNUF: "VIETNAM, Thanhhoa Prov., Pu Luong NR, Son village, 20°28′54″N; 105°14′43″E, 875 m a.s.l., secondary forest, 10–25.iv.2016, Van Bac Bui leg." Male at VNUF: "VIETNAM, Thanhhoa Prov., Pu Luong NR, Son village, 20°28′54″N; 105°14′41″E, 867 m a.s.l., secondary forest, 10–25.iv.2016, Van Bac Bui leg." Female at VNUF: "VIETNAM, Thanhhoa Prov., Pu Luong NR, Son village, 20°28′51″N; 105°14′44″E, 860 m a.s.l., secondary forest, 10–25.iv.2016, Van Bac Bui leg." Female at VNUF: "VIETNAM, Thanhhoa Prov., Pu Luong NR, Son village, 20°28′55″N; 105°14′28″E, 958 m a.s.l., primary forest, 10–25.iv.2016, Van Bac Bui leg." Male at NMPC: "VIETNAM, Thanhhoa Prov., Pu Luong NR, Son village, 20°28′53″N; 105°14′41″E, 856 m a.s.l., secondary forest, 10–25.iv.2016, Van Bac Bui leg." Male at RMNH: "VIETNAM, Thanhhoa Prov., Pu Luong NR, Son village, 20°28′53″N; 105°14′42″E, 853 m a.s.l., secondary forest, 10–25.v.2016, Van Bac Bui leg." Male at PLNR: "VIETNAM, Thanhhoa Prov., Pu Luong NR, Son village, 20°28′52″N; 105°14′43″E, 866 m a.s.l., secondary forest, 10.–25.v.2016, Van Bac Bui leg."

Type locality. Central Vietnam, Thanhhoa Province, Pu Luong Nature Reserve, Son Ba Muoi area, Son village, 20°28′53″N; 105°14′42″E, 850–960 m.

Etymology. The specific epithet *sonensis* refers to the name of the type locality, Son village, Son Ba Muoi area, Thanhhoa Province, central Vietnam.

Collecting details. During intensive surveys of dung beetle communities inhabiting ecosystems on limestone bedrock in the two nature reserves, 12 specimens of *C. sonensis* sp. n. were col-



Figs 35, 36. Dorsal habitus. 35 – *Copris* (*Copris*) *sonensis* sp. n., small male, showing clypeal apex with wide and shallow emargination; 36 – *C.* (*C.*) *sinicus,* male, showing clypeal apex with narrow and deep emargination.

lected in Pu Luong Nature Reserve. Habitats of *C. sonensis* sp. n. comprised primary forest and secondary forest that were characterized by a complex vertical structure with various forest layers, at an altitudinal range from 850–960 m and forest canopy cover ranging from 75 to 100%. No specimens of *C. sonensis* sp. n. were found in meadows during our surveys.

Copris (*Copris*) *szechouanicus* Balthasar, 1958

Figs 47, 67, 73

Comments. This species is here recorded for the first time from Vietnam (Caobang Province and Thanhhoa Province). Based on 18 measured specimens, we provide additional measurements of this species (Table 2).

Type material examined. Holotype male, allotype female, 6 male paratypes and 1 female paratype in NMPC. Holotype male: “Kuatun [= nowadays Guadun], Fukien, China, 15.06.46, leg. Tschung-Sen.” Allotype female: “Giufu Shan [= nowadays Jinfo Shan], Szechuan, 1500–2000 m, Reitter E.” Two male paratypes: “Kuatun, 2300 m, 27.40°N; 117.40°E, L.J. Klapperich, 15.5.1938, (Fukien).” Two male paratypes: “Kwangtseh-Fukien, J. Klapperich, 8.10.1937.” One male paratype: “Tatsienlu, Yüling Süd, Szechuan China.” One female paratype: “Kuatun, Fukien, China, 15.6.46, leg. Tschung-Sen.” One male paratype: “Nördl Szechuan, China, Kwanhsien Em. Reitter.”

Additional material examined. 254 specimens (VNUF), all from Vietnam, baited pitfall traps, B. V. Bac leg. 234 specimens, Thanhhoa Prov., Pu Luong NR, 752–965 m, 20°28′54″–29′11″N; 105°14′22–41″E, 5.–20.iv.2016; 20 specimens, Caobang Prov., Pia Oac NR, 1154–1223 m, 22°34′3–24″N; 105°52′48″–53′3″E, 5.–20.v.2016.

Distribution and ecology. *Copris* (*C.*) *szechouanicus* has hitherto been known from China (Sichuan Province and Fujian Province) (e.g., Balthasar, 1963). In Vietnam it was found in both Pia Oac and Pu Luong NR with a higher number of individuals collected in the latter with 6 individuals/trap, compared with < 1 individual/trap in the former. *Copris szechouanicus* showed a strong preference for forest with 6.6 ± 1.1 and 8.9 ± 1.6 individuals/trap in primary and secondary forest, compared to 1.9 ± 0.4 individuals/trap in meadows ($F = 10.19$, $p < 0.001$) (Fig. 37).

Updated checklist of species of *Copris* in Vietnam

Balthasar (1939, 1958, 1963) divided *Copris* species occurring in the Oriental and Palearctic Regions into three subgenera: *Copris*, *Paracopris* and *Microcopris*, based on differences in the elytral and pronotal structures. This classification was used for the Southeast Asian species by Kabakov & Napolov (1999), Hanboonsong et al. (2003) and Ochi et al. (2004, 2008, 2009). Subsequently, the subgenus *Sinocopris* Ochi, 2009 was erected. Using Balthasar’s (1963) classification, we can place in subgenera almost all Vietnamese species, except the new species *C. caobangensis* sp. n., whose morphological characters do not fit any of the known subgenera in South East Asia.

The checklist of Vietnamese *Copris* below was mainly updated from Balthasar (1963), Kabakov & Napolov (1999), Hanboonsong et al. (2003), Ochi & Kon (2004) and Heyes et al. (2009). For the six species recorded in our

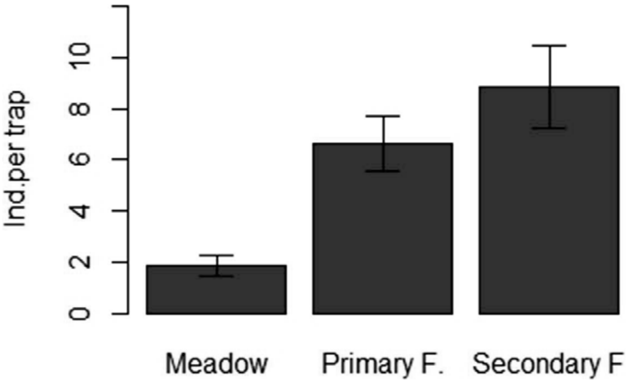


Fig. 37. Mean (± SE) numbers of *Copris* (*C.*) *szechouanicus* collected per trap-day in three areas with different land use intensities (F – forest).

field surveys we provide collecting details and their habitat preferences in limestone ecosystems.

Subgenus *Copris* Geoffroy, 1762

1. *Copris* (*Copris*) *angusticornis* Arrow, 1933. Distribution in Vietnam: North Vietnam (Caobang, Langson, Sonla provinces). Habitat recorded: montane tropical forest, 600–1500 m a.s.l. (Balthasar, 1963; Kabakov & Napolov, 1999).

Elsewhere: China and Thailand (Balthasar, 1963; Hanboonsong et al., 2003; Kabakov & Shokhin, 2014).

2. *Copris* (*Copris*) *carinicus* Gillet, 1910. Distribution in Vietnam: North Vietnam (Tuyenquang, Thainguyen, Backan, Vinhphuc, Sonla, Dienbien provinces), Central Vietnam (Thanhhoa Province) and South Vietnam (Gialai, Kontum provinces). Habitats recorded: primary tropical rainforest, secondary tropical forest and secondary savannah, 10–1800 m a.s.l. (Kabakov & Napolov, 1999; Heyes et al., 2009).

Elsewhere: India, Myanmar, Thailand and China (Balthasar, 1963; Hanboonsong et al., 2003; Boonrotpong et al., 2004; Kabakov & Shokhin, 2014).

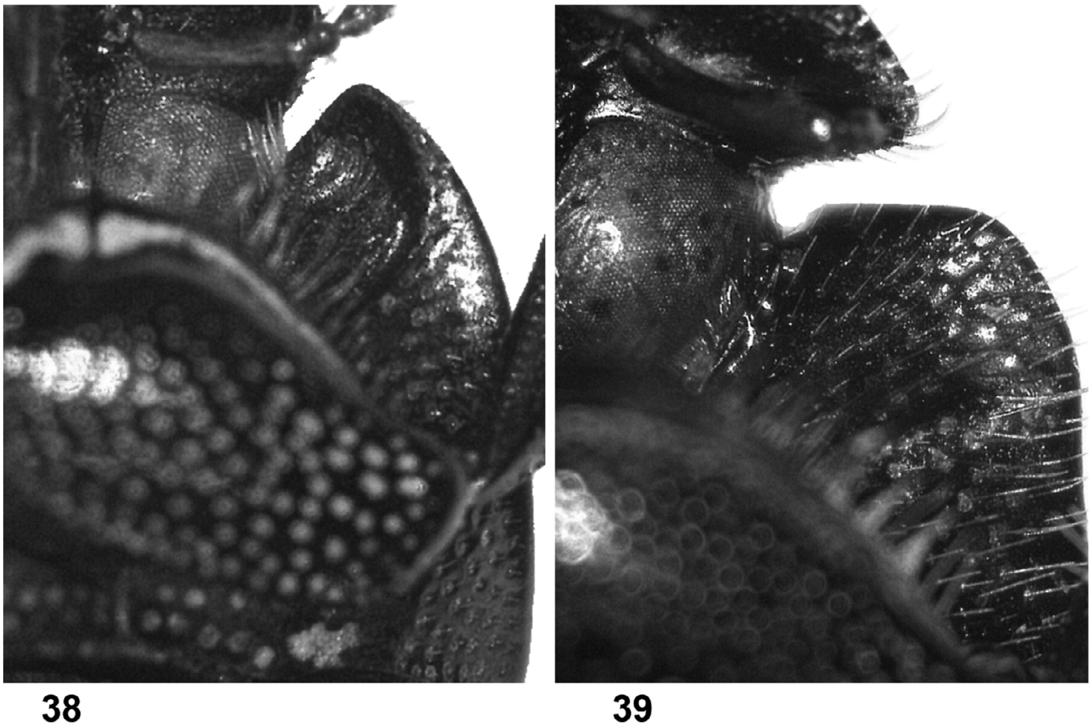
3. *Copris* (*Copris*) *confucius* Harold, 1877. Distribution in Vietnam: Thanhhoa Province, 750–950 m a.s.l., primary forest (15 individuals), secondary forest (4 individuals) and meadows (5 individuals). Outside the region studied, it was recorded widely in North Vietnam (Hagiang, Tuyenquang, Thainguyen, Vinhphuc, Quangninh, Laocai, Sonla provinces) and Central Vietnam (Nghean, Quangbinh provinces) (Balthasar, 1963; Kabakov & Napolov, 1999).

Elsewhere: Malaysia, Myanmar, Thailand, Laos, Cambodia and China (Balthasar, 1963; Hanboonsong et al., 2003; Kabakov & Shokhin, 2014).

4. *Copris* (*Copris*) *corpulentus* Gillet, 1910. Distribution in Vietnam: North Vietnam (Hagiang, Tuyenquang, Thainguyen, Vinhphuc, Quangninh, Sonla provinces) and Central Vietnam (Thanhhoa, Nghean, Hatinh, Quangbinh provinces). Habitats recorded: semiarid semi-deciduous tropical forest, montane tropical forest, secondary tropical forest and secondary savannah, 100–1600 m a.s.l. (Balthasar, 1963; Kabakov & Napolov, 1999).

Elsewhere: India, Myanmar, Thailand, Laos and China (Balthasar, 1963; Hanboonsong et al., 2003; Sewak, 2009; Kabakov & Shokhin, 2014).

5. *Copris* (*Copris*) *iris* Sharp, 1875. Distribution in Vietnam: this species occurs in Vietnam according to Balthasar (1963) and Hanboonsong et al. (2003), but there is no locality data recorded for it.


38
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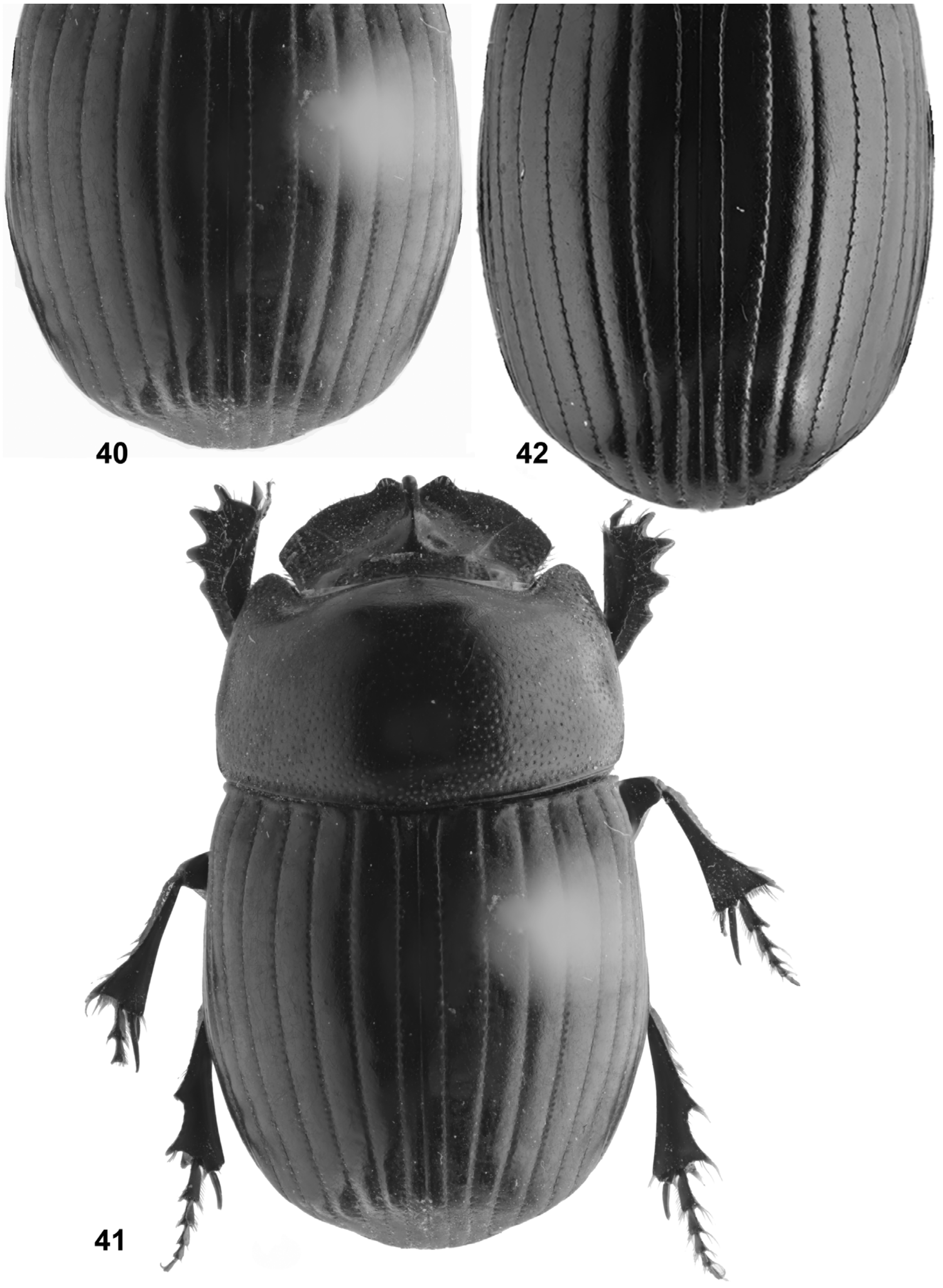
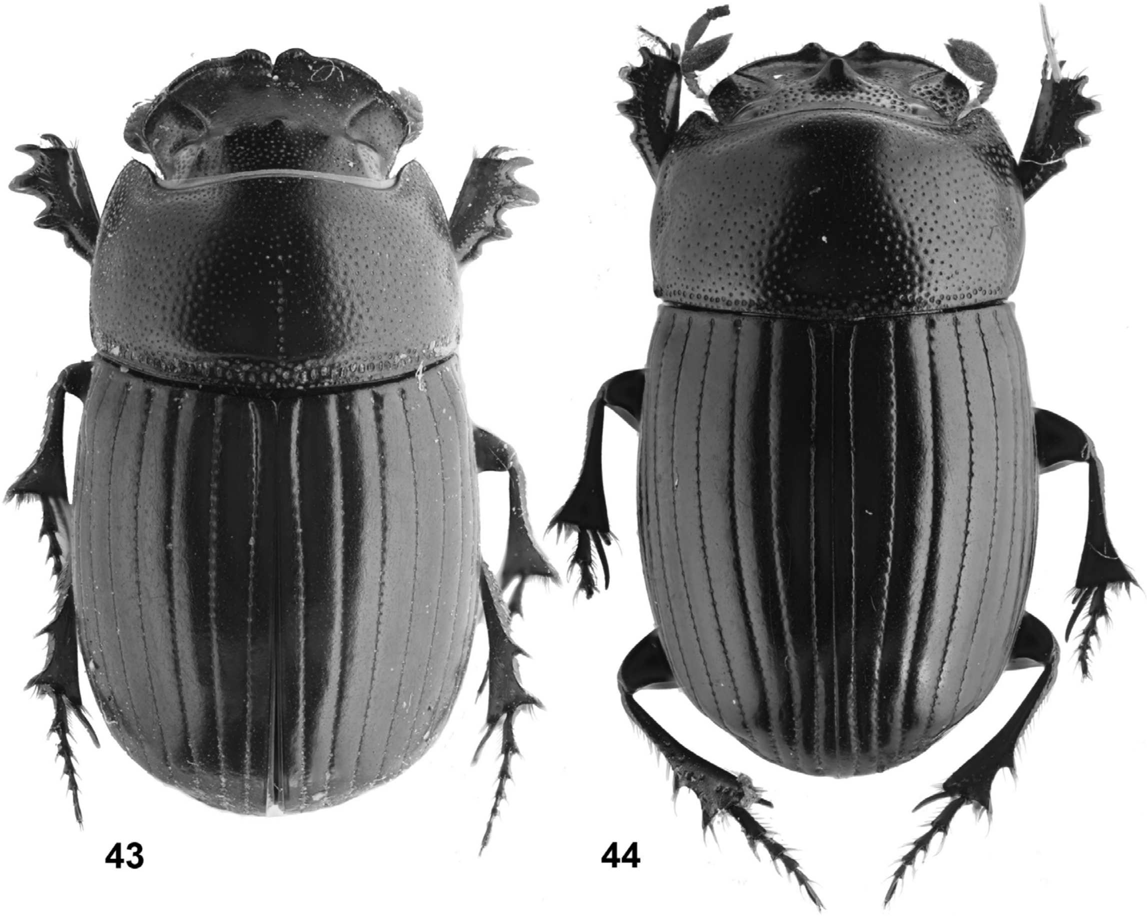
Figs 38, 39. Front angles of prothorax in ventral view. 38 – *Copris* (*Microcopris*) *propinquus* showing the angle at the front of prothorax with deep excavation; 39 – *C.* (*Copris*) *magicus* showing the angle at the front of prothorax without excavation.



Figs 40–42. Dorsal habitus and elytral characters. 40, 41 – *Copris* (*Microcopris*) *doriae*, male, elytra and dorsal habitus; 42 – *C.* (*M.*) *propinquus*, elytra.

Elsewhere: India, Malaysia, Myanmar, Laos, Thailand and China (Balthasar, 1963; Hanboonsong et al., 2003; Sewak, 2009).

6. *Copris* (*Copris*) *magicus* Harold, 1881. Distribution in Vietnam: According to Kabakov & Napolov (1999), this species occurs in Sapa (1700–2000 m a.s.l.) and Fansipan (2000–2600 m a.s.l.) (Laocai Province, northern Vietnam) and Muongxen (800–1100 m a.s.l.) (Nghean Province, central Vietnam), in montane tropical forest. In our study, this species was newly recorded for Caobang Province



Figs 43, 44. Dorsal habitus. 43 – *Copris* (*Microcopris*) *reflexus*; 44 – *C.* (*M.*) *propinquus*, male.

(northern Vietnam), 1150–1220 m a.s.l., meadows (16 individuals) and primary forest (1 individual).

Elsewhere: India, Laos, Myanmar, Thailand and China (Balthasar, 1963; Hanboonsong et al., 2003; Kabakov & Shokhin, 2014).

7. *Copris* (*Copris*) *nevinsoni* Waterhouse, 1891. Distribution in Vietnam: Binhduong Province (South Vietnam). Habitat recorded: semiarid semi-deciduous tropical forest (Balthasar, 1963; Kabakov & Napolov, 1999).

Elsewhere: Malaysia, Laos and Thailand (Balthasar, 1963; Hanboonsong et al., 2003).

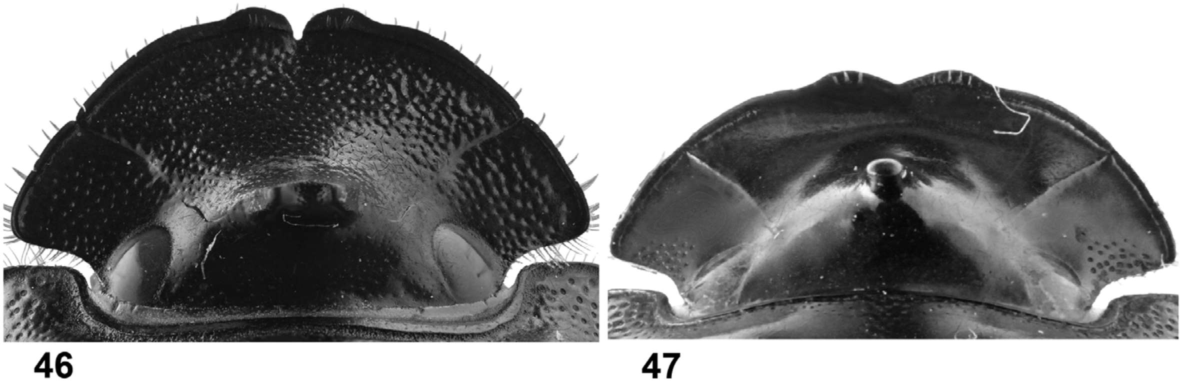
8. *Copris* (*Copris*) *numa* Lansberge, 1886. Distribution in Vietnam: Nghean Province (Central Vietnam). Habitats recorded: semiarid semi-deciduous tropical forest and montane tropical forest, 300–1000 m a.s.l. (Kabakov & Napolov, 1999).

Elsewhere: India, Myanmar, Malaysia, Indonesia and Thailand (Balthasar, 1963; Hanboonsong et al., 2003; Sewak, 2009).

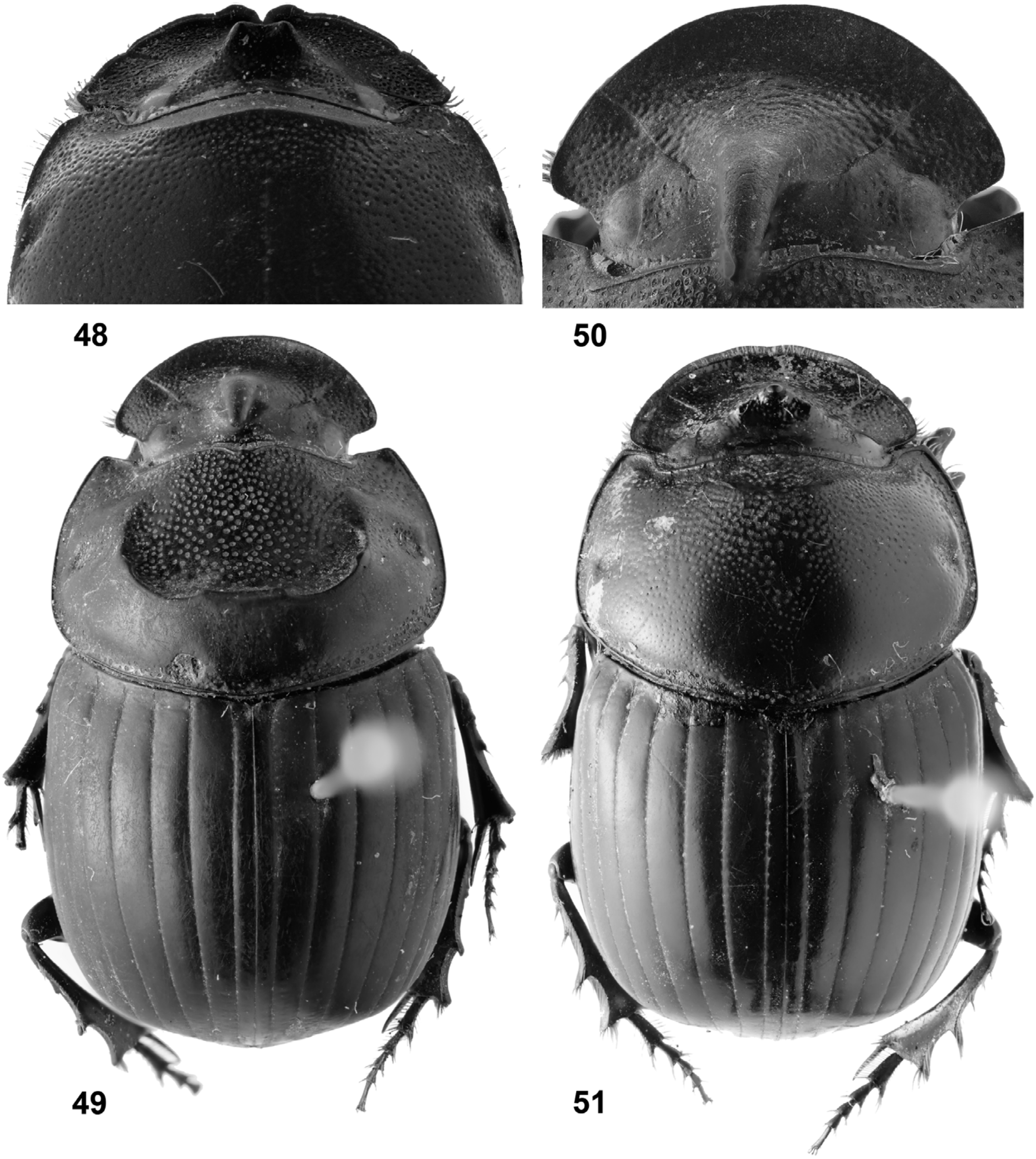
9. *Copris* (*Copris*) *repertus* Walker, 1858. Distribution in Vietnam: Nghean Province (Central Vietnam). Habitats recorded: montane tropical forest, secondary tropical forest and secondary savannah, 300–1100 m a.s.l. (Kabakov & Napolov, 1999).

Elsewhere: India, Sri Lanka and China (Balthasar, 1963; Sabu et al., 2006; Sewak, 2009; Kabakov & Shokhin, 2014).

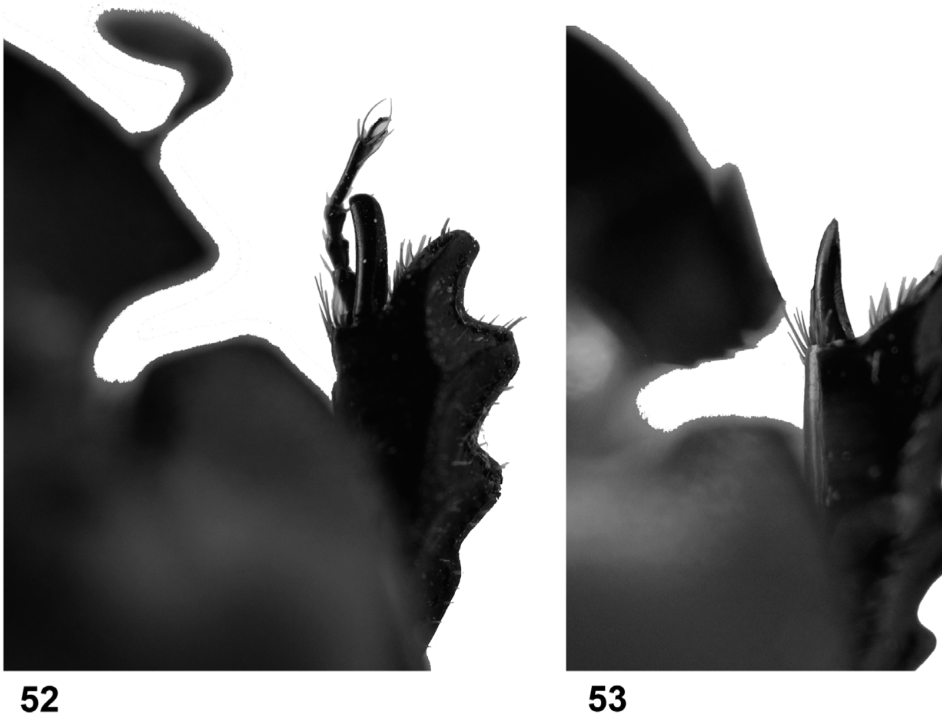
Fig. 45. *Copris* (*Paracopris*) *punctulatus*, dorsal habitus, male.



Figs 46, 47. Clypeal surfaces. 46 – *Copris* (*Copris*) *sinicus* showing clypeus with deep and distinct punctures; 47 – *C.* (*C.*) *szechouanicus* showing clypeus without punctures.



Figs 48–51. Dorsal habitus and form of clypeal apex and pronotal structures. 48 – *Copris* (*Copris*) *carinicus* female, showing clypeal apex with distinct emargination and pronotum with median sulcus; 49–51 – *C.* (*C.*) *iris*, male dorsal habitus, clypeal apex, and female dorsal habitus showing clypeal apex without emargination and male pronotum with a large excavation.



Figs 52, 53. Form of protibial spurs. 52 – *Copris* (*Copris*) *sinicus* showing protibial spur curved inwards near apex; 53 – *C.* (*C.*) *magicus* showing protibial spur curved outwards near apex.

10. *Copris* (*Copris*) *sinicus* Hope, 1842. Distribution in Vietnam: North Vietnam (Hagiang, Tuyenquang, Vinhphuc, Quangninh, Sonla, Dienbien provinces), Central Vietnam (Thanhhoa, Nghean, Quangbinh provinces) and South Vietnam (Gialai, Kontum, Dongnai provinces). Habitats recorded: semiarid semi-deciduous tropical forest, secondary tropical forest and cultural landscape; 10–1800 m a.s.l. (Kabakov & Napolov, 1999).

Elsewhere: India, Malaysia, Myanmar, Cambodia and China (Balthasar, 1963; Davis et al., 2001; Hanboonsong et al., 2003; Kabakov & Shokhin, 2014).

11. *Copris* (*Copris*) *sonensis* sp. n. Collecting details: Thanhhoa Province, 850–960 m a.s.l., secondary forest (9 individuals) and primary forest (3 individuals).

12. *Copris* (*Copris*) *sorex* Balthasar, 1942. Distribution in Vietnam: Tamdao National Park (Vinhphuc Province, northern Vietnam). Habitat recorded: montane tropical forest; 900–1000 m a.s.l. (Kabakov & Napolov, 1999).

Elsewhere: China (Balthasar, 1963).

13. *Copris* (*Copris*) *szechouanicus* Baltharsar, 1958, a newly recorded species for Vietnam. Distribution in Vietnam: Thanhhoa and Caobang provinces. This species was mainly found in forest with 102 and 125 individuals collected in primary and secondary forest, respectively, while only 27 individuals were collected in meadows; 780–1200 m a.s.l.

Elsewhere: China (Balthasar, 1963).

14. *Copris* (*Copris*) *vietnamicus* Kabakov, 1994. Known only from Vietnam: Tamdao National Park (Vinhphuc Province, northern Vietnam). Habitat recorded: montane tropical forest; 900–1000 m a.s.l. (Kabakov & Napolov, 1999).

Subgenus *Paracopris* Balthasar, 1939

15. *Copris* (*Paracopris*) *cariniceps* Felsche, 1910. Distribution in Vietnam: North Vietnam (Hagiang, Tuyenquang, Backan provinces) and Central Vietnam (Thanhhoa, Nghean provinces). Habitat recorded: lowland evergreen forest (Kabakov & Napolov, 1999; Heyes et al., 2009).

Elsewhere: China, Thailand (Balthasar, 1963; Hanboonsong et al., 2003; Kabakov & Shokhin, 2014).

16. *Copris* (*Paracopris*) *punctulatus* Wiedeman, 1823. Distribution in Vietnam: North Vietnam (Sonla, Dienbien provinces) and Central Vietnam (Quangbinh Province) (Balthasar, 1963; Kabakov & Napolov, 1999).

Elsewhere: India, Indonesia, Malaysia, Myanmar, Laos, Cambodia, Thailand and China (Balthasar, 1963; Hanboonsong et al., 2003; Sewak, 2009; Shahabuddin, 2010; Bai et al., 2011).

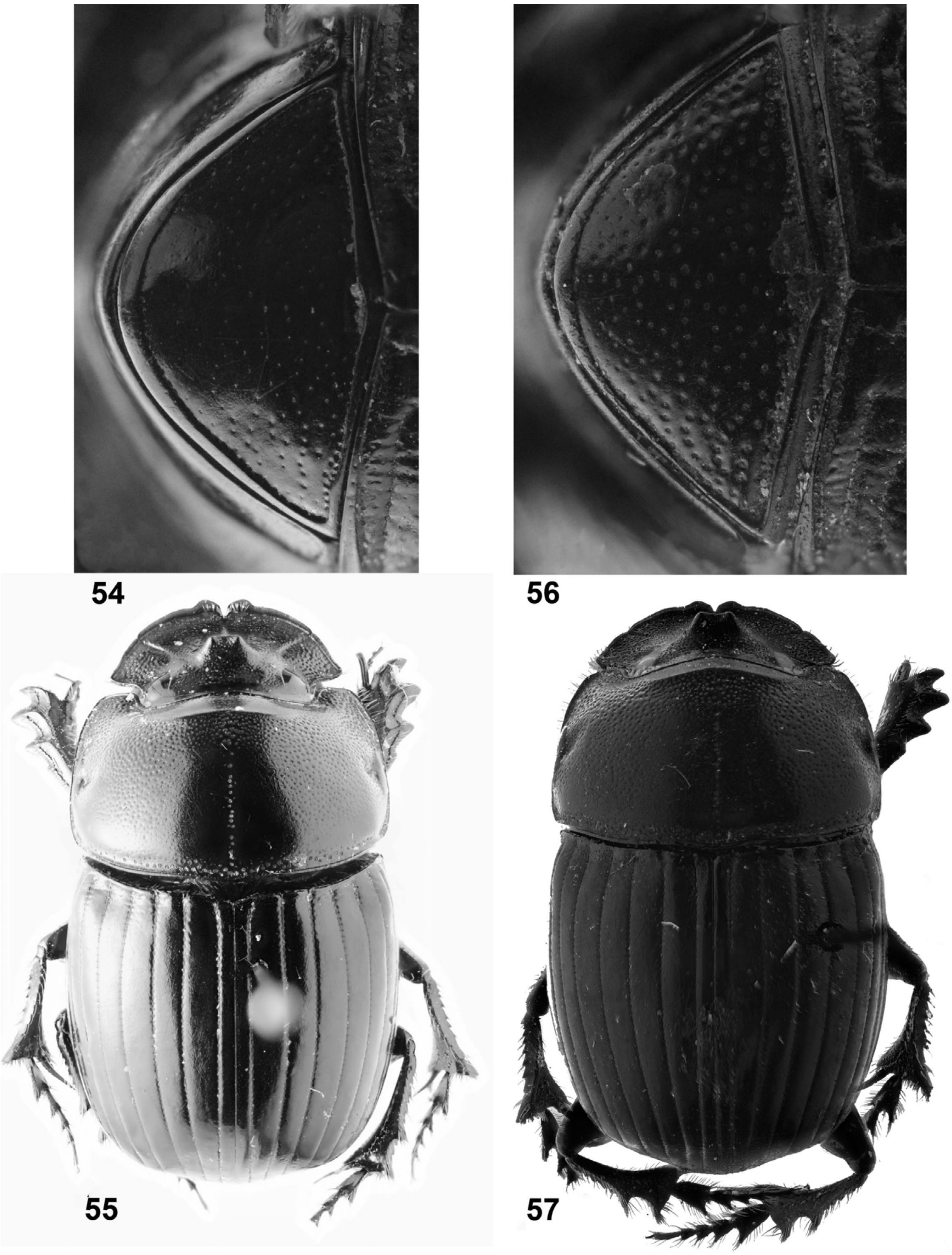
Subgenus *Microcopris* Balthasar, 1958

17. *Copris* (*Microcopris*) *doriae* Harold, 1877. Distribution in Vietnam: North Vietnam (Vinhphuc, Laocai provinces) and Central Vietnam (Nghean Province). Habitats recorded: montane tropical forest and secondary savannah, 500–1700 m a.s.l. (Kabakov & Napolov, 1999).

Elsewhere: Malaysia, Indonesia, “Indochina” and Myanmar (Arrow, 1931; Balthasar, 1963; Davis et al., 2001; Qie et al., 2011; Doll et al., 2014).

18. *Copris* (*Microcopris*) *miyakei* Ochi & Kon, 2004. Known only from Vietnam: Caobang Province (North Vietnam) (Ochi & Kon, 2004).

19. *Copris* (*Microcopris*) *propinquus* Felsche, 1910. Distribution in Vietnam: in our surveys, almost all specimens were collected in Thanhhoa Province (115 speci-

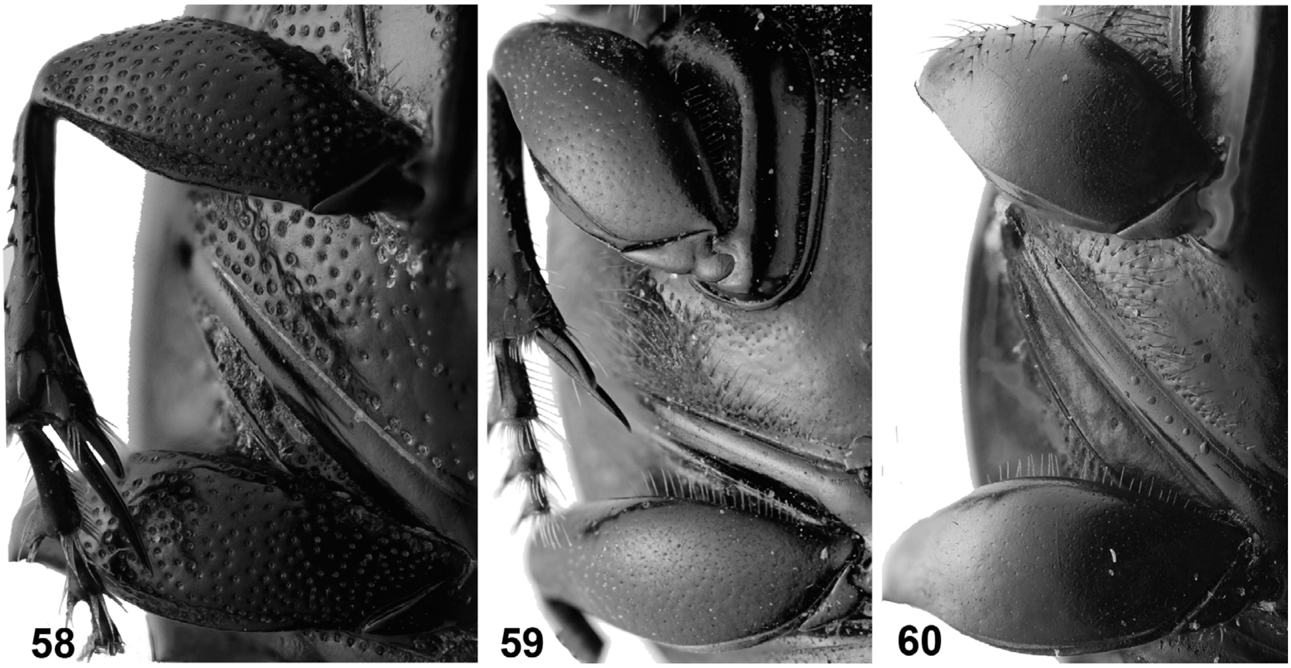


Figs 54–57. Dorsal habitus and pygidium. 54, 55 – *Copris* (*Copris*) *sinicus*, female, pygidium and habitus; 56, 57 – *C.* (*C.*) *carinicus*, female, pygidium and habitus.

mens) and only 7 specimens in Caobang Province. Strong preference of *C.* (*M.*) *propinquus* for secondary forest with 65 specimens collected in this habitat compared to 44 and 6 specimens in meadows and primary forest, respectively. No specimen was collected in meadows and primary forest in Caobang. According to Kabakov & Napolov (1999), this species is widespread in North Vietnam (Tuyenquang, Thainguyen, Backan, Vinhphuc, Quangninh provinces), Central Vietnam (Thanhhoa, Nghean, Hatinh, Quangbinh provinces) and South Vietnam (Gialai, Kontum provinces). Habitats recorded: semiarid semi-deciduous tropical forest, montane tropical forest, secondary tropical forest, cultural landscape and secondary savannah; 10–1100 m a.s.l. (Kabakov & Napolov, 1999; Heyes et al., 2009).

Elsewhere: China, Laos (Balthasar, 1963; Kabakov & Shokhin, 2014).

20. *Copris* (*Microcopris*) *reflexus* Fabricius, 1787. Distribution in Vietnam: North Vietnam (Hanoi, Hagiang,



Figs 58–60. Ventral surfaces of right meso- and metafemora. 58 – *Copris* (*Copris*) *angusticornis*, showing deep and coarse punctures; 59 – *C.* (*C.*) *repertus*, showing shallow but distinct punctures, 60 – *C.* (*C.*) *magicus*, showing indistinct punctures.

Caobang, Backan, Tuyenquang, Thainguyen, Vinhphuc, Langson, Quangninh, Haiphong, Laocai, Hoabinh, Sonla, Laichau, Dienbien provinces), Central Vietnam (Thanhhoa, Nghean, Hatinh, Quangbinh, Quangtri provinces) and South Vietnam (Gialai, Kontum provinces). Habitats recorded: various habitats from forest, meadows to cultural landscape; 10–2000 m a.s.l. (Kabakov & Napolov, 1999; Heyes et al., 2009).

Elsewhere: "Indochina", Thailand, Myanmar, Malaysia, Indonesia, China and Taiwan (Balthasar, 1963; Davis et al., 2001; Boonrotpong et al., 2004; Kabakov & Shokhin, 2014).

21. *Copris* (subgenus incertae sedis) *caobangensis* sp. n. Collecting details: Caobang Province, primary forest (3 individuals).

Key to species of *Copris* recorded from Vietnam

The key to 21 Vietnamese *Copris* is based on the specimens examined by us in NMPC, RMNH and VNUF, and data published by Arrow (1931), Balthasar (1933, 1958, 1963), Kabakov (1994), Hanboonsong et al. (2003) and Ochi & Kon (2004).

The key makes separation of sexes possible for 15 species. Females of two species, *C.* (*Microcopris*) *miyakei* and *C.* (*Copris*) *vietnamicus* are unknown. Both sexes are similar externally (and thus not separated in the key) in four species: *C.* (*Microcopris*) *reflexus, C.* (*Copris*) *corpulentus*, *C.* (*C.*) *confucius* and *C.* (*C.*) *numa.*

1 Anterior angles of prothorax with deep excavation on ventral side (Fig. 38).. 2
– Anterior angles of prothorax flat, without excavation on ventral side (Fig. 39) 5
2 Pronotum with transverse carina on the upper part of the anterior declivity (males only, females unknown) .... *C.* (*Microcopris*) *miyakei*
– Pronotum without transverse anterior carina....................... 3
3 Body length 12–16 mm. Maximum elytral width greater than maximum elytral length. Males: cephalic horn short, slender, and curved backwards (Figs 40, 41). Females: cephalic horn indistinct ....*C.* (*Microcopris*) *doriae*
– Body length 7–11 mm. Maximum elytral length greater than maximum elytral width (Fig. 42)... 4
4 Clypeal apex with narrow and deep emargination. Both sexes alike externally, with cephalic horn indistinct (Fig. 43) .... *C.* (*Microcopris*) *reflexus*
– Clypeal apex with wide and shallow emargination. Males: cephalic horn short but distinct (Fig. 44). Females: cephalic horn indistinct.......................... *C.* (*Microcopris*) *propinquus*
5 Elytral interstriae deeply punctate (Figs 13, 15).................. 6
– Elytral interstriae shallowly or indistinctly punctate (Figs 17, 19)... 9
6 Pronotum with sharp anterior declivity. Males: pronotal disc armed with two forwardly directed prominences on dorsal side and one upwardly directed prominence on each side, and with deep excavation on each side. Females: pronotal disc unarmed and without excavations 7
– Pronotum without sharp anterior declivity. Both sexes: pronotal disc unarmed and without excavations....................... 8
7 Body length 11.8–12.0 mm. Punctures on interstriae and pronotum equal in size. Males: cephalic horn long, curved backwards; clypeal apex with weak emargination (Figs 1, 4). Females: cephalic horn short, straight, excavated at apex; clypeal apex with strong emargination (Figs 7, 10) ....*C.* (subg. incertae sedis) *caobangensis* sp. n.
– Body length 14.5 mm. Punctures on interstriae smaller than those on pronotum. Males: cephalic horn nearly straight; clypeal apex with deep emargination. Females unknown .... *C.* (*Copris*) *vietnamicus*
8 Pronotum and elytra sparsely punctate. Males: clypeal apex protrudes upwards (Fig. 45). Females: clypeal apex truncate. .... *C.* (*Paracopris*) *punctulatus*
– Pronotum and elytra densely punctate. Males: clypeal apex indistinctly emarginated and not protruding upwards; ce-

Figs 61–64. Male protibial spurs and dorsal habitus. 61, 62 – *Copris* (*Copris*) *angusticornis*; 63, 64 – *C.* (*C.*) *sorex*.

phalic horn short but distinct. Females: clypeal apex deeply emarginated; cephalic horn indistinct.. *C.* (*Paracopris*) *cariniceps*

9 Clypeus and anterior part of genae rugose or deeply punctate (Fig. 46) 10

– Clypeus and anterior part of genae smooth, almost impunctate (Fig. 47) 16

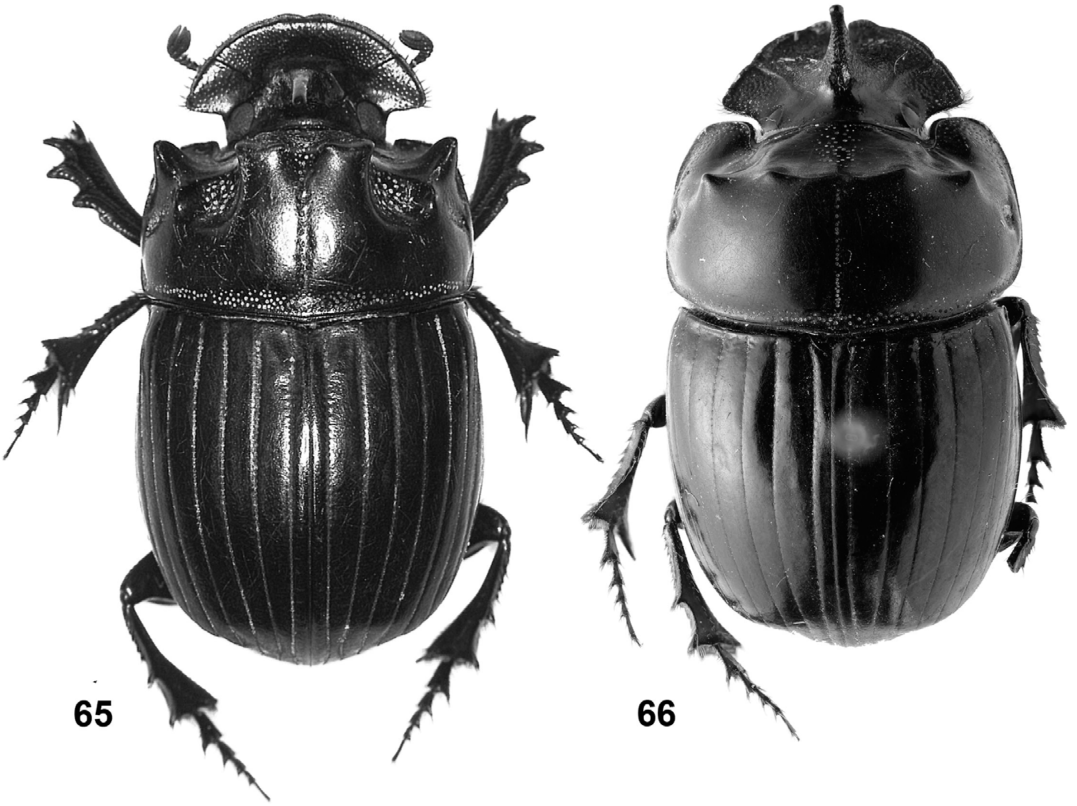
10. Clypeal apex with distinct emargination. Pronotum with median sulcus (Fig. 48) 11

– Clypeal apex without emargination. Pronotum without median sulcus. Males: cephalic horn long, strongly curved backwards; pronotal disc with large excavation (Figs 49, 50). Females: cephalic horn short, straight; pronotal disc without excavation (Fig. 51)...*C.* (*Copris*) *iris*

11. Protibial spur curved inwards near apex (Fig. 52).............. 12

– Protibial spur straight or curved outwards near apex (Fig. 53).. 13

12 Pygidium sparsely, weakly and unevenly punctate. Males: pronotal disc with weak prominences; cephalic horn long, slender and with two minute teeth at base. Females: pronotal disc without prominences; cephalic horn short, straight and deeply excavated at apex (Figs 54, 55)..... *C.* (*Copris*) *sinicus*



Figs 65, 66. Dorsal habitus. 65 – *Copris* (*Copris*) *magicus*, large male; 66 – *C.* (*C.*) *repertus*, large male.

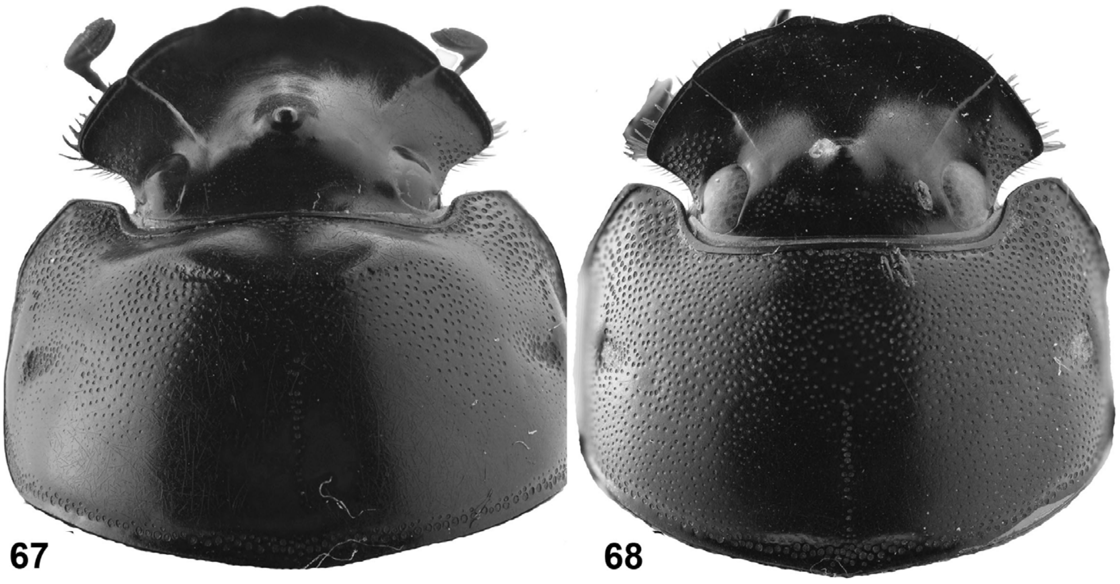
– Pygidium densely, deeply and evenly punctate. Males: pronotal disc with weak prominences; cephalic horn relatively long, slender and without teeth at base. Females: pronotal disc without prominences; cephalic horn short, straight and slightly excavated at apex (Figs 56, 57) .... *C.* (*Copris*) *carinicus*

13 Mesofemora and metafemora strongly and coarsely punctate (Fig. 58) 14

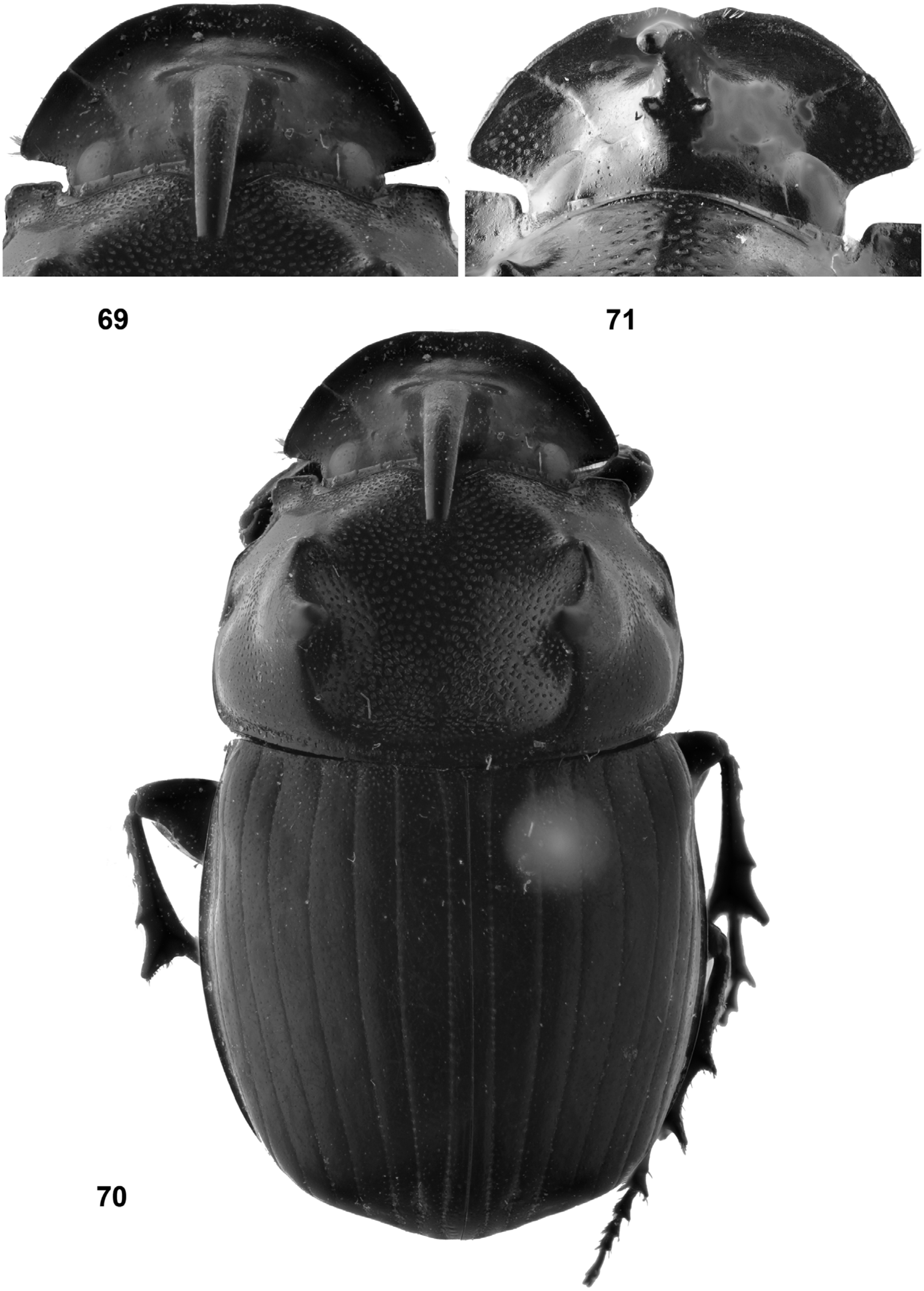
– Mesofemora and metafemora weakly (Fig. 59) or indistinctly punctate (Fig. 60).. 15

14 Body length 11.5–14.0 mm. Protibial spur curved outwards near apex. Males: cephalic horn long (4.5–5.5 mm); pronotal disc with strong prominences on dorsal side and with deep excavations on each side (Figs 61, 62). Females: cephalic horn short (1.5–2 mm); pronotal disc without prominences and not excavated on each side...... *C.* (*Copris*) *angusticornis*

– Body length 9.5–11.0 mm. Protibial spur straight. Males: cephalic horn short (approximately 1.5 mm); pronotal disc without prominences on dorsal side, and with a weak excavation on each side (Figs 63, 64). Females: cephalic horn indistinct; frons slightly swollen; pronotal disc without prominences, and not excavated ....*C.* (*Copris*) *sorex*



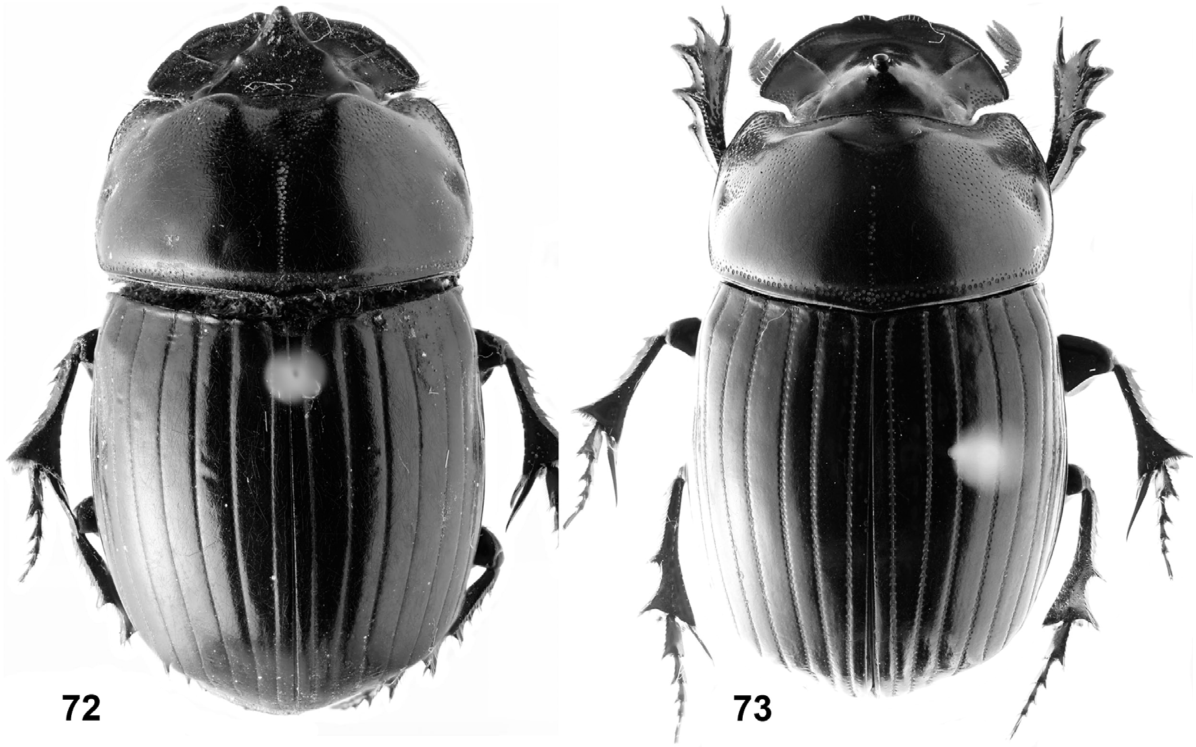
Figs 67, 68. Form of pronotum. 67 – *Copris* (*Copris*) *szechouanicus* showing pronotum with sharp anterior declivity; 68 – *C.* (*C.*) *numa* showing pronotum without sharp anterior declivity.



Figs 69–71. Dorsal habitus and form of clypeal apex. 69, 70 – *Copris* (*Copris*) *nevinsoni*, male, showing clypeal apex without emargination; 71 – *C.* (*C.*) *sonensis* sp. n. showing clypeal apex with emargination.

15 Body length 18–22 mm. Elytra strongly striate. Mesofemora and metafemora indistinctly punctate. Males: cephalic horn pointed and curved backwards; large individuals: pronotal disc with deep excavation on each side (Fig. 65); small individuals: pronotal disc with weak excavation on each side. Females: cephalic horn excavated at apex; pronotal disc indistinctly excavated .... *C.* (*Copris*) *magicus*

– Body length 16–22 mm. Elytra weakly striate. Mesofemora and metafemora shallowly but distinctly punctate. Males: cephalic horn long, slightly curved backwards, pointed and with



Figs 72, 73. Dorsal habitus. 72 – *Copris* (*Copris*) *corpulentus*; 73 – *C.* (*C.*) *szechouanicus*, female.

two small teeth at base; large individuals: pronotal disc with weak excavation on each side (Fig. 66); small individuals without excavations; Females: cephalic horn short, straight and excavated at apex .... *C.* (*Copris*) *repertus*

16 Pronotum with sharp anterior declivity (Fig. 67) 17

– Pronotum without sharp anterior declivity (Fig. 68) 20

17 Clypeal apex without emargination. Males: cephalic horn long and strongly curved backwards; pronotal disc with one large central excavation (Figs 69, 70). Females: cephalic horn short and straight; pronotal disc without excavation .... *C.* (*Copris*) *nevinsoni*

– Clypeal apex with distinct emargination (Fig. 71) 18

18 Medium sized species, body length 13.3–15.2 mm (n = 9). Males: pronotum with a deep excavation along each side; cephalic horn long, slightly curved backwards (Figs 20, 32). Females: pronotum without excavations; cephalic horn short, straight and strongly excavated at apex (Figs 27, 29) .... *C.* (*Copris*) *sonensis* sp. n.

– Large species, body length 15–21 mm. Both sexes: pronotum without excavations on each side; cephalic horn short, straight and pointed (not excavated).................................. 19

19 Anterior part of pronotum with pair of protuberances. Both sexes alike externally (Fig. 72)......... *C.* (*Copris*) *corpulentus*

– Pronotum with transverse carina on upper part of anterior declivity. Males: pronotal carina interrupted by longitudinal sulcus. Females: pronotal carina not interrupted (Fig. 73)..... .... *C.* (*Copris*) *szechouanicus*

20 Vertex with deep and contiguous punctures. Punctures on genae deep, dense and surround eyes. Clypeal apex with narrow and deep emargination. Both sexes alike externally (Figs 74, 75)... *C.* (*Copris*) *confucius*

– Vertex with punctures separate. Punctures on genae shallow and do not surround eyes. Clypeal apex with wide and shallow emargination. Both sexes alike externally (Figs 75, 76) . ... *C.* (*Copris*) *numa*

Molecular analysis

Analysis of the cytochrome oxidase I sequences (Table 1; *Onthophagus* was used as outgroup) resolved monophyletic and well supported genera *Copris* and *Catharsius* (Appendix 1). Both Maximum Likelihood analysis and MrBayes provided trees with the same conformation. *Copris sonensis* sp. n. was clearly distant from other available *Copris* species and the male and female showed only slight differences (three base pairs) in their COXI gene sequences.

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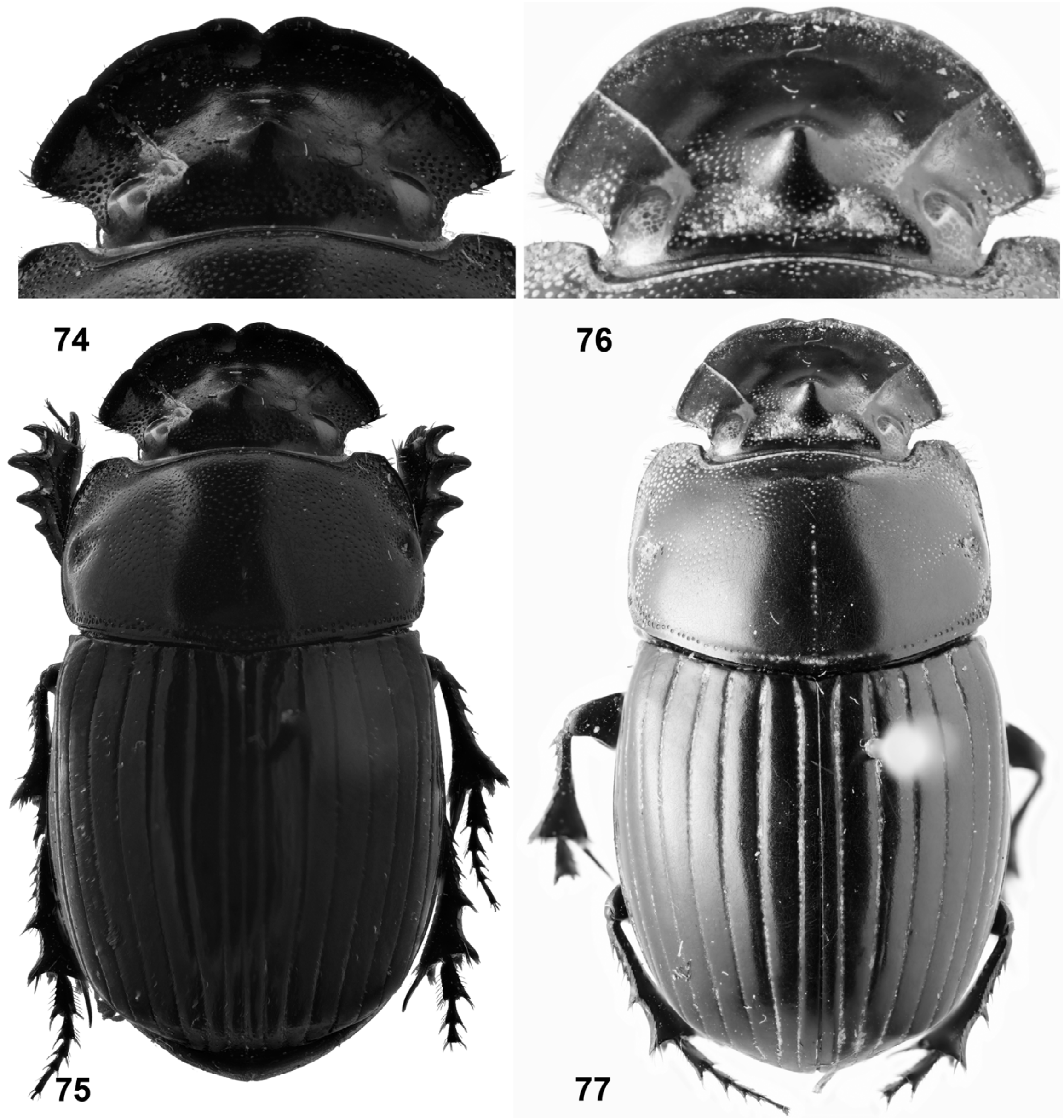

Figs 74–77. Dorsal habitus and form of clypeus. 74, 75 – *Copris* (*Copris*) *confucius* showing clypeal apex with narrow and deep emargination; 76, 77 – *C.* (*C.*) *numa* showing clypeal apex with wide and shallow emargination.

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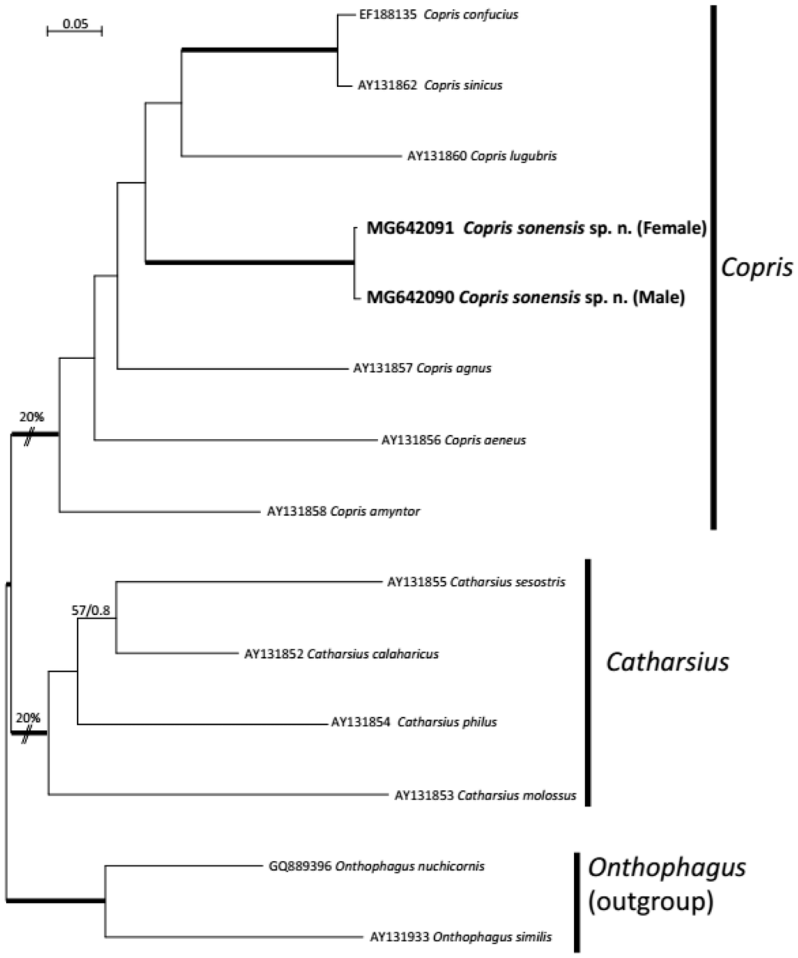

Appendix 1. Molecular relationships of *Copris* and *Catharsius* based on COXI; *Onthophagus* was used as the outgroup. Shown is the maximum likelihood tree obtained using the PhyML GTR+I+G analyses including 14 sequences and 837 aligned sites of which 67.03% were invariant. The support levels of the PhyML and the Bayesian analysis are shown on the respective branches (ML/BI) if support was over 50 BP/0.8 PP. Bold lines indicate bootstrap support > 99%. Support under 50% or 0.8 are omitted. Some branches were reduced to 20% of their branch length (//) to improve readability of the tree. The beetles sequenced in this study are highlighted in bold.

Manuscript prepared for publication:

Copris (*Paracopris*) Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae) from Asia with description of a new species, and redescription of *Copris* (*Paracopris*) *punctulatus*

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Key words. Coleoptera, Scarabaeidae, *Copris*, *Paracopris*, taxonomy, new species, Asia, Indonesia, Java.

Abstract

We present the first checklist of Asian members of the *Copris* (*Paracopris*) Balthasar, 1939 and provide data on the distribution of the Asian *Paracopris* species. In addition, *Copris* (*Paracopris*) *javanensis* **sp. nov.** from Java (Indonesia) is described as a new species of *Copris* (*Paracopris*) Balthasar, 1939 and illustrated and *Copris* (*Paracopris*) *punctulatus* is thoroughly re-described and morphologically compared with *C. javanensis* **sp. nov.** based on a series of new materials from Vietnam and Indonesia.

Introduction

The genus *Copris* Geoffroy, 1762 is globally distributed with currently more than 235 species formally being described (Davis et al., 2008). Over a third of all species have been recorded in the Palaearctic and Oriental Region (Balthasar, 1963; Davis et al., 2008). The genus *Copris* is commonly divided into the four subgenera *Copris*, *Paracopris*, *Microcopris* and *Sinocopris* according to morphological characteristics of the elytra and the pronotum (Balthasar, 1939, 1958 & 1963; Ochi et al., 2009). Many of the Asian *Copris* species have been only recently discovered and described (Ochi et al., 2004, 2008, 2009 & 2018; Bui et al., 2018). Yet, we still have an incomplete understanding of these taxa, especially in the subgenus *Copris* (*Paracopris*) Balthasar, 1939 with only the species, *Copris* (*Paracopris*) *kasagii* Ochi & Kon, 1996 being described since the work of Balthasar (1939). *Paracopris* is particularly problematic, due to only minute morphological differences in the elytral and pygidial punctures between species, coupled with significant intraspecific morphological variation across different habitats. These poorly defined morphological boundaries between *C.* (*Paracopris*) species pose major problems for the delineation and identification of *C.* (*Paracopris*) species. In order to enable a reliable species identification of the Asian dung beetles in the subgenus *Paracopris*, we morphologically re-examined numerous Asian *Copris* species deposited in the Muséum National D'Histoire Naturelle (MNHN) (Paris, France) and the National Museum, Prague, Czech Republic (NMPC), and found one undescribed *Copris* species from Java (Indonesia). This species could be assigned to the subgenus *Copris* (*Paracopris*) due to the possession of distinctly punctate elytral intervals and an anteriorly untruncated pronotum. The external morphology of the undescribed species bears much resemblance to *Copris* (*Paracopris*) *punctulatus* Wiedemann, 1823, especially in the upwards protruded clypeal apex, but it consistently differed from the latter due to its densely, but separately punctate pygidium. In addition, morphological differences of the aedeagi clearly separate both species. Accordingly we describe this new species, and re-describe its resembling species *C.* (*P.*) *punctulatus*, with the detailed illustrations of both sexes and the male genitalia. We complement these species descriptions with the checklist of the Asian members of the subgenus *Copris* (*Paracopris*) along with data on the distribution of the known Asian *Paracopris* species.

Materials and methods

Specimens and collections: comparative materials of the following species were examined in the Muséum National D'Histoire Naturelle (Paris, France) (MNHN) (curator: O. Montreuil) and the National Museum, Prague, Czech Republic (NMPC) (curator: J. Hájek): *Copris* (*Paracopris*) *cariniceps* Felsche, 1910, *Copris* (*Paracopris*) *excisus* Waterhouse, 1891, *Copris* (*Paracopris*) *furciceps* Felsche, 1910, *Copris* (*Paracopris*) *imitans* Felche, 1910, *Copris* (*Paracopris*) *punctulatus* Wiedemann, 1823 and *Copris* (*Paracopris*) *signatus* Walker, 1858.

Measurements: The following morphological traits were measured

BoL	body length from anterior margin of clypeus to posterior margin of elytra;
BoW	maximum body width;
HeadL	head length from anterior most point of clypeus to posterior margin of head;
HeadW	maximum head width;
PronL	maximum pronotum length;
PronW	maximum pronotum width;
ElyL	elytra length from apex to base;
PyL	maximum pygidium length;
PyW	maximum pygidium width;
PhaW	maximum phallobase width
PaW	maximum paramere width

Qualification of the density of punctures on the surface of elytra, pygidium and pro-meso-metafemora as follow:

Contiguous punctures (0)	distance between punctures: 0
Very dense punctures (1)	distance between punctures: < 1 x diameter of the puncture
Dense punctures (2)	distance between punctures: 1–2 x diameter of the puncture
Sparse punctures (3)	distance between punctures: >2 x diameter of the puncture

The elytral punctures were measured at the middle of the second elytral interval, the pygidial punctures were measured at middle, and the femoral punctures were also measured at middle.

Checklist of species of the subgenus *Copris* (*Paracopris*) Balthasar, 1939 in Asia

The below checklist of the Asian *Copris* (*Paracopris*) species was compiled based on Arrow (1931), Balthasar (1963), Ochi and Kon (1996), Kabakov and Napolov (1999), Kabakov and Shokhin (2014), Hanboonsong et al. (2003), Sewak (2009), Shahabuddin (2010), Bai et al. (2011), Sabu and Vinod (2011) and Cheung et al. (2018) as well as locality information on the labels of the materials deposited in MNHN and NMPC.

1. *Copris* (*Paracopris*) *andrewesi* Waterhouse, 1891. Distribution: India (Karnataka, Madhya Pradesh, Maharashtra, Orissa, Rajasthan) (Arrow, 1931; Balthasar, 1963; Sewak, 2009).

2. *Copris* (*Paracopris*) *anomiopseoides* Boucomont, 1924. Distribution: Laos, Myanmar and "Indo-China" (Arrow, 1931; Balthasar, 1963).

3. *Copris* (*Paracopris*) *cariniceps* Felsche, 1910. Distribution: China (Hong Kong, Jiujiang, Fujian, Jiangxi, Jiangxu, Shanghai, Taiwan, Yunnan, Zhejiang, Nanjing, Yunnan, Sichuan), Vietnam (Hagiang, Tuyenquang, Backan,Thanhhoa, Nghean), Laos and Thailand (Balthasar, 1963; Kabakov & Napolov, 1999; Hanboonsong et al., 2003; Kabakov & Shokhin, 2014; Cheung et al., 2018).

4. *Copris* (*Paracopris*) *compressipennis* Gillet, 1910. Distribution: India (Sikkim, Assam) (Arrow, 1931; Balthasar, 1963).

5. *Copris* (*Paracopris*) *cribratus* Gillet, 1927. Distribution: India (Arunachal Pradesh, Gujarat, Kerala, Meghalaya, Rajasthan, Uttar Pradesh) (Arrow, 1931; Balthasar, 1963; Sewak, 2009; Sabu & Vinod, 2011).

6. *Copris* (*Paracopris*) *davisoni* Waterhouse, 1891. Distribution: Central and South India (Arrow, 1931; Balthasar, 1963; Sabu & Vinod, 2011).

7. *Copris* (*Paracopris*) *excisus* Waterhouse, 1891. Distribution: India (Arrow, 1931; Balthasar, 1963).

8. *Copris* (*Paracopris*) *furciceps* Felsche, 1910. Distribution: India (Arunachal Pradesh, Gujarat, Meghalaya, Rajasthan, Uttar Pradesh), Myanmar, Laos, Thailand and China (Arrow, 1931; Balthasar, 1963; Hanboonsong et al., 2003; Sewak, 2009; Sabu & Vinod, 2011).

9. *Copris* (*Paracopris*) *imitans* Felche, 1910. Distribution: India (Goa, Gujarat, Karnataka, Madhya Pradesh, Maharashtra, Rajasthan) (Arrow, 1931; Balthasar, 1963; Sewak, 2009).

10. *Copris (Paracopris) kasagii* Ochi & Kon, 1996. Distribution: Indonesia (Sumatra) (Ochi & Kon, 1996).

11. *Copris* (*Paracopris*) *pedarioides* Lansberge, 1886. Distribution: Malaysia, Indonesia (Java) and India (Madhya Pradesh) (Balthasar, 1963).

12. *Copris* (*Paracopris*) *punctulatus* Wiedemann, 1823. Distribution: India (Arunachal Pradesh, Assam, Rajasthan), Indonesia (Java), Malaysia, Myanmar, Vietnam (Sonla, Dienbien, Quangbinh), Thailand, Cambodia, Laos and China (Yunnan, Anhui) (Arrow, 1931; Balthasar, 1963; Kabakov & Napolov, 1999; Hanboonsong et al., 2003; Sewak, 2009; Shahabuddin, 2010; Bai et al., 2011).

13. *Copris* (*Paracopris*) *punjabensis* Gillet, 1921. Distribution: India (Arrow, 1931; Balthasar, 1963).

14. *Copris* (*Paracopris*) *ramosiceps* Gillet, 1921. Distribution: India, Myanmar, Malaysia, “Indo-China” and Southern China (Arrow, 1931; Balthasar, 1963).

15. *Copris* (*Paracopris*) *signatus* Walker, 1858. Distribution: Sri Lanka, India (Himachal Pradesh, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Rajasthan, Tamil Nadu) and Laos (Arrow, 1931; Balthasar, 1963; Sewak, 2009; Sabu & Vinod, 2011).

16. *Copris* (*Paracopris*) *surdus* Arrow, 1931. Distribution: Central India (Arrow, 1931; Balthasar, 1963; Sabu & Vinod, 2011).

TAXONOMY

Genus *Copris* Geoffroy, 1762

Type species: *Scarabaeus lunaris* Linnaeus, 1758 (designated by Latreille, 1810).

Copris (*Paracopris*) *javanensis* sp. nov.

Figs 1-A–E, 2-A, 3-A, C&E

Description of holotype male. Total body length 15.5 mm, maximum body width 7.5 mm. Whole surface chocolate brown. Mouthparts and antennomeres 1–6 reddish brown. Antennal club and setae on legs yellow.

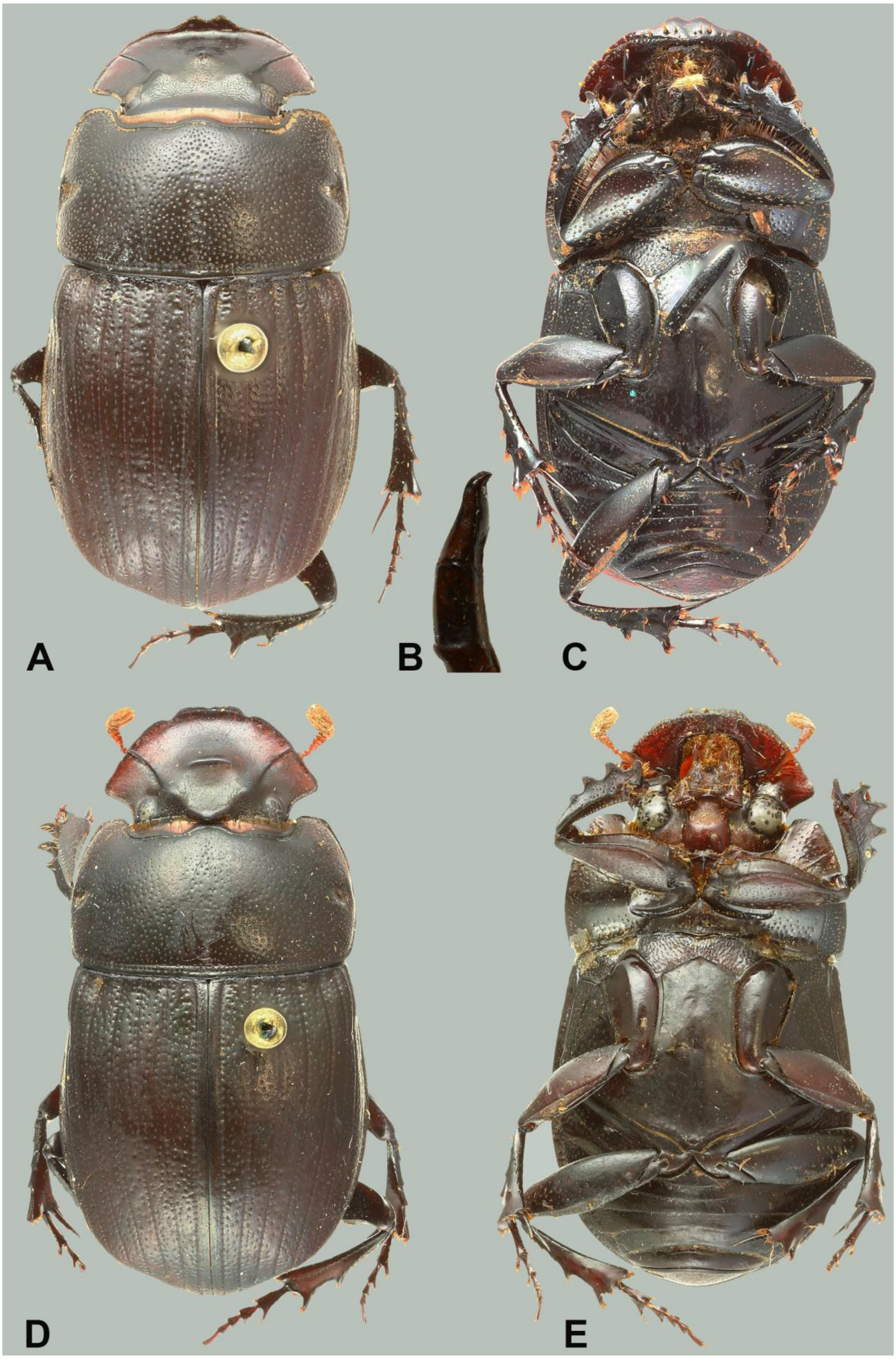
Head 4 mm long and 5 mm wide. Clypeal surface smooth and impunctate; clypeal apex strongly upwards protruded, and widely and shallowly emarginate. Genae rectangular, distinctly separated from clypeus by well-defined suture; most surface of genae smooth, except for small areas in middle sparsely and weakly punctate. Surface of vertex distinctly punctate; punctures denser and deeper at areas near eyes. Cephalic horn small but distinct. Antenna with 9 antennomeres; antennomere 1 longer than antennomeres 2–6 combined and also antennal club.

Pronotum 5.2 mm long and 6.8 mm wide, and without anterior declivity. Pronotal anterior margin slightly forwards curved in middle; anterolateral angles obtuse. Pronotal disc with weak median sulcus; sulcus not extending to pronotal anterior margin. Whole surface of pronotum deeply and densely punctate; most punctures equal in size, except for punctures near sulcus slightly larger. Each pronotal side with one deep and large excavation.

Anterior angles of prothorax flat, and shallowly and sparsely punctate on ventral side.

Elytra (ElyL 8.5 mm) deeply striate; striae weakly, sparsely and equally punctate. Elytral intervals convex, and deeply and densely punctate; interval punctures evenly distributed and relatively equal in size. Each elytron with one rather abrupt vertical flattening near sutural angle.

Mesepimeron and metepisternum flat and weakly punctate. Mesosternum strongly rugose. Metasternum relatively smooth, and with median distinct groove; sides of metasternum sparsely and shallowly punctate, and without setae.



Figs. 1-A–E. *Copris* (*Paracopris*) *javanensis* **sp. nov.** A–C – male, holotype. A – dorsal habitus. B – aedeagus, lateral view. C – ventral habitus. D–E – female, paratype. D – dorsal habitus. E – ventral habitus

Legs. Ventral surface of profemora strongly punctate; punctures unevenly distributed, and unequal in size, becoming denser and smaller towards anterior margin of profemora; a few punctures at posterior half of profermora with yellow and long setae. Anterior margin of profemora with yellow, dense and long setae. Protibia with four lateral teeth, and protibial surface strongly and unevenly punctate. Protibial spurs pointed, slightly curved outwards near apex, and equal in length to protarsomeres 2–4 combined. Protarsomere 1 and 5 equal in length, and both slightly longer than individual protarsomere 2–4. Mesofemora smooth and impunctate on ventral side. Mesotibia smooth and broadly dilated at posterior end; mesotibia with two spurs, one of which blunt, one longer and pointed. Mesotarsus with five tarsomeres, and all mesotarsomeres with yellow scanty setae; basal mesotarsomere elongated, almost equal in length to mesotibial spurs. Most ventral surface of metafemora smooth and impunctate, except for apical third sparsely punctate. Metatibia smooth and broadly dilated at posterior end, and with one spur pointed. Metatarsus with five tarsomeres covered with yellow scantly setae; basal metatarsomere apically enlarged, and shorter than metatibial spur.

Abdomen and pygidium. Abdominal ventrites smooth, impunctate, and narrower at midline. Pygidium (PyL 1.5 mm; PyW 3.1 mm) with margin complete; pygidial surface slightly convex, and deeply punctate; punctures dense but clearly separated.

Aedeagus. Phallobase slightly longer and wider than parameres. A broad angle almost reaching 180° formed by phallobase and parameres. Parameres slightly curved downwards in apical part.

Sexual dimorphism. Females differ from the male holotype in the following characters: Clypeal anterior margin not protruded in middle, and without emargination. Head with one slightly curved transverse carina between clypeus and frons. Pronotal anterior margin strongly forwards curved in middle.

Variation. Body length 11.5–16.5 mm, body width 6–7.5 mm (n =12: five males and seven females). The two males are larger, compared to the holotype, possess more strongly protruded clypeus upwards but similar in the remaining characters. There are no significant differences in external morphology among the female specimens examined.

Differential diagnosis. The new species has many morphological similarities to *Copris* (*Paracopris*) *punctulatus* Wiedemann, 1823 that was widely distributed in Asia: Vietnam, Laos, Cambodia, Thailand, Indonesia, Malaysia, Myanmar, China and India, but has consistently different pygidial surface and pronotal anterior margin (see detailed diagnostic characters separating these two species in Table 1).

TABLE 1. Diagnostic characters separating the new species from *Copris* (*P.*) *punctulatus* (also see Fig. 2-A–F)

Characters	***C.* (*P.*) *javanensis* sp. nov. (12 specimens examined)**	***C.* (*P.*) *punctulatus* (9 specimens examined)**
Colaration	Chocolate brown	Reddish brown
Anterior margin of pronotum in males	Slightly forwards curved in middle (Fig. 2-A)	Slightly backwards curved in middle (Fig. 2-B)
Anterior margin of pronotum in females	Strongly forwards curved in middle (Fig. 1-D)	Slightly forwards curved in middle (Fig. 4-D)
Punctures on pygidium surface	Clearly separated (Fig. 2-C)	Contiguous (Fig. 2-D)
Phallobase width relative to parameres width	PhaW slightly wider than PaW (Fig. 2-E)	PhaW greatly wider than PaW (Fig. 2-F)
Shape of parameres	Slightly curved downwards in apical part (Fig. 2-E)	Strongly curved downwards in apical part (Fig. 2-F)

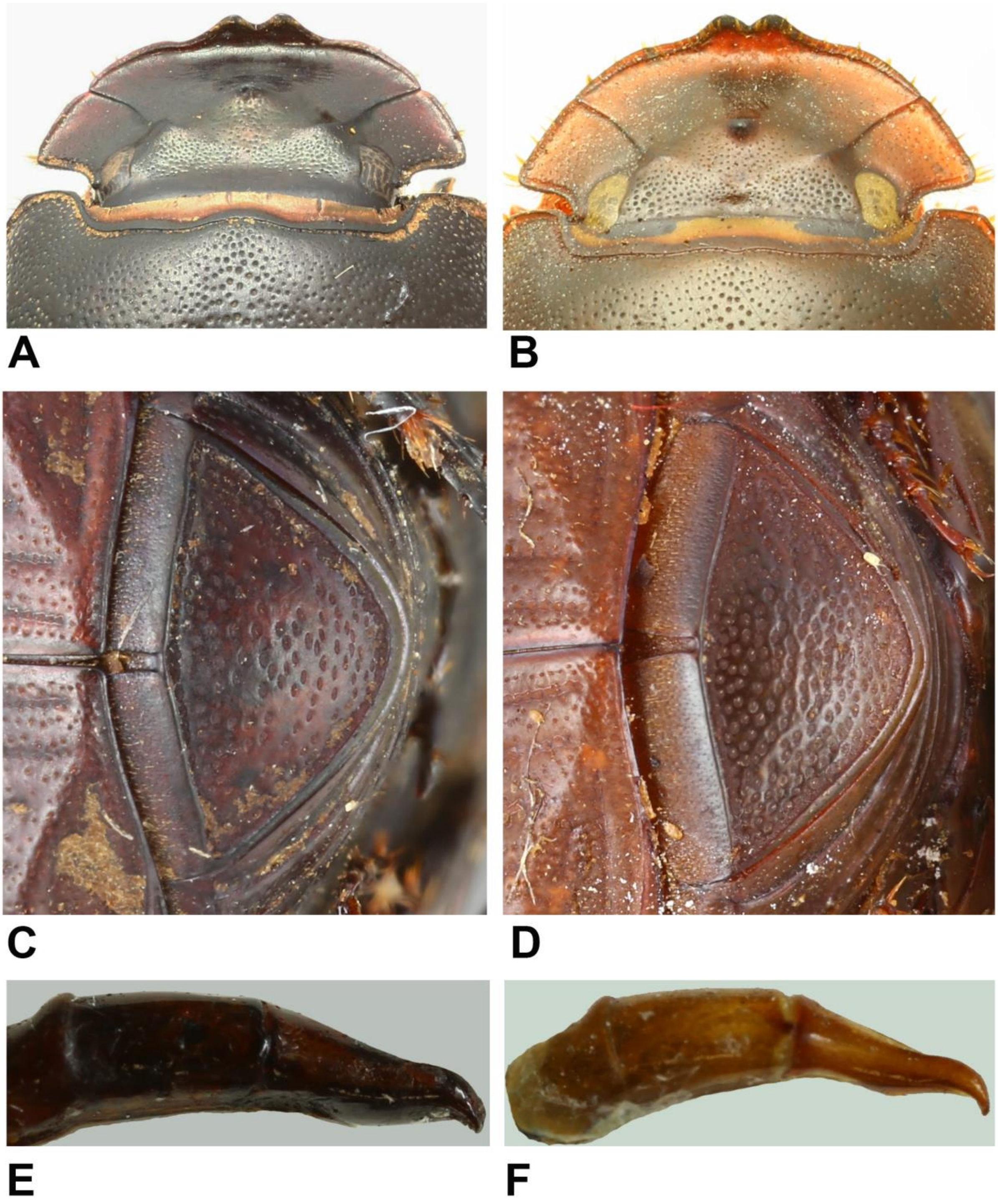


Fig. 2-A–F. Diagnostic characters separating *Copris* (*Paracopris*) *javanensis* **sp. nov.** from *Copris* (*Paracopris*) *punctulatus*. A, C & E –Pronotal anterior margin, pygidium and aedeagus of *C.* (*P.*) *javanensis* **sp. nov.** B, D & F– Pronotal anterior margin, pygidium and aedeagus of *C.* (*P.*) *punctulatus*.

The males of both *C.* (*P.*) *javanensis* **sp. nov.** and *C.* (*P.*) *punctulatus* possess a clypeal apex strongly upwards protruded and shallowly and widely emarginated, making these two species distinct from most Asian members of the subgenus *C.* (*Paracopris*) (for details see Table 2), except for *C.* (*P.*) *pedarioides*, *C.* (*P.*) *surdus* and *C.* (*P.*) *cariniceps*. The three latter can be clearly distinguished from the two former due to having very densely to contiguously punctate elytra and very densely and deeply punctate genae (Fig. 3-A–C). In addition, characters on the male cephalic horn clearly differentiate *C.* (*P.*) *pedarioides* and *C.* (*P.*) *surdus* from *C.* (*P.*) *javanensis* **sp. nov.** and *C.* (*P.*) *punctulatus*. In the two former, the male cephalic horn is relatively long, whereas in the two latter, the male cephalic horn is small. The males of *C.* (*P.*) *cariniceps* bear a clypeus strongly longitudinally carinate in middle, distinctly separating this species from *C.* (*P.*) *javanensis* **sp. nov.** and *C.* (*P.*) *punctulatus* whose clypeus without longitudinal carinae.

TABLE 2. Diagnostic characters of clypeus separating the new species from the other *Copris* (*Paracopris*) species (based on the specimens examined by us in MNHN and NMPC, and data published by Wiedemann, 1823; Arrow, 1931; Balthasar, 1939 & 1963; Ochi & Kon, 1996; Hanboonsong et al.,2003)

Species	**Character of clypeus (males)**
C. (*P.*) *javanensis* **sp. nov.**	Clypeal apex distinctly upwards protruded, and widely and shallowly emarginated.
C. (*P.*) *anomiopseoides*	Clypeal apex deeply and almost semicircularly emarginated; middle part of emargination strongly protruded upwards, and bifurcated.
C. (*P.*) *andrewesi*	Clypeal apex strongly reflexed and emarginated; middle part of emargination protruded, forming a rounded lobe.
C. (*P.*) *compressipennis*	Clypeal apex widely emarginated, and not protruded.
C. (*P.*) *cribratus*	Clypeal apex distinctly emarginated, and not protruded.
C. (*P.*) *davisoni*	Clypeal apex upwards protruded, forming one backwardly curved and pointed horn.
C. (*P.*) *excisus*	Clypeal apex widely and deeply emarginated, forming a pair of slender lateral processes forwards directed.
C. (*P.*) *furciceps*	Clypeal apex deeply and widely emarginated, and with one backwards and pointed horn in middle.
C. (*P.*) *imitans*	Clypeal apex reflexed, and weakly emarginated; middle part of emargination upwards protruded, forming one short erect process.

C. (*P.) kasagii* (*)	Clypeal anterior margin distinctly bidentate in middle, and not protruded.
C. (*P.*) *punjabensis*	Clypeal apex shallowly emarginated; middle part of emargination protruded, forming a rounded tongue-like lobe.
C. (*P.*) *ramosiceps*	Clypeal apex protruded, forming one upwards protruded horn which widely bifurcated; two branches upwards and backwards curved.
C. (*P.*) *signatus*	Clypeal apex with two narrow and almost parallel processes.

(*) Ochi and Kon (1996) originally showed the clypeus of *Copris (Paracopris) kasagii* with distinct emargination "Clypeus produced as a reflexed point in the middle, which is medially notched as obtuse angle and distinctly bidentate, from anterior aspect" (Ochi & Kon, 1996: p. 25), though the illustrated photos (Ochi & Kon, 1996: p. 26) showed indistinctly emarginated clypeal anterior margin. However, both the descriptions and photos of *C.* (*P.*) *kasagii* by Ochi and Kon (1996) showed the clypeal anterior margin not protruded, making this species clearly distinct from the new species.

Type material. Holotype male in MNHN was labelled: "INDONESIA | JAVA | MT Moeria 3 – 4000' | R. Oberthür | male". Paratype female (one at MNHN) was labelled: "INDONESIA | JAVA | MT Moeria 3 – 4000' | R. Oberthür| female"

Type locality. Indonesia, Java,

Etymology. The specific epithet javanensis refers to the name of the type locality, Java (Indonesia)

Collecting details. Unknown

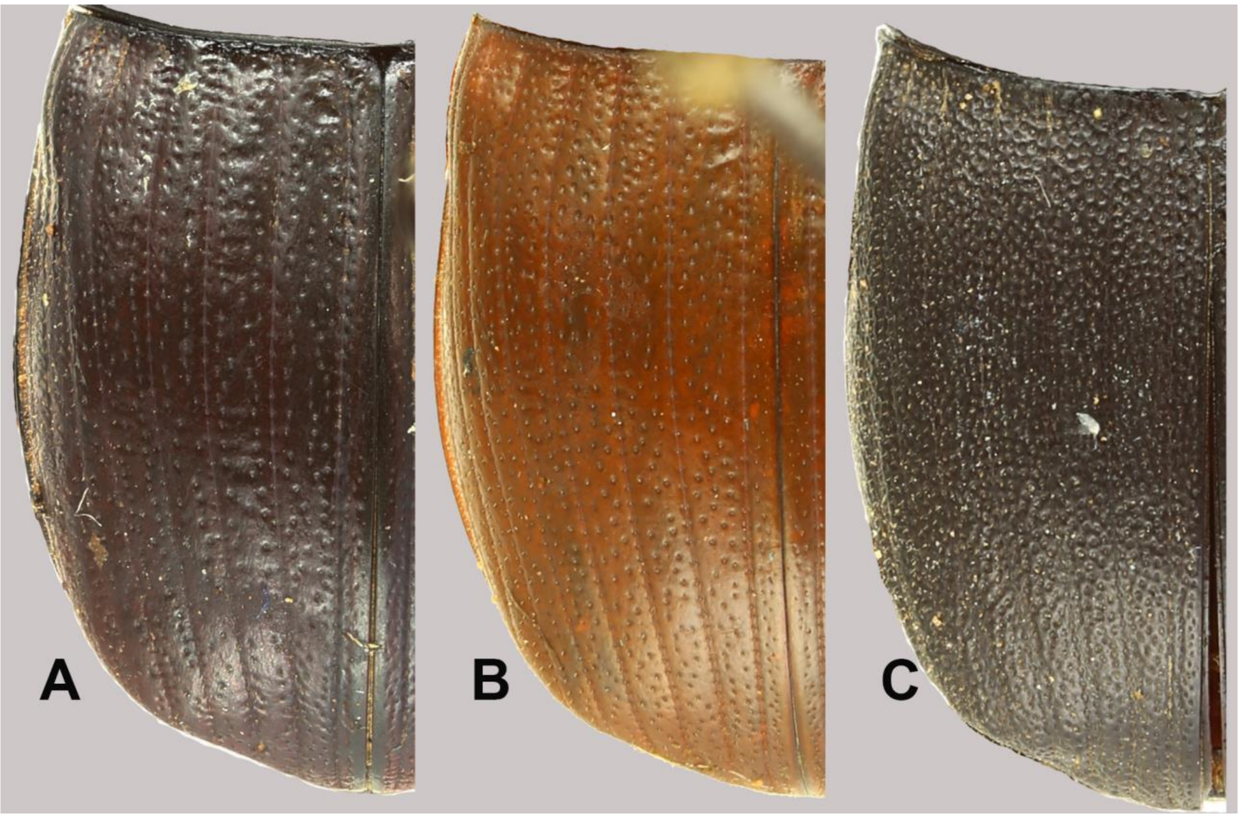


Fig. 3-A–C – Surface of elytral intervals of *Copris* (*Paracopris*) species. A&B – *C.* (*P.*) *javanensis* **sp. nov.** and *C.* (*P.*) *punctulatus* with elytral intervals sparsely punctate. C – *C.* (*P.*) *cariniceps* with intervals very densely to contiguously punctate

***Copris* (*Paracopris*) *punctulatus* Wiedemann, 1823**: 11 (original description)

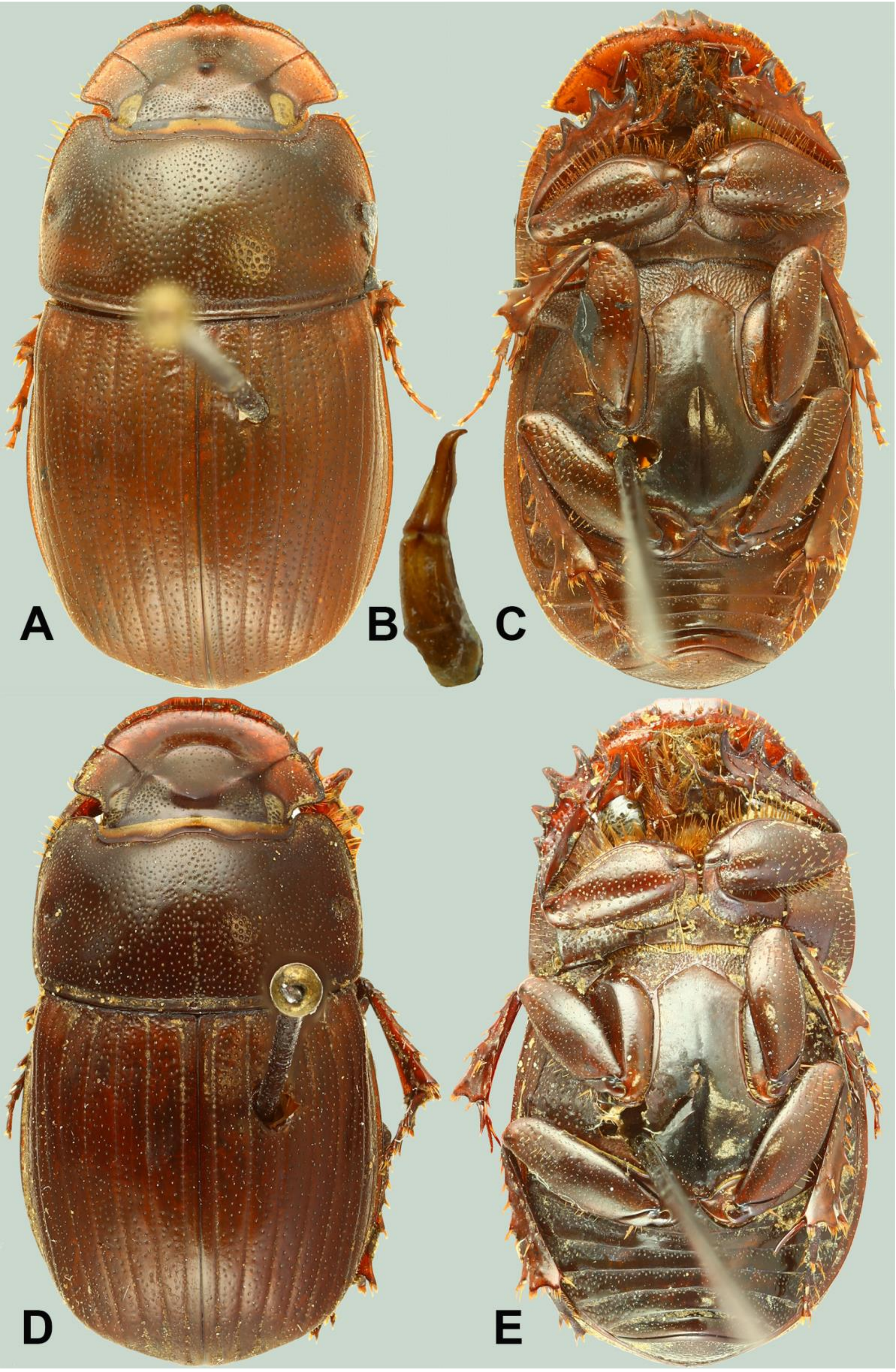
Figs 2-B, D, F, 3-B, 4-A–E

Additional information:

Copris punctulatus Wiedemann, 1823: p.126 (Arrow, 1931);

Copris (*Paracopris*) *punctulatus* Wiedemann, 1823: p. 370, fig. 133 (Balthasar, 1963);

Copris (*Paracopris*) *punctulatus* Wiedemann, 1823: p. 27, figs. 25–26 (Ochi & Kon, 1996);
Copris (*Paracopris*) *punctulatus* Wiedemann, 1823: figs. 65–68 (Hanboonsong et al., 2003);
Copris (*Paracopris*) *punctulatus* Wiedemann, 1823: fig. 45 (Bui et al., 2018)



Figs. 4-A–E. *Copris* (*Paracopris*) *punctulatus* A–C – male, holotype. A – dorsal habitus. B – aedeagus, lateral view. C – ventral habitus. D–E – female, paratype. D – dorsal habitus. E – ventral habitus

Description of males. Total body length 13–17.5 mm, body width 6.5–9 mm. Whole surface reddish brown. Mouthparts and antennomeres 1–6 reddish. Antennal club and setae on legs red.

Head almost semicircular (HeadL 3.5–4.5 mm, HeadW 5.5–7 mm). Clypeus smooth and impunctate; clypeal surface near anterior margin very shining; clypeal apex distinctly upwards protruded, and widely and shallowly emarginate. Genae rectangular, separated from clypeus by well-defined clypeo-genal suture; genal surface minutely and sparsely punctate. Vertex strongly and densely punctate; punctures of vertex unevenly distributed and unequal in size, denser and coarser at areas near eyes. Cephalic horn small but distinct.

Pronotum (PronL 5–6.2 mm, PronW 6.5–7.5 mm) without anterior declivity; anterior margin slightly downwards curved in middle; anterolateral angles obtuse. Pronotal median sulcus weak; sulcus not extending to pronotal anterior margin. Whole surface of pronotum deeply and densely punctate; punctures slightly larger in middle than in sides and also in anterior part. Each side of pronotum with one deep and large excavation in middle; surface of excavation coarsely but shallowly punctate.

Ventral surface of anterior angles of prothorax flat, and shallowly and sparsely punctate.

Elytra (ElyL 6.9–9.3 mm) deeply striate; striae sparsely and equally punctate. Elytral intervals convex, and strongly punctate; interval punctures dense, evenly distributed, and relatively equal in size; interval punctures slightly deeper than strial punctures. Each elytron with one rather abrupt vertical flattening near sutural angle.

Mesepimeron flat; surface weakly punctate. Metepisternum flat; surface sparsely but distinctly punctate. Mesosternum flat; surface strongly rugose.

Metasternal plate smooth, and with median deep groove at basal half; metasternal sides sparsely but distinctly punctate, and without setae.

Legs. Ventral surface of profemora strongly punctate; punctures unevenly distributed, and unequal in size, becoming denser and coarser at posterior half of femora; a few punctures near profemoral posterior margin with yellow setae. Profemoral margin with yellow, dense and long setae. Protibia with four lateral teeth, and protibial surface smooth and impunctate. Protibial spurs broadly dilated in middle, relatively pointed and slightly curved outwards near apex. Protarsus with five tarsomeres; protarsomere 1 and 5 equal in length, and both slightly longer than individual protarsomere 2–4.

Most ventral surface of mesofemora impunctate, except for small area behind anterior margin with a few strong but sparse punctures. Mesotibia smooth and broadly dilated at posterior end. Two mesotibial spurs almost equal in length and pointed. Mesotarsus with five tarsomeres; tarsomeres elongated, almost equal in length, and with yellow scanty setae.

Almost whole ventral surface of metafemora smooth and impunctate, except for apical areas near anterior margin distinctly punctate; punctures with relatively long and red setae. Metatibia smooth and broadly dilated at posterior end, with one spur long and pointed. Metatarsus with five tarsomeres, all bear red and scantly setae; basal metatarsomere slender, and slightly longer than individual metatarsomeres 2–4; basal metatarsomere, metatarsomere 5 and metatibial spur almost equal in length.

Abdomen and pygidium. Abdominal ventrites slightly narrower at midline; most surface of abdomen smooth, except for small areas at sides distinctly punctate. Pygidium (PyL 1.2–1.6 mm; PyW 2.7–3.3 mm) with complete margin; surface slightly convex and deeply punctate; pygidial punctures very dense to contiguous.

Aedeagus. Phallobase greatly longer and wider than parameres. A broad angle almost reaching 180º formed by phallobase and parameres. Parameres strongly curved downwards in apical part.

Sexual dimorphism. Females differ from males in the following characters: Clypeal anterior margin not protruded, and without emargination. Head with one strongly curved transverse carina between clypeus and frons. Pronotal anterior margin distinctly forwards curved in middle.

Variation. There is a significant difference in size of the protruding part of clypeal apex between small and large-bodied males with the latter having more strongly protruded clypeal apex upwards. Females have no significant differences in external morphology between large and small-bodied individuals.

Remarks. *Copris* (*Paracopris*) *punctulatus* Wiedemann, 1823 was originally described with only 20 lines and without illustrated photos. Although this species was re-described by Balthasar (1963), Ochi & Kon (1996), the intraspecific morphological variation is still lacking. Additionally the lack of illustrated photos of this species probably poses great challenge for practical identification of this species and its morphologically similar species. We for the first time provided characters of numerous morphological traits of this species based on a series of examined materials along with the detailed photographs of this species.

This may help to identify the potentially important morphological species boundaries of this species as well as its close relatives of the subgenus *Paracopris*, and therefore may help to discover potentially novel *Paracopris* species.

Type material. Nine specimens examined in MNHN. Of which four (one male and three females) were labelled: "ANNAM | PHUC-SON | Nov. Dez | H. Fruhstorfer" and five (two males and three females) were labelled: "INDONESIA | JAVA | MT Moeria 3 – 4000' | R. Oberthür".

CONCLUSION

Limited access to the scattered museum materials combined with the poorly defined species boundaries of the subgenus *Copris* (*Paracopris*) Balthasar, 1939 has hindered taxonomic work, and the subgenus has been neglected for many years. Increasing interest in Asian dung beetle taxonomy and ecology (Hayes et al. 2009; Senior 2012; Raine et al. 2018) created a need to re-examine collected type material and to define reliable morphological species boundaries in the subgenus *Paracopris*. By examining various morphological traits of a series of specimens of the morphologically similar *Paracopris* species, we determined the clypeal apex, the pronotal anterior margin and the structure of clypeal, pronotal, elytral intervals, as well as pygidial and femoral punctures as potentially important morphological traits to confine species boundaries in the subgenus *Paracopris* spp.. The discovery of *C.* (*P.*) *javanensis* **sp. nov.** increases the number of known species of *Paracopris* Balthasar, 1939 to 20, of which 17 have been so far only recorded from Asia. Only three species have been recorded elsewhere, including *Paracopris bihimatus* Balthasar, 1965 (synonymized with *Copris fidius* (Olivier, 1789)) from the north east highlands of South Africa along the eastern escarpment (Davis et al. 2013); *Paracopris ciprianii* Balthasar, 1939 (synonymized with *Copris coriarius* Gillet, 1907) from Zambia **(**Nguyen-Phung, 1988; Bezděk & Hájek, 2012), and *Paracopris similis* Balthasar, 1939 (synonymized with *Copris mesacanthus* Harold, 1878) from Belgian Congo, Southern Rhodesia, Transvaal, Natal and Cape Province (Nguyen-Phung, 1988). This suggests that the subgenus *Copris* (*Paracopris*) is almost exclusively confined to Asia and that current sampling efforts are likely far from comprehensive. Further studies focusing the Asian *Paracopris* species seem indispensable to improve our knowledge on the diversity, evolution and distribution of this subgenus.

Acknowledgement

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CHAPTER 4 A REVIEW OF THE GENUS *SYNAPSIS* BATES (COLEOPTERA: SCARABAEIDAE)

***Manuscript prepared for publication*:**

An illustrated key and diagnoses of beetle species in the genus *Synapsis* Bates (Coleoptera: Scarabaeidae)

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Key words. Coleoptera, Scarabaeidae, *Synapsis*, taxonomy, identification key, dung beetles

Abstract

We provide a thoroughly illustrated key to all worldwide known species of the genus *Synapsis* Bates, 1868. The key is mainly based on morphological examinations of a great number of type specimens housed at the Muséum National D'Histoire Naturelle (MNHN) (Paris, France), the National Museum, Prague, Czech Republic (NMPC) along with recently recorded material from Vietnam. This key took into account recent changes in both the species composition and diagnostic characters of the genus. The key contains a detailed photographic guide, hence it may be broadly useful for both specialists and non-specialists in the identification of all worldwide members of this genus. Also given herein are the diagnoses and distribution of all 24 *Synapsis* species known to date.

Introduction

The genus *Synapsis* Bates, 1868 comprises large-bodied beetles with a body length ranging between 17–52 mm (Zidek & Pokorny, 2010). *Synapsis* spp. are generally classified as tunnelling species that habitually store dung as breeding and nesting material in tunnels below dung patches. Their ability to interlock their head and thorax provides an adaptive advantage for *Synapsis* spp. over other tunnelling dung beetles in the excavation of tunnels (Arrow, 1931; Balthasar, 1963). Dung removal is the key ecosystem function of dung beetles, contributing to nutrient cycling, secondary seed dispersal and biological control of vertebrate parasites (Nichols et al., 2008). The body size of dung-beetle species is positively associated with dung removal rate. Therefore large-bodied beetles like *Synapsis* spp. are important contributor to this key ecosystem function (Nervo et al., 2014; Tixier et al., 2015; Frank et al., 2017). Like other large-bodied dung beetles whose brood masses typically require a large amount of dung for nutrition, *Synapsis* spp. rely heavily on the availability of dung resources of large-bodied mammals. This dependence on the composition and abundance of large mammals makes *Synapsis* spp. important indicators of habitat change. At the same time these large-bodied dung beetles are extremely vulnerable to habitat loss, and as *Synapsis* spp. have been found mainly in SE Asian tropical forests (Král, 2002; Bui & Bonkowski, 2018), they may be considered as ideal indicator species for undisturbed forests of this area.

The genus *Synapsis* currently comprises 24 species (Zidek & Pokorny, 2010; Bui & Bonkowski, 2018) and is taxonomically challenging. Although several identification keys to the *Synapsis* species occurring in specific regions (Paulian, 1945; Krikken, 1987;

Hanboonsong & Masumoto, 1999; Král, 2002) or worldwide (Balthasar, 1963; Zidek & Pokorny, 2010) existed, the species status of some taxa underwent repeated changes and inconsistences between keys make comparisons infeasible. For example, Balthasar (1935) synonymized *Synapsis yunnana* Arrow, 1933 with *Synapsis tridens* Sharp, 1981, while, Zidek and Pokorny (2010) recently synonymized *Synapsis cambeforti* Krikken, 1987 and *Synapsis thoas* Sharp, 1875 with *Synapsis ritsemae* Lansberge, 1874. There are some important reasons leading to erroneous and inconsistent species identifications. First, the existing keys include different diagnoses to identify *Synapsis* species. Second, the existing keys are not easily accessible as they are published in different languages (e.g., German, French). Third, accurate taxonomy is hampered by the lack of detailed pictorial descriptions of the main morphological characters, posing major problems for the practical identification of *Synapsis* spp., particularly between species whose morphological boundaries are poorly defined. Finally, morphological traits of *Synapsis* spp. show significant intraspecific variation, e.g., body size, hind legs, across different land uses (Raine et al., 2018). Therefore species description based on only a single specimen and distinguished from the known *Synapsis* species by unequivocal characteristics should be considered as unreliable species. In order to overcome these obstacles, we here provide a thoroughly illustrated key to the species of the genus *Synapsis* along with many detailed photos of type specimens. Additionally, compiled diagnoses of all *Synapsis* species known to date are presented based on morphological examinations of a great number of type specimens housed at the Muséum National D'Histoire Naturelle (MNHN) (Paris, France), the National Museum, Prague, Czech Republic (NMPC) and the Vietnamese National University of Forestry (VNUF).

Materials and methods

We morphologically examined the *Synapsis* species whose materials are deposited in MNHN, NMPC and VNUF, including *Synapsis birmanicus* Gillet, 1907; *S. brahmina* (Hope, 1831); *S. cambeforti* Krikken, 1987; *S. davidis* Fairmaire, 1878; *S. horaki* Zídek & Pokorný, 2010; *S. naxiorum* Král & Rejsek, 2000; *S. ochii* Masumoto, 1995; *S. ovalis* Boucomont, 1920; *S. puluongensis* Bui & Bonkowski, 2018; *S. ritsemae* Lansberge, 1874; *S. simplex* Sharp, 1875; *S. strnadi* Král, 2002; *S. thoas* Sharp, 1875; *S. tmolus* (Fischer von Waldheim, 1821); *S. tridens* Sharp, 1881; *S. yama* Gillet, 1911 (for details see the diagnosis part).

Examined morphological traits

The important morphometric traits examined include: body length – measured from anterior margin of clypeus to posterior margin of elytra; body width – measured at the widest part; frons (at 10x magnification); genae (at 10x); hypomeral cavity (HyC, at 10x); mesepisternal cavity (MeC, at 10x); elytral striae (30x), punctures on elytral striae (30x), elytral interval shape; interval punctures (at 30x); the second interval near base (at 10x); femora (at 20x, ventral sides).

Ranking of the density of punctures on the surface of elytra and femora as:

Contiguous punctures (0)	distance between punctures: 0
Very dense punctures (1)	distance between punctures: < 1 x diameter of puncture
Dense punctures (2)	distance between punctures: 1–2 x diameter of puncture
Sparse punctures (3)	distance between punctures: >2 x diameter of puncture

The elytral punctures were measured at the middle of the second elytral interval, and the femoral punctures were measured at the middle of the ventral sides

Key to species of the genus Synapsis

1. Genae expanded (Fig. 1-A–C) 2
- Genae unexpanded (Fig. 1-D–F) ..……………..……………………..……………7

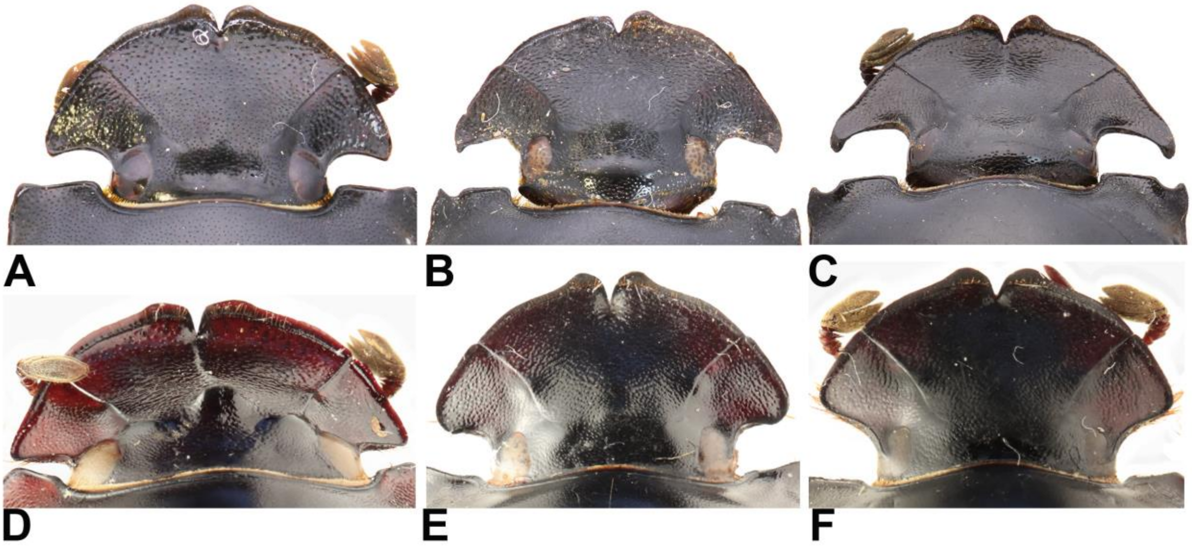


Fig. 1-A–F – Head structure of *Synapsis* species. A – *S. cambeforti* Krikken, 1987. B – *S. ritsemae* Lansberge, 1874. C – *S. thoas* Sharp, 1875. D – *S. simplex* Sharp, 1875, E – *S. ovalis* Boucomont, 1920, F – *S. strnadi* Kral, 2002.

2. Anterior angles of prothorax with deep excavation on ventral side (Fig. 2-A–C) ……3
- Anterior angles of prothorax flat, without excavation on ventral side (Fig. 2-D–F) ….5

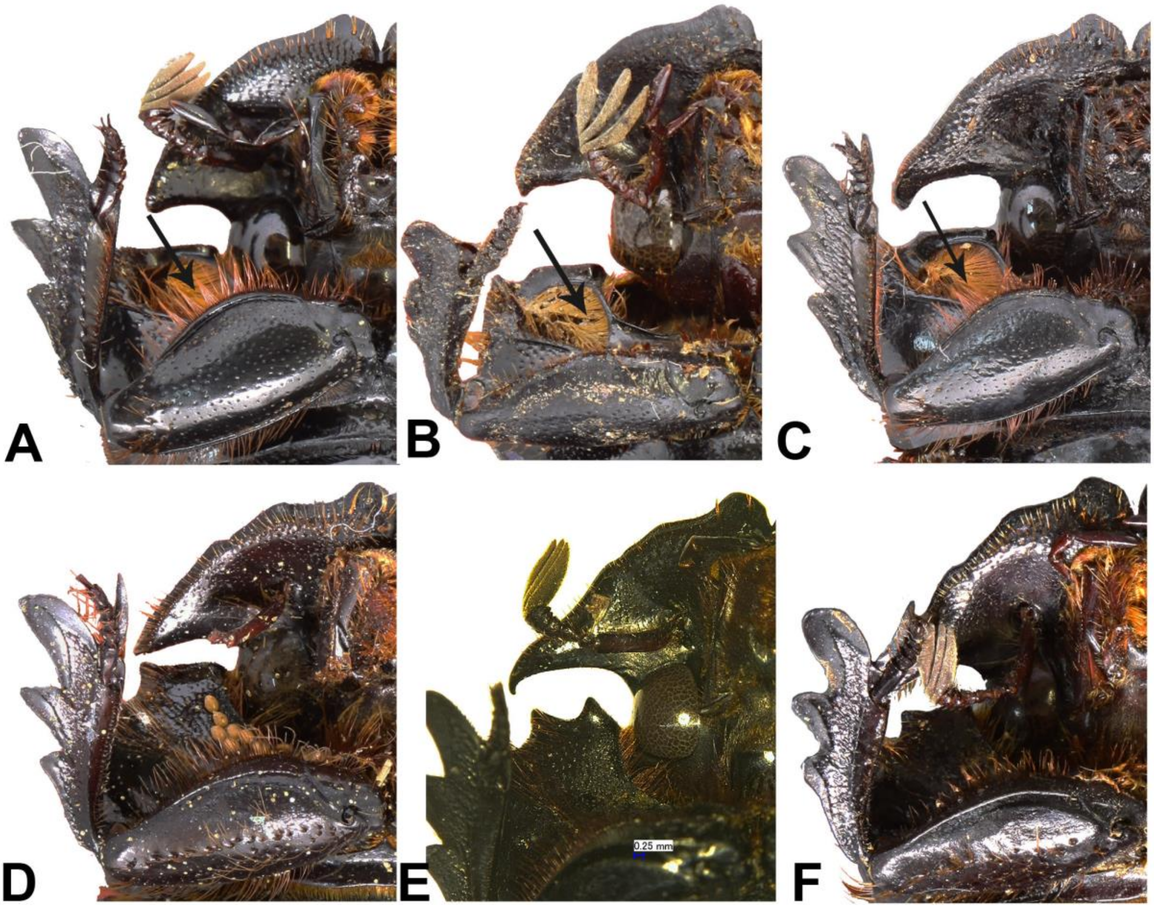


Fig. 2- A–F – Structure of anterior angles of prothorax of *Synapsis* species. A–C – Anterior angles of prothorax with deep excavation (arrow). A – *S. cambeforti* Krikken, 1987. B – *S. ritsemae* Lansberge, 1874. C – *S. thoas* Sharp, 1875. D–F – Anterior angles of prothorax without excavation. D – *S. brahmina* Hope 1831, E – *S. tridens* Sharp, 1881, F – *S. davidis* Fairmaire, 1878.

3. Anterior pronotal margin weakly sinusoidal, genal apex relatively rounded; surface of clypeus and frons strongly, evenly but sparsely punctate (I-A&D)………………..…... ………………………………………………………...***S. cambeforti* Krikken, 1987**
- Anterior pronotal margin strongly sinusoidal to excised, genal apex pointed; surface of frons and clypeus strongly rugose ....………….…...………….....……...…4

4. Elytral striae shallow and minutely punctate. Metatibial underside slightly concave near apex (Fig. I-B&E) ..…………………....…………..***S. ritsemae* Lansberge, 1874**
- Elytral striae deep and distinctly punctate. Metatibial underside strongly concave near apex (Fig. I-C&F) ...……..…..…………………………………. ***S. thoas* Sharp, 1875**

5. Anterolateral margins of pronotum with two teeth (Fig. II-A&D)……………………
…………………..……………………………………………...***S. brahmina*** **Hope, 1831**

- Anterolateral margins of pronotum with three teeth ……………...……..……………6

6. Elytra striae deep, pronotum with shallow median sulcus (Fig. II-B&E) ……………...
…………………..……………………….………....…...…...***S. tridens*** **Sharp, 1881**

- Elytra striae shallow, pronotum with deep median sulcus (Fig. II-C&F) ....
……………………………………………...………...***S. davidis*** **Fairmaire, 1878**

7. Frons distinctly armed (Fig. 3-A) ..………...……..……………………………...8

- Frons unarmed (Fig. 3-B&C) ………………..………….………..………………10

Fig. 3-A–C – Frons of *Synapsis* species. A – *S. simplex* Sharp, 1875 showing frons with distinct horn. B–C: *S. naxiorum* Kral & Rejsek, 2000 and *S. yama* Gillet, 1911 showing frons without horn

8. Body length >35 mm, elytral striae deep and strongly punctate (Fig. III-A) ...………...
…..…………………………………………………….***S. tmolus*** **(Fischer, 1821)**

- Body length<30 mm, elytral striae shallow and indistinctly punctate …..…..…..……9

9. Frons with strong and large horn; horn apex truncated (Fig. III-B)……...……………..
...………………………………………...………….***S. simplex*** **Sharp, 1875**

- Frons with distinct tubercle ………….. ***S. kiuchii*** **Hanboonsong & Masumoto, 1999**

10. Mesepisternal cavities present (Fig. 4-A&B) …...………………...……..…….…11

- Mesepisternal cavities absent (Fig. 4-C–E) ….……………..…...……………..…14

11. Anterolateral angles of pronotum nearly rectangular (90°)…………………………..12

- Anterolateral angles of pronotum >130°……………………..……...………….13

12. Genal apex acute and posteriorly curved...
……………………………...……***S. boonlongi*** **Hanboonsong & Masumoto, 1999**

- Genal apex rounded and not posteriorly curved (Fig. IV-A)….………………………..
…………………………………………………………***S. ovalis*** **Boucomont, 1920**

13. Metafemora in ventral view densely punctate (Fig. IV-B)…..…. ***S. strnadi*** **Kral, 2002**

- Metafemora in ventral view impunctate …………...…...…….... ***S. gilleti*** **Arrow, 1931**

14. Elytral interval II near base not swollen (Fig. 5-A&B) ...…...…………………...…..15

- Elytral interval II near base distinctly swollen (Fig. 5-C) ..………...…………………19

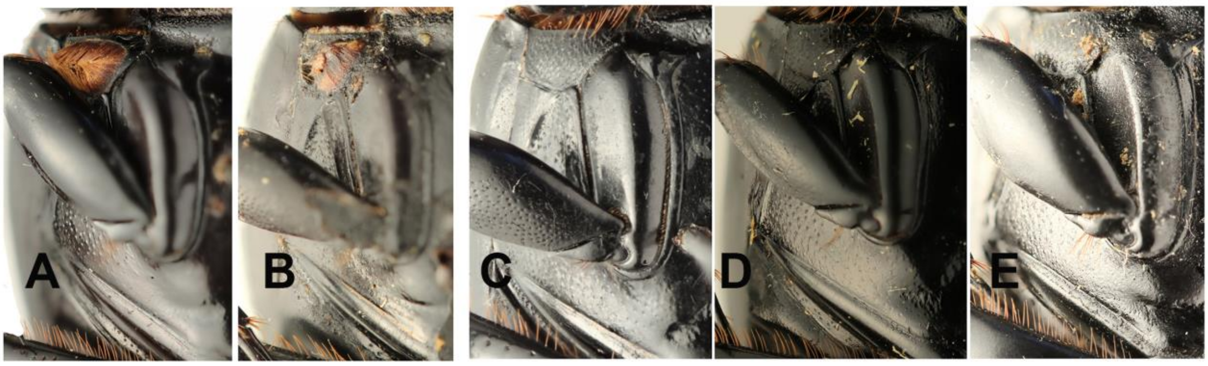


Fig. 4-A–E – Mesepisternal structure of *Synapsis* species. A–B – Mesepisternal cavities present: A – *S. ovalis* Boucomont, 1920; B – *S. strnadi* Kral, 2002. C–E – Mesepisternal cavities absent: C – *S. puluongensis* Bui & Bonkowski, 2018; D – *S. naxiorum* Kral & Rejsek, 2000; E – *S. yama* Gillet, 1911

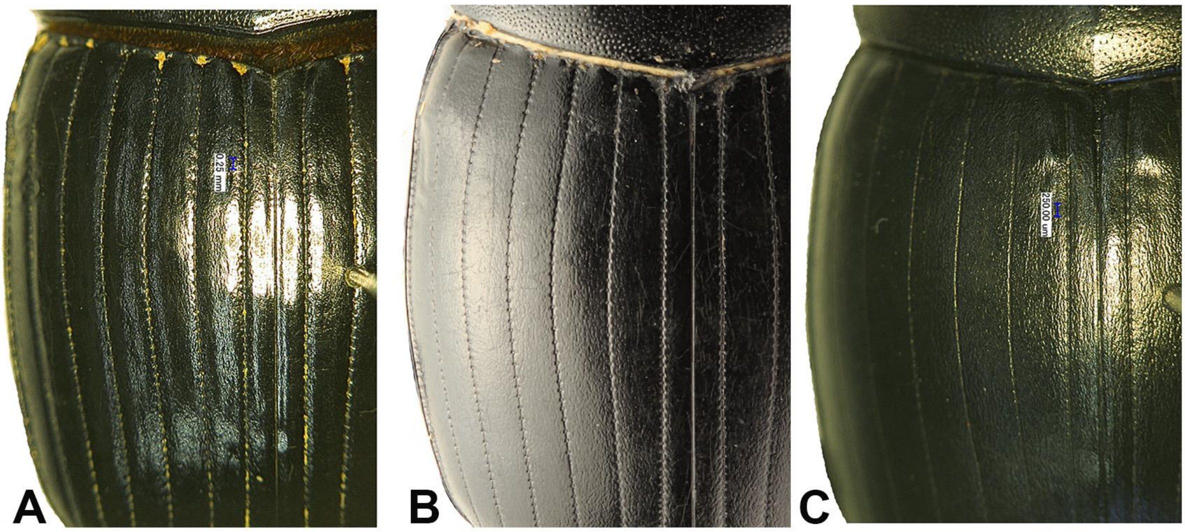


Fig. 5-A–B – Structure of elytral interval 2 of *Synapsis* species. A& B – Elytral interval II not swollen: A – *S.puluongensis* Bui & Bonkowski, 2018, B – *S. birmanicus* Gillet, 1907. C – Elytral interval II swollen: *Synapsis horaki* Zidek & Pokorny 2010

15. Excavation of anterior angles of prothorax (ventral side) without brush of rusty macrosetae (Fig. 6-A)..16
- Excavation of anterior angles of prothorax (ventral side) with brush of rusty macrosetae (Fig. 6-B&C)……………...……………………...…………………….…17

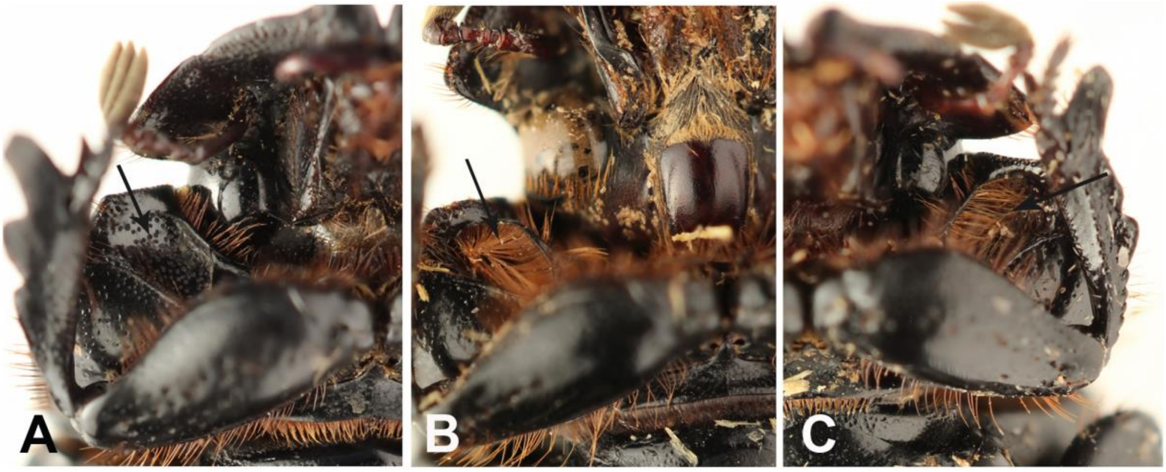


Fig. 6-A–C – Prothorax with characteristic excavation of anterior angles (arrow). A – *S. puluongensis* Bui & Bonkowski, 2018, showing excavation without brush of rusty macrosetae. B–C: *S. naxiorum* Kral & Rejsek, 2000 and *S. birmanicus* Gillet, 1907, showing excavation with brush of rusty macrosetae

16. Elytral intervals flat, margins of elytral intervals punctate …………………………….
..………………………………….……***S. punctatus* Ochi, Kon and Kawahara, 2008**

- Elytral intervals convex, margin of elytral intervals impunctate (Fig. V-A) ….…...…..
..………………..…………………………***S. puluongensis* Bui & Bonkowski, 2018**

17. Elytral intervals convex, elytral striae deep and weakly punctate (Fig. V-B).………….
……………………...……..…………………...…..***S. naxiorum* Kral & Rejsek, 2000**

- Elytral intervals flat, elytral striae shallow and strongly punctate...……....…………18

18. Strial punctures slightly notch interval margins (Fig. V-C).***S. birmanicus* Gillet, 1907**

- Strial punctures clearly notch interval margins……………………………………….
……………………………..………...***S. roslihashimi* Ochi, Kon & Kawahara, 2008**

19. Most surface of metafemora in ventral view impunctate (Fig. 7-A&B) ..…...….….…..20

- Metafemora in ventral view punctate (Fig. 7-C) ...……………………......……………21

20. Excavation of anterior angles of prothorax with brush of rusty macrosetae (Fig. VI-A)
……………………………………………..…..………***S. ochii* Masumoto, 1995**

- Excavation of anterior angles of prothorax without brush of rusty macrosetae (Fig. VI-B) ………………...………………………………...……………..***S. yama* Gillet, 1911**

21. Ventral surface of metafemora densely punctate (Fig. VI-C)………..…………………
……………………..……………………...…….***S. horaki* Zídek & Pokorný, 2010**

- Ventral surface of metafemora sparsely punctate …….……...……………………..22

Fig. 7-A–C – Ventral femora of *Synapsis* species. A – *S. ochii* Masumoto, 1995. B – *S. yama* Gillet, 1911. C – *S. horaki* Zídek & Pokorný, 2010

22. Anterolateral angles of pronotum projecting ………….…. ***S. masumotoi*** **Ochi, 1992**

- Anterolateral angles of pronotum not projecting……….…………………………...
………………………….………..…….***S. dickinsoni*** **Hanboonsong & Masumoto, 1999**

Diagnoses and distribution of all 24 *Synapsis* species known to date

Synapsis cambeforti **Krikken, 1987: 311, figs. 1–3 (original description)**

(Figs. 1-A, 2-A, I-A&D)

Type locality. Brunei, Telisai

Material examined. One paratype (female) in MNHN, labelled "Brunei | 5 km E Telisai | 4°44' N, 114°36' E + 20 m | 12.–30.xi.1980 | Forest: human feces | W.D. Edmonds, col. || Paratype || Synapsis cambeforti | J. Krikken ms 1986 | Paratype || Muséum Paris | coll. Générale || MNHN EC1887"

Habitat and distribution: Tropical forest in Borneo (Malaysia) and Brunei (Krikken 1987)

Diagnosis. Clypeus and frons strongly and evenly punctate. Frons armed with minor horn. Genae expanded; genal apex relatively rounded. Anterior pronotal margin weakly sinusoidal. Anterior angles of prothorax with deep excavation on ventral side; excavation surface covered by long, dense and rusty setae. Elytral striae deep, and strongly and densely punctate; elytral interval 2 not swollen near base. Mesepisternal surface flat and weakly and sparsely punctate. Posterior half of metafemora densely punctate on ventral side

Synapsis ritsemae **Lansberge, 1874: 143 (original description)**

(Figs. 1-B, 2-B, I-B&E)

Type locality. Indonesia, Sumatra

Material examined. Two specimens in MNHN: one paralectotype (sex unknown) labelled "Java Or. || Ritsemae Lansb. | Java | Type || Ex-Museum Van Lansberge || Paralectorype ||

Museum Paris | ex coll. R. Oberthur || MNHN EC1892”; one (sex: unknown) labelled “Java orient. | Mantes Tengger | 4000 | 1890 | H.Fruhstorfer || S. ritsemae Lamb. || Ex Museo N Van De Poll || Muséum Paris 1838 | Coll. A. Boucomont”.

Six specimens in NMPC: one labelled “Indonesia | S Java Sukamade | 300 – 400 m | i. 1997 | Stanley Jakl legt.”; three with the same label “Indonesisa | S Kalimantan | Kandangan district, 17 km NE Loksado | 15.11.1997 – 15.1.1998 | Stanley Jakl lgt.”; one labelled “Indonesia | Sumatra | March 1992 | Mts Leuser Nat. Park, Ketambe | local collector lgt.”; one labelled “Indonesia | 10 – 14/ii. 1999 | West Sumatra prov. | 600 m, Mt. Singgalang – Annai vall. | fish trap | Stanley Jakl lgt.”

Habitat and distribution: Java, Sumatra (Indonesia)

Diagnosis. Surface of frons and clypeus strongly rugose. Frons armed with minor horn. Genae expanded; genal apex not curved downwards. Anterior angles of prothorax with deep excavation on ventral side; Excavation surface covered with long, dense and rusty setae. Anterior pronotal margin strongly sinusoidal to excised. Elytral striae shallow and minutely punctate. Elytral intervals convex, and sparsely punctate. Second intervals near base not swollen. Mesepisternal surface flat and weakly and relatively smooth. Ventral surface of metafemora impunctate. Metatibial underside slightly concave near apex

Synapsis thoas Sharp, 1875: 44 (original description)

(Figs. 1-C, 2-C, I-C&F)

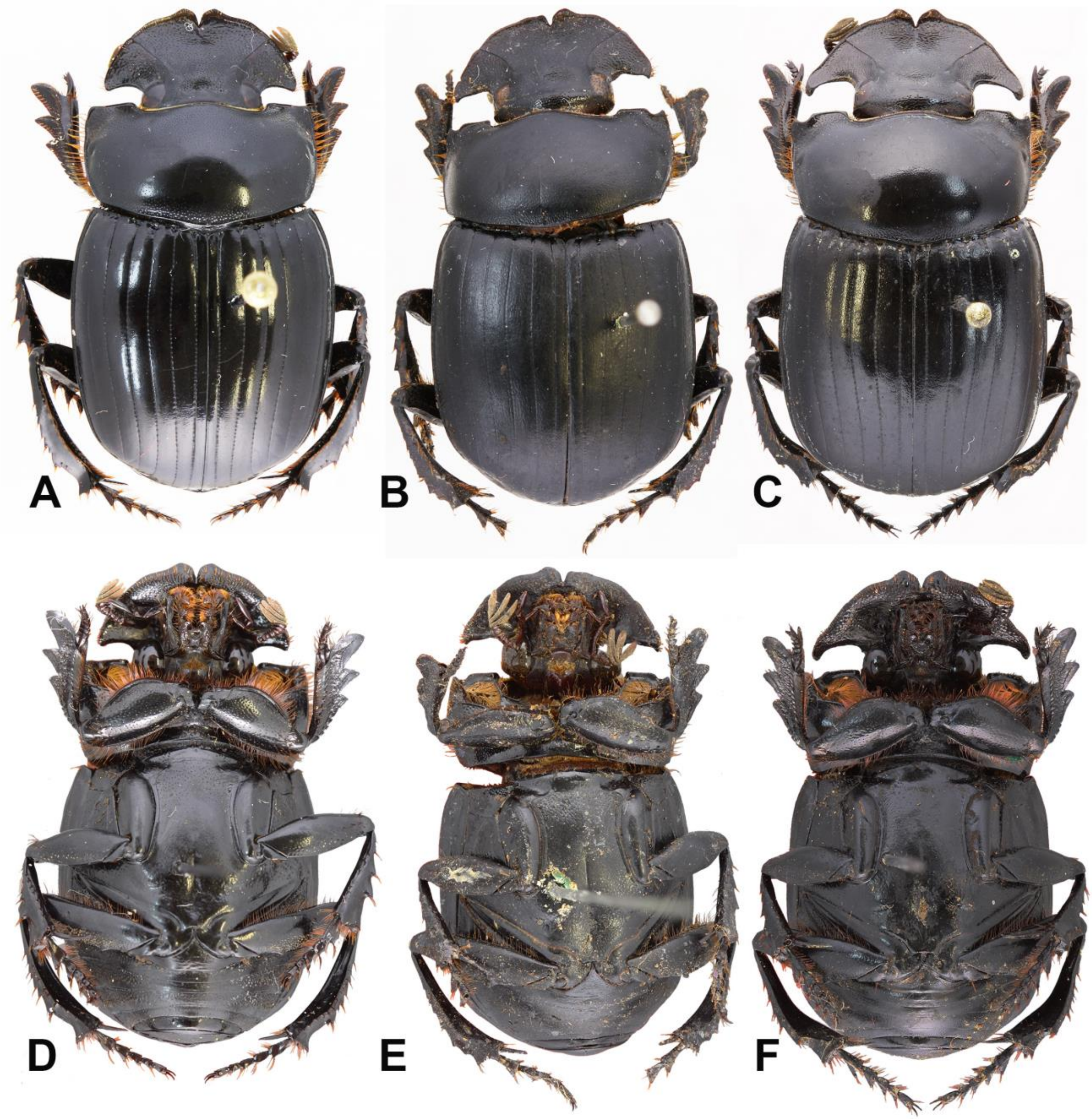
Type locality. Unrecorded

Material examined. Holotype (sex: unknown) in MNHN labelled “LAFERTE. 4458. | Synapsis thoas Type. 08 | Ex Museo D.Sharp 1890 | MNHN EC1895 | Museum Paris 1952. Coll. R.

Habitat and distribution: Java and Sumatra (Indonesia) (Balthasar 1963)

Diagnosis. Surface of frons and clypeus strongly rugose. Frons armed with minor horn. Genae strongly expanded; genal apex pointed, and strongly curved downwards. Anterior angles of prothorax with deep excavation on ventral side; Excavation surface covered with long, dense and rusty setae. Anterior pronotal margin strongly sinusoidal to excised. Elytra deeply striate; striae distinctly punctate. Elytral intervals weakly convex, and sparsely punctate. Second intervals near base not swollen. Mesepisternal surface flat and weakly and sparsely punctate. Most ventral surface of metafemora impunctate, except for small area surrounding metafemoral teeth with dense and deep punctures. Metatibial underside strongly concave near apex.

Remarks. *Synapsis thoas* Sharp, 1875 was regarded as subspecies of *S. ritsemae* by Krikken (1987) and *Synapsis ritsemae* Lansberge 1874 syn. nov. by Zidek and Pokorny (2010). Given that the morphology of genae poses an important mating barriers of the genus(Arrow, 1931; Balthasar, 1963; Zidek & Pokorny 2010), the strongly expanded genal apex of *S. thoas* compared to *S. ritsemae* most likely represents a valid species border separating both species.



Figs. I. A–F. Dorsal and ventral habitus of *Synapsis* species. A&D – *S. cambeforti* Krikken, 1987. B&E – *S. ritsemae* Lansberge, 1874. C&F – *S. thoas* Sharp, 1875.

Synapsis brahmina Hope, 1831: 22 (original description)

(Figs. 2-D, II-A&D)

Type locality. Unrecorded

Material examined. One specimen in MNHN labelled "Museum Paris 1952 | coll. R. Oberthur | North India | MNHN EC1902". Three specimens in NMPC; one labelled "Bootan Indep. | native collect. | 1918 | Slg. R. Oberthur | (Coll. O. Martin) Eing. Nr. 4, 1956"; one labelled "East Nepal 1992 | Jiri – Dolaka D. | 2200 m | (Janakpur) | leg. M. Limbu" one labelled "Napal | Bagiuati | Ganjual | 2700 m | coll. Tistze".

Habitat and distribution: Bhutan, India, Nepal, Pakistan (Arrow 1931, Balthasar 1963, Zidek & Pokorny, 2010)

Diagnosis. Clypeus strongly rugose. Frons coarsely and densely punctate; frons distinctly armed. Genae expanded; genal surface near eyes strongly and densely punctate, surface near outer margin strongly rugose. Whole pronotal surface deeply and densely punctate; disc with a distinct median sulcus running from base to anterior margin of pronotum. Anterolateral margins of pronotum with two teeth. Anterior angles of prothorax without excavation on ventral side. Elytral striae deep; striae deeply, coarsely and densely punctate; elytral interval 2 not swollen near base. Mesepisternal surface flat and weakly and sparsely punctate. Most ventral surface of metafemora impunctate, except for small area near base with sparse and shallow punctures.

Synapsis tridens Sharp, 1881: 92 (Original description)

(Figs. 2-E, II-B&E)

Type locality. Unrecorded

Material examined. One male lectotype (D. Král des. 2002) in MNHN labelled "Ex Museum D. Sharp 1890 | MNHN EC1896 | Assam | Museum Paris 1952. Coll. R. Oberthur"|. Four specimens in NMPC, one labelled "China | N – Yunnan, Yulongahan mts. | 2500 – 2800 m | Ganha IZI/LiJiang road | lgt. D. Král | 24. –26.7.90"|, one labelled "China | Yunnan | 2000 – 3000 m | 27.20N 100.11E | Habashan mts. Se slope | 10 -13.7 | David Král leg. 92"|, one labelled "China |Yunnan | Lijiang | 3300 m | 23.6.93 | lgt. Bocak", one labelled "China | Yunnan prov. | 4km SW Ancient Dali Chang Shan | 3000 m | J. Stastný | 29.10.1999"

Habitat and distribution: India, China, Bengal, Laos, Myanmar, Thailand, Vietnam (Arrow 1931, Balthasar 1963, Zidek & Pokorny, 2010, Bui & Bonkowki 2018)

Diagnosis. Clypeus strongly rugose. Frons with distinct horn; base of horn strongly rugose; horn apex with sparse punctures. Genae strongly expanded; genal apex pointed and slightly downwards curved. Pronotal surface strongly punctate on sides, base and anterior areas, but impunctate in middle; pronotal disc without median sulcus. Anterolateral margins of pronotum with three teeth. Anterior angles of prothorax without excavation on ventral side. Elytral striae shallow but distinct; striae indistinctly punctate; elytral interval 2 not swollen near base. Mesepisternal surface flat and weakly and sparsely punctate. Ventral surface of metafemora impunctate.

Synapsis satoi Ochi and Kon, 2007: 91 (original description)

Type locality: Laos - Myanmar border, Laos

Remarks: The species was originally described based on only the male holotype collected from the border between Laos and Myanmar. According to the original morphological comparison, this species "is closely related to *Synapsis tridens* SHARP from India, Myanmar and Thailand, but can easily be distinguished from the latter by the following character states: 1) the body clearly smaller (29.5 mm in length), whereas in *S. tridens*, it is larger (30.0–36.0mm) …. 3) the pronota1 anterior angle with four teeth instead of being thee…" (Ochi and Kon, 2007).

We have not examined the holotype of this species. However, as commended by Zidek & Pokorny (2010), we regard this species as synonym of *S. tridens*. First, the body sizes of *Synapsis* spp. show significant intraspecific variation (Raine et al. 2018), and species cannot be reliably separated by small differences in body length. *Synapsis tridens* has a wide distribution from NE India, Myanmar, SW China, North Vietnam, Laos to Thailand (Arrow, 1931; Balthasar, 1963; Zidek & Pokorny, 2010; Bui & Bonkowski, 2018) and its body length varies between 28–40 mm (Arrow, 1931; Balthasar, 1963; Zidek & Pokorny, 2010).

According to Ochi and Kon (2007), the pronotal anterior angle of *S. satoi* bears four teeth, further differentiating this species from *S. tridens* whose pronotal anterior angle has three teeth, but Fig. 1 in Ochi & Kon (2007) (p. 92) shows *S. satoi* possessing only three pronotal teeth (also commented by Zidek & Pokorny, 2010). Also the remaining morphological traits described for *S. satoi* are all within the expected morphological variation of *S. tridens*.

Synapsis davidis Fairmaire, 1878: 96 (original description)

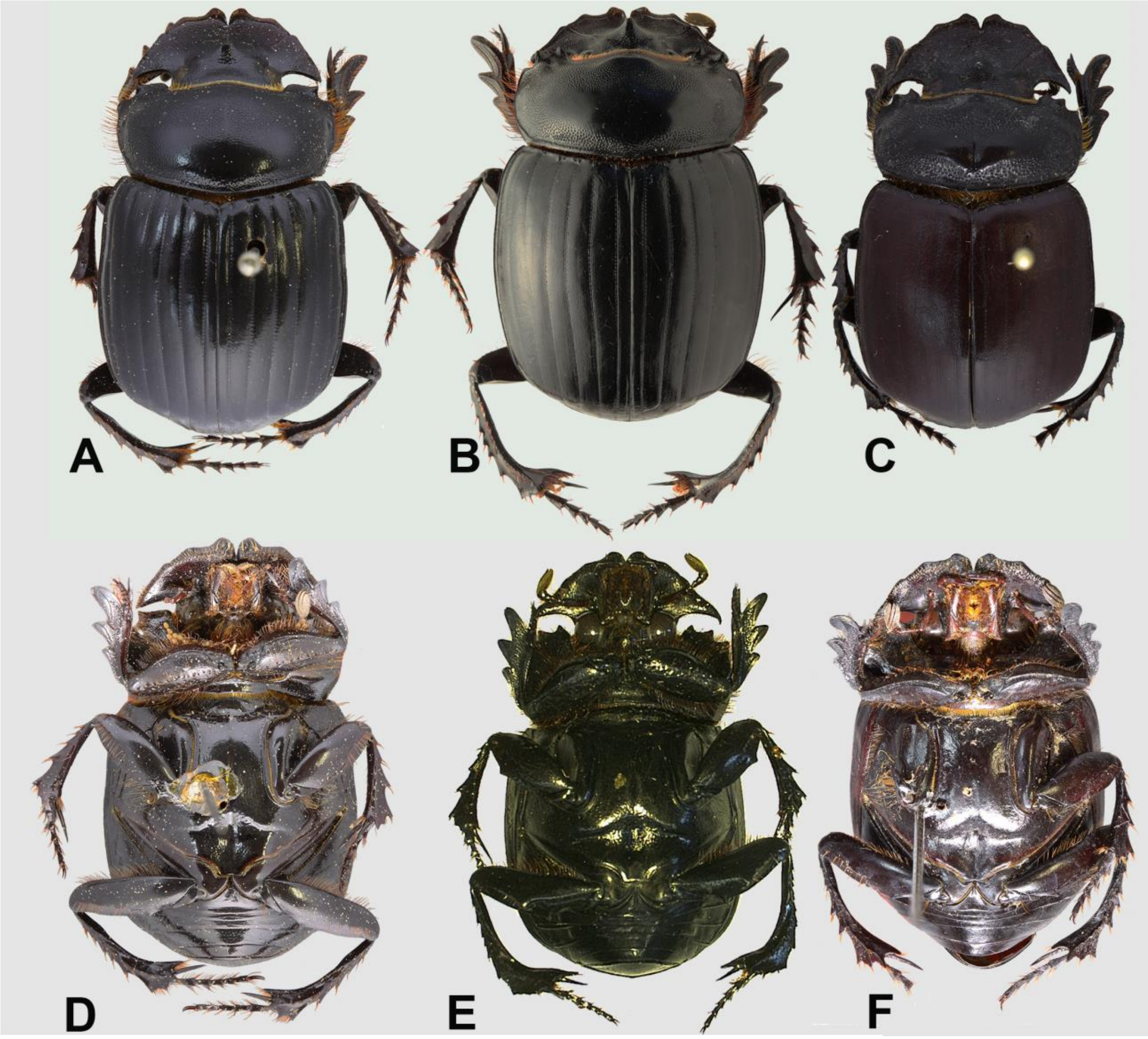
(Figs. 2-F, II-C&F)

Type locality. Unrecorded

Material examined. Lectotype (sex; unknown) (David Král des. 2002) in MNHN labelled "MNHN EC1891 | Laos | Tran Ninh | Vitalis. 1917", one paralectotype (sex: unknown) (David Král des. 2002) in MNHN labelled "MNHN EC1904 | Museum Paris | Moupin | A. David 1870". Three specimens (sex: unknown) in NMPC, one labelled "C Sichuan (Kangding) | Gogga Shan massive | ± 1000 m | Hoki village (SSW of Luding) | 29°40'N 102°06'E | 24.5–7.6.1993 | leg. B. Brezina", one labelled "Sichuan | 2. –6.vii.1994 | 29.36 N 102.06 E | 1500–2900 m | Gonggashan Hall Jougou | lgt. D. Král & J. Farkae", one labelled "China | Sichuan | 29°13N 102°10E | 1600 m | 2.vii.1998 | D. Král leg."

Habitat and distribution: China, Taiwan (Balthasar 1963, Zidek & Pokorny, 2010)

Diagnosis. Clypeus strongly rugose. Frons distinctly armed. Vertex strongly and densely punctate. Genae expanded; most surface of genae strongly rugose, except for small area near eyes deeply and sparsely punctate. Pronotal surface deeply, densely and coarsely punctate on sides, bases and anterior areas, but impunctate in middle; disc with deep median sulcus running from base to anterior margin of pronotum. Anterolateral margins of pronotum with three teeth. Anterior angles of prothorax without excavation on ventral side. Elytra minutely striate; elytral interval 2 not swollen near base. Mesepisternal surface flat and weakly and sparsely punctate. Metepisternum covered with yellow setae. Whole ventral surface of metafemora impunctate.



Figs. II. A–F. Dorsal and ventral habitus of *Synapsis* species. A&D – *Synapsis brahmina* Hope, 1831. B & E – *Synapsis tridens* Sharp, 1881. C & F – *S. davidis* Fairmaire, 1878.

***Synapsis tmolus* (Fischer von Waldheim, 1821): 11 (original description)**

(Figs. III-A)

Type locality. Unrecorded

Material examined. Five specimens in NMPC: one labelled "N. Afghanistan | Prov. Kataghan | coll. J. Simek | (32) Kundus, 400 m | 18–22.4.1996"; one labelled " USSR, Tadzikistan | 18.4.1978 | Babatag Mt. | cca 800 m | J. Strejcek lgt."; one labelled "BUCHARA | Repetek 5. 1900 | Coll. Hauser"; one labelled "Neize Bubad | Baba Tau | Asia centr. | Coll. Obenberger."; one labelled "USSR – Tadzikistan | 18.4.1978 | Babatag Mt. | cca 800 m | J. strejcek leg".

Habitat and distribution: Afghanistan, Iran, Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan and China (Balthasar, 1963; Zidek & Pokorny, 2010)

Diagnosis. Body very large, reaching a length of 52 mm. Whole surface of clypeus, frons and genae strongly rugose; frons with distinct horn. Genae unexpanded. Pronotal surface shallowly but distinctly punctate; pronotal disc without median sulcus in middle. Anterolateral margins of pronotum with one distinct tooth. Anterior angles of prothorax without excavation on ventral side. Elytra deeply striated; striae deeply and densely punctate. Elytral interval 2 not swollen near base. Mesepisternal surface flat, and with long but scanty setae. Whole ventral surface of metafemora impunctate.

Synapsis simplex **Sharp, 1875: 45 (original description)**

(Figs. 3-A, III-B)

Type locality. Laos

Material examined. Holotype (sex: unknown) in MNHN labelled "Laos | Mouhot | MNHN EC1893 | Museum Paris 1952 | coll. R. Oberthur". Two specimens in NMPC: one labelled "Laos – N. Phongsalay prov. | 21º41.2"N 102º6.8'E, | 28.v–20.vi.2003 | Phongsalay env., 1500m | Vit Kuban leg.", one labelled "Thailand N. | 1700 m | Mae Hong Son env. | Ban Hual Po | 24– 30.6 | J. Schneider legt. | 1993"

Habitat and distribution: China (Yunnan), Myanmar, Thailand, Laos (Xiangkhouang Prov.), North Vietnam (Dienbien Prov.) (Balthasar, 1963; Zidek & Pokorny, 2010)

Diagnosis. Clypeal surface strongly rugose. Surface of frons strongly but sparsely punctate; frons with distinct horn. Genae unexpanded; genal surface strongly, densely and evenly punctate. Most surface of pronotum impunctate, except for small areas near lateral margins being sparsely but distinctly punctate; pronotal disc without median sulcus. Anterolateral margins of pronotum without teeth. Anterior angles of prothorax without excavation on ventral side. Elytra deeply striated; striae impunctate. Elytral interval 2 not swollen near base. Mesepisternal surface flat, and weakly and sparsely punctate. Whole ventral surface of metafemora impunctate.

Figs. III. A–B. Dorsal habitus of *Synapsis* species. A – *Synapsis tmolus* (Fischer von Waldheim, 1821). B – *Synapsis simplex* Sharp, 1875.

Synapsis kiuchii Hanboonsong & Masumoto, 1999: 455 (original description)

Type locality Chiang Mai Prov., North Thailand

Habitat and distribution: This species has so far been known only from Thailand

Remarks: This species was originally described as being similar to *S. simplex* in external morphology. Both species possess unexpanded genae, the anterior angles of prothorax not excavated, and mesepisternal cavities absent. However, frons of *S. kiuchii* with distinct tubercles differentiate it from *S. simplex* whose frons bears a strong and large horn.

Synapsis ovalis Boucomont, 1920: 307 (original description)

(Figs. 4-A, IV-A)

Type locality. Tran Ninh Prov.

Material examined. One male lectotype (David Král des. 2002) in MNHN labelled "Laos | Prov. Tran Ninh | Vitalis. 1917 | MNHN EC1891". One (sex: unknown) in NMPC labelled "Khao Yai | viii. 86 | Thailand | Dr. F. Garnier"

Habitat and distribution: Laos, Thailand, Vietnam (Kral 2002; Balthasar, 1963; Zidek & Pokorny, 2010)

Diagnosis. Clypeal surface strongly rugose. Surface of frons deeply but unevenly punctate; punctures coarser and denser at areas near eyes; frons unarmed. Genae unexpanded; genal apex rounded and not posteriorly curved; genal surface strongly rugose. Surface of pronotum shallowly punctate; punctures stronger at base; pronotal disc without median sulcus. Anterolateral margins of pronotum almost rectangular (90°). Elytra feebly striated; striae impunctate. Elytral interval 2 not swollen near base. Mesepisternal cavity present; surface with dense rusty setae. Most ventral surface of metafemora impunctate, except for apical part shallowly and sparsely punctate.

Synapsis boonlongi Hanboonsong & Masumoto, 1999: p. 460 (original description)

Additional information

Synapsis boonlongi sp. nov.: p. 456–457 (the photos of dorsal and ventral habitus) (Hanboonsong & Masumoto, 1999)

Synapsis boonlongi Hanboonsong and Masumoto, 1999: p. 280 (distribution) (Král, 2002)

Synapsis boonlongi Hanboonsong and Masumoto, 1999: p. 9 (diagnosis in the identification key) (Zidek & Pokorny, 2010)

Type locality. Phukieo, 800 m alt., Chaiyaphum prov., NE Thailand.

Material examined. We have not been able to examine this species. Its diagnosis was compiled based on the original description with photos and on additional information in Král (2002) and Zidek & Pokorny (2010)

Habitat and distribution. Dry dipterocarp forest Thailand.

Diagnosis: This species is morphologically similar to *S. ovalis* but can be distinguished from the latter by an acute and posteriorly curved genal apex.

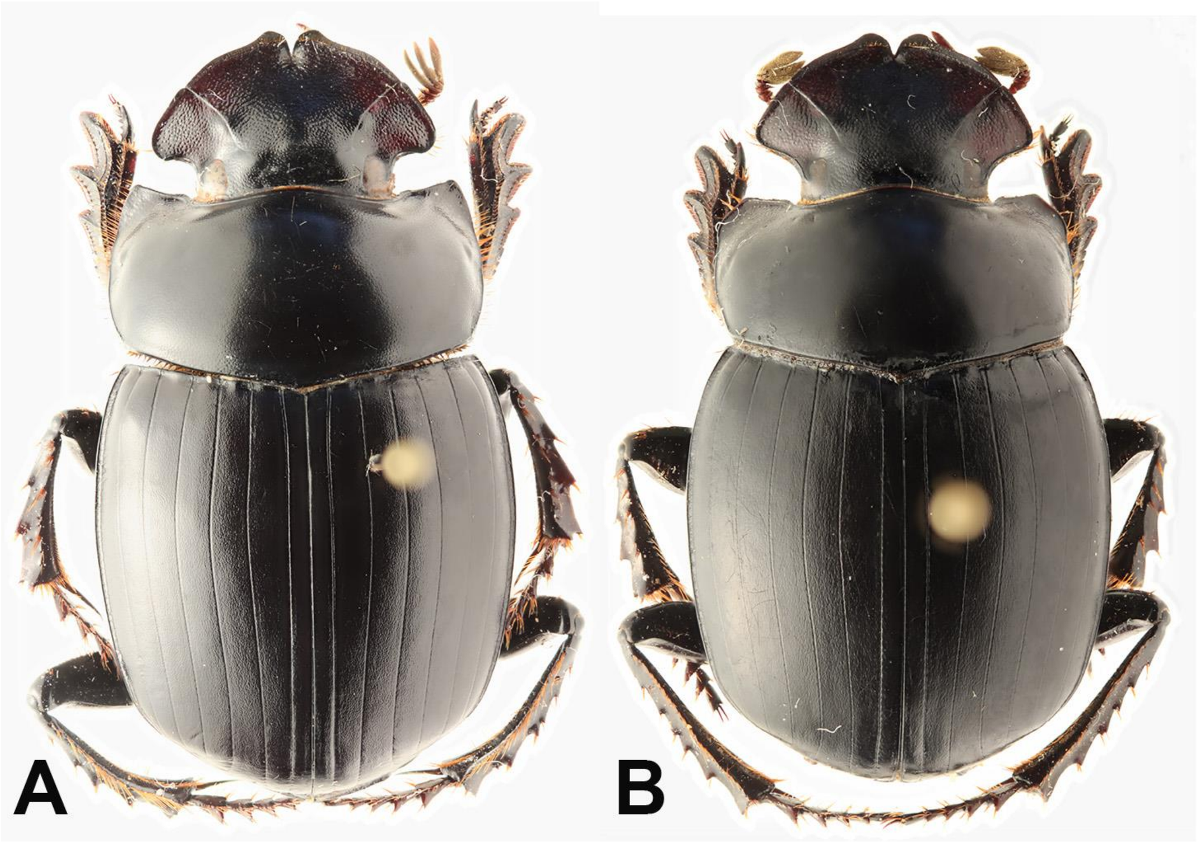
Synapsis strnadi Král, 2002: 283 (original description)
(Figs. IV-B)

Type locality. Vietnam

Material examined. Holotype (female) in NMPC, labelled "VIETNAM N. | TamDao – 900 m |16.–23.v.1991 | Strnad Jan lgt."; one paratype (female), labelled "VIETNAM N. | 1990 | SaPa | 11.–19.vi. | 1800 m | Hoang Lien Son prov. | Strnad Jan lgt."

Habitat and distribution: All specimens collected in human excrement in forests. Vietnam (Vinhphuc, Laocai provinces) (Král 2002)

Diagnosis. Clypeal surface strongly rugose. Surface of frons deeply punctate; frons unarmed. Genae unexpanded; Gena nearly rectangular laterally; genal surface strongly rugose. Most surface of pronotum impunctate, except for middle area sparsely and shallowly punctate; pronotal disc without median sulcus. Anterolateral margins of pronotum > 130°. Elytra feebly striated; striae impunctate. Elytral interval 2 not swollen near base. Mesepisternal cavity present; surface with dense rusty setae. Ventral surface of metafemora deeply and densely punctate in posterior part.



Figs. IV. A–B. Dorsal habitus of *Synapsis* species. A – *Synapsis ovalis* Boucomont, 1920. B – *Synapsis strnadi* Král, 2002.

Synapsis gilleti Arrow, 1931: 83 (original description)

Additional information:

Synapsis gilleti Arrow, 1931: p. 291 (key); p. 297 (re-description) (Balthasar, 1963)

Synapsis gilleti Arrow, 1931: p. 281 (distribution); p. 284 (Fig. 6) (Král, 2002)

Synapsis gilleti Arrow, 1931: p. 14 (Fig. 5, 6) (Zidek & Pokorny, 2010)

Type locality. Bengal, Darjeeling District

Diagnosis. We have not morphologically examined the specimens of this species. The diagnosis was compiled based on the original description and also Balthasar (1963), Král (2002); Zidek & Pokorny (2010).

Clypeal surface strongly rugose and punctate. Surface of frons strongly rugose and punctate; frons unarmed. Genae unexpanded; Gena nearly rectangular laterally; genal surface strongly rugose. Pronotal surface minutely punctate; pronotal disc without median sulcus. Anterolateral margins of pronotum > 130°. Anterior angles of prothorax without excavation on ventral side. Elytra distinctly striated; striae impunctate. Elytral interval 2 not swollen near base. Mesepisternal cavity present; surface with dense rusty setae. Ventral surface of metafemora impunctate.

Synapsis puluongensis Bui & Bonkowski, 2018: p. 408 (original description)
(Figs. 4-C, 5-A, 6-A, V-A)

Type locality. Vietnam, Thanh Hoa Province, Puluong Nature Reserve, 20º28′54″N 105°14′31″E, 950 m a.s.l.

Material examined. Holotype (male) in VNUF, five paratype specimens (one male, four females) in VNUF, NMPC and PLNR (for details see Bui & Bonkowski, 2018)

Habitat and distribution: all specimens of this species were collected in primary forests in Puluong NR (Thanhhoa Prov., Vietnam)

Diagnosis (for details see Bui & Bonkowski, 2018). Clypeal surface strongly rugose. Surface of frons very unevenly punctate; frons unarmed, only slightly swollen. Genae unexpanded, and rectangular; genal surface densely and evenly punctate. Pronotal surface distinctly punctate, punctures denser at sides; pronotal disc without median sulcus. Anterolateral margins of pronotum > 130°. Anterior angles of prothorax with a shallow cavity; surface of cavity sparsely punctate, and without macrosetae. Elytra strongly striated; striae strongly and densely punctate. Elytral interval 2 near base not swollen. Mesepisternal cavity absent. Posterior half of metafemora deeply and densely punctate.

Synapsis naxiorum Král & Rejsek, 2000: p. 268 (original description)

(Figs. 3B, 4D, 6-B, V-B)

Type locality. China, Hutiaoxia

Material examined. All examined specimens were in NMPC: Holotype (male), labelled "Yunnan | 2000 m | 27.15 N 100.09 E | Hutiao gorge | Jinsha r. | 18–22/7 | David Král leg. 92"; one paratype (female), labelled "China | N–Yunnan | 27°18 N 100°13 E | Jinsha r. vall. | 1900 m | Daju | Hutiao gorge | legt. D. Král | 16–17.7.90"; one specimen, labelled " Yunnan | 2000 m | 27.15 N 100.09 E | Hutiao | gorge Jinsha r. | 18– 22.7.92 | Vit Kuban leg."; six specimens with the same label: "Yunnan | 2000m | 27.15 N 100.09 E | Hutiao gorge | Jinsha r. | 18–22/7 |David Král leg. 92".

Habitat and distribution: China (Yunnan)

Diagnosis. Clypeal surface densely and coarsely punctate. Surface of frons deeply, densely but separately punctate; frons unarmed. Genae unexpanded and rectangular; genal surface evenly, densely but separately granulate. Pronotal surface shallowly, parsley and evenly punctate; pronotal disc without median sulcus. Anterolateral margins of pronotum > 130°. Anterior angles of prothorax with one deep cavity; surface of cavity with dense macrosetae. Elytra strongly striated; striae sparsely and almost evenly punctate. Elytral interval 2 near base not swollen. Mesepisternal cavity absent. Metafemora sparsely and irregularly punctate.

Synapsis birmanicus Gillet, 1907: p. 600 (original description)

(Figs. 5-B, 6-C,V-C)

Type locality. Karen Hills (as Carin Cheba), Myanmar

Material examined. All examined specimens were in NMPC: two spec., labelled "Laos | Attapeu prov, |Annam highlands | Dong Amphan NBCA | ca. 1160m | 15^{0}05.9$^{'}$N 107^{0}25.6$^{'}$E | leg. Jiří Hájek | 30. iv – 6.v.2010"; one spec., labelled "Thailand South | Khao Sok rainforest | 38 km E – TaKua PA | leg. Rejsek J. | 21.11.1996".

Habitat and distribution: Rainforests, China (Yunnan), Malaysia (Malay peninsula), Myanmar, Sumatra, Thailand (Balthasar, 1963; Zidek & Pokorny, 2010)

Diagnosis. Clypeal surface strongly rugose; Surface of frons deeply, coarsely and sparsely punctate; frons unarmed. Genae unexpanded and almost rectangular; genal surface evenly, densely punctate. Pronotal surface deeply and sparsely punctate; most punctures evenly distributed and equal in length, except for basal punctures denser and coarser; pronotal disc without median sulcus. Anterolateral margins of pronotum > 130°. Anterior angles of prothorax with one deep cavity; surface of cavity with dense macrosetae. Elytra shallowly striated; striae deeply and evenly punctate. Elytral interval 2 near base not swollen. Mesepisternal cavity absent. Metafemora strongly punctate.

Synapsis punctatus Ochi, Kon and Kawahara, 2008: p. 194 (original description)

Additional information

Synapsis punctatus sp. nov. p. 193 (photos of dorsal habitus), p. 195 (photos of aedeagus) (Ochi et al. 2008)

Type locality. Myanmar, ne Kachin, Chudo Rozi

Habitat and distribution. Myanmar

Diagnosis: So far, this species is known only from the holotype from Myanmar. According to the original description, *S. punctatus* is morphologically similar to *S. birmanicus* but can be distinguished from the latter due to the possession of hypomeral cavity (HyC) without a brush of rusty macrosetae (in *S. birmanicus*, HyC with a brush of rusty macrosetae). Characters on elytral intervals differentiate *S. punctatus* from the recently described new species, i.e., *S. puluongensis* Bui & Bonkowski. *Synapsis punctatus* possess punctate interval margins, while *S. puluongensis* has impunctate interval margins (Bui & Bonkowski, 2018).

Synapsis roslihashimi Ochi, Kon & Kawahara, 2008: 191 (original description)

Type locality: Ulu Gombak, 220 m, Selangor, West Malaysia

Habitat and distribution: Malay Peninsula and Sumatra

Remarks: *Synapsis roslihashimi* Ochi, Kon & Kawahara, 2008 was originally described based on 22 specimens from Malaysia and Indonesia, showing similar external morphological characters to *S. birmanicus* Gillet, particularly in possessing HyC with a brush of rusty macrosetae and elytral striae shallow and strongly punctate. Also documented in the original description, the strial punctures strongly notch the elytral margins in *S. roslihashimi*, differentiating it from *S. birmanicus*.

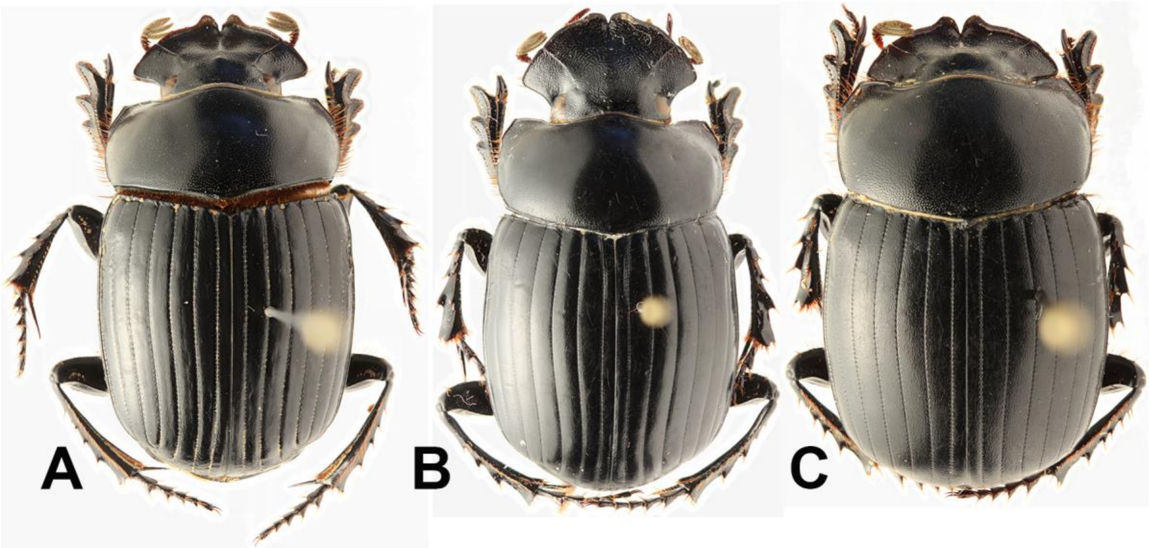


Fig. V-A–C – Habitus of *Synapsis* species. A – *S. puluongensis* Bui & Bonkowski, 2018. B – *S. naxiorum* Kral & Rejsek, 2000. C – *S. birmanicus* Gillet, 1907.

Synapsis ochii Masumoto, 1995: p. 81 (original description)

(Figs. 7-A, VI-A)

Type locality. Thailand (Chiang Mai)

Material examined. Paratype (sex: unknown), labelled “MNHN EC1890 // MUSÉUM PARIS | coll. GÈNÈRALE // Doi Angkhang | Chiang Mai prov. | THAILAND | 13-vii-1991 | Y. MANIT leg. // Paratype, Synapsis ochii MASUMOTO”

Habitat and distribution: Chiang Mai, Thailand

Diagnosis. Surface of clypeus mostly strongly rugose, except for small areas near anterior margin sparsely and shallowly punctate. Surface of frons strongly rugose; frons unarmed. Genae unexpanded, and nearly rectangular; genal surface strongly rugose. Pronotal surface indistinctly punctate; pronotal disc without median sulcus. Anterolateral margins of pronotum > 130°. Anterior angles of prothorax with one deep cavity; surface of cavity with brush of rusty setae. Elytra shallowly striated; striae distinctly punctate. Elytral interval 2 near base swollen. Mesepisternal cavity absent. Ventral surface of metafemora mostly impunctate, except for small area near metatrochanter very sparsely punctate.

Synapsis yama Gillet, 1911: 313 (original description)

(Fig. 3-C, 4-E, 7-B, VI-B)

Type locality: Vietnam, Tuyenquang

Examined material: Holotype (male) in MNHN, labelled “MUSEUM PARIS | TONKIN CENTR. | Env. de TUYEN-QUAN [QUANG] | A. Weiss, 1901 || TYPE || Juill. – Sept. || Synapsis yama Gillet, n. sp. || Synapsis yama Gillet, 1911 | Holotypus | David Krasl des. 2002”.

Nine spec. in NMPC: six spec. labelled “Lao – N., Phongsaly prov. | 21º41.2N 102º06.8'E | 28.v–20.vi. 2003 | Phongsaly env. | 1500m | Vit Kuban leg. |; three spec. labelled “Lao – N. Phongsaly prov. | 21º41.2N 102º06.8'E | Phongsaly env. | 6–17. v. 2004 | 1500m | Vit Kuban leg”.

Habitat and distribution. Vietnam and Laos (Balthasar 1963, Kabakov & Napolov 1999; Zidek & Pokorny, 2010)

Diagnosis. Surface of clypeus strongly rugose. Surface of frons densely punctate; punctures near eyes deeper; frons unarmed. Genae unexpanded and nearly rectangular; genal surface strongly rugose. Pronotal surface minutely punctate; punctures at base slightly coarser; pronotal disc without median sulcus. Anterolateral margins of pronotum > 130°. Anterior angles of prothorax with one deep cavity; surface of cavity without brush of rusty setae. Elytra minutely striated; striae impunctate. Elytral interval 2 near base swollen. Mesepisternal cavity absent. Ventral surface of metafemora impunctate.

Synapsis horaki Zidek & Pokorny, 2010: 18 (original description)

(Figs. 5-C, 7-C, VI-C)

Type locality. Vietnam, Vinh Phuc Province, Tam Dao, 900 m a.s.l.

Type material examined. Holotype (male) in NMPC, labelled “6–10.v.1990 | Tam Dao | Vinh Phu Distr. | Vietnam | 900 m | Jan Horák leg.” Four additionally examined specimens in VNUF (for details see Bui & Bonkowski, 2018)

Habitat and distribution. Primary forests, Tamdao National Park and Piaoac Nature Reserve (Vietnam)

Diagnosis. Surface of clypeus strongly rugose. Surface of frons weakly punctate and rugose; frons unarmed, only slightly swollen. Genae unexpanded and almost rectangular; genal surface strongly rugose and shallowly punctate. Surface of pronotum mostly impunctate, except for small shallowly and sparsely punctate areas near base and sides; pronotal disc without median sulcus. Anterolateral margins of pronotum > 130°. Anterior angles of prothorax with one deep cavity; surface of cavity without brush of rusty setae. Elytra minutely striated; striae impunctate. Elytral interval 2 near base swollen. Mesepisternal cavity absent. Third posterior part of ventral surface of metafemora strongly and densely punctate.

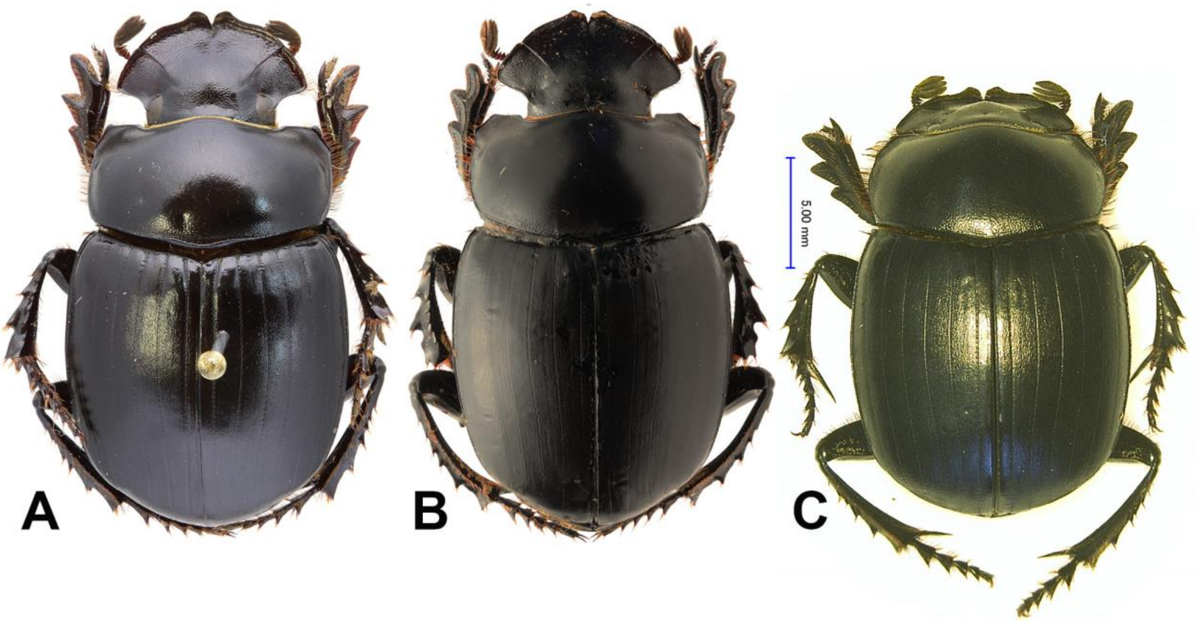


Fig. VI-A–C – *Synapsis* species. A - *S. ochii* Masumoto, 1995. B – *S. yama* Gillet, 1911. C – *S. horaki* Zídek & Pokorný, 2010

Synapsis masumotoi Ochi, 1992: 9 (original description)

Type locality. Taiwan

Material examined. None specimens examined in this study

Habitat and distribution. Taiwan (Ochi, 1992; Král, 2002; Zidek & Pokorny, 2010)

Remarks. This species was originally described based on three male specimens from Taiwan, being similar to *S. yama* in external morphology. Particularly both species possess metafemora with a strong tooth in the middle of posterior margin of the femora, and a protruding anterolateral angle of pronotum. However, punctures on the metafemora of *S. masumotoi* distinguish this species from *S. yama* whose metafemora are without punctures.

Synapsis dickinsoni Hanboonsong & Masumoto, 1999: 457 (original description)

Type locality: Thailand, Phukieo, 1000 m

Material examined. None of the specimens were examined in this study

Habitat and distribution: Evergreen forests, Thailand (Chaiyaphum)

Remarks: According to the original description (p. 457–459) and illustrated photos fig. 5 (p. 456) (Hanboonsong & Masumoto, 1999), *S. dickinsoni* is morphologically similar to *S. masumotoi* but can be distinguished from the latter due to its pronotum with a not protruding anterolateral angle.

Acknowledgement

We would like to thank O. Montreuil from the French National Museum of Natural History, Paris, France (MNHN), J. Hájek from the National Museum, Prague, Czech Republic (NMPC) for permission to examine the reference collections deposited in their museums. The Bui's research stays in MNHN and NMPC received support from the program "IPaK - Promoting International Doctorates at the University of Cologne" financed by German Academic Exchange Service (DAAD) and from the SYNTHESYS Project (http://www.synthesys.info/) financed by the European Community Research Infrastructure Action under the FP7 Integrating Activities Programme, respectively.

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***<u>Publication</u>*:**

Synapsis puluongensis sp. nov. and redescription of *Synapsis horak*i (Coleoptera: Scarabaeidae), with a key to Vietnamese species.

Van Bac Bui

Michael Bonkowski

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RESEARCH PAPER

Synapsis puluongensis sp. nov. and redescription of *S. horaki* (Coleoptera: Scarabaeidae), with a key to Vietnamese species

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Abstract. A new species of coprophagous scarabaeid, *Synapsis puluongensis* sp. nov., is described based on six specimens collected in Pu Luong Nature Reserve in central Vietnam. The new species can be clearly distinguished from the remaining species of *Synapsis* Bates, 1868 by the following characters: hypomeral cavities present but not covered by red macrosetae; mesepisternal cavities absent; elytral striae extremely strong, bearing close and strong punctures; metafemora with dense and strong punctures in ventral view. Redescription of *S. horaki* Zídek & Pokorný, 2010 based on new material is also presented. Key to species of the genus *Synapsis* from Vietnam is provided.

Key words. Coleoptera, Scarabaeidae, *Synapsis*, dung beetles, new species, taxonomy, identification key, Vietnam, Oriental Region

Zoobank: http://zoobank.org/urn:lsid:zoobank.org:pub:8187447B-B951-4D73-973B-0AB6BB038A81

Introduction

Synapsis Bates, 1868 is an Asian genus of Coprinae dung beetles, i.e. true dung beetles of the tunneler group, which burrow vertical tunnels near or below the dung pat and use it for dung removal (Hanski & Cambefort 1991). Currently, the genus comprises 23 valid species and is divided into five groups: the *Synapsis ovalis* group (*S. boonlongi* Hanboonsong & Masumoto, 1999, *S. gilleti* Arrow, 1931, *S. ovalis* Boucomont, 1920 and *S. strnadi* Král, 2002), the *S. birmanica* group (*S. birmanica* Gillet, 1907, *S. dickinsoni* Hanboonsong & Masumoto, 1999, *S. horaki* Zídek & Pokorný, 2010, *S. masumotoi* Ochi, 1992, *S. naxiorum* Král & Rejsek, 2000, *S. ochii* Masumoto, 1995, *S. punctata* Ochi, Kon & Kawahara, 2008, *S. roslihashimi* Ochi, Kon & Kawahara, 2008 and *S. yama* Gillet, 1911), the *S. ritsemae* group (*S. cambeforti* Krikken, 1987, *S. ritsemae* Lansberge, 1874 and *S. thoas* Sharp, 1875), the *S. brahmina* group (*S. brahmina* (Hope, 1831), *S. davidis* Fairmaire, 1878, *S. satoi* Ochi & Kon, 2007 and *S. tridens* Sharp, 1881), and the *S. tmolus* group (*S. kiuchii* Hanboonsong & Masumoto, 1999, *S. simplex* Sharp, 1875 and *S. tmolus* (Fischer von Waldheim, 1821)) (Balthasar 1963, Krikken 1987, Hanboonsong & Masumoto 1999, Král 2002, Ochi et al. 2008, Zídek & Pokorný 2010, Bezděk & Hájek 2012). In Vietnam, six species of the genus have been recorded so far: *S. ovalis* from Binh Phuoc and Song Be provinces, *S. strnadi* from Vinh Phuc and Lao Cai provinces, *S. yama* from Tuyen Quang and Thanh Hoa provinces, *S. horaki* from Vinh Phuc Province, *S. tridens* from Lao Cai and Nghe An provinces, and *S. simplex* from Dien Bien and Nghe An provinces (Balthasar 1963, Kabakov & Napolov 1999, Král & Rejsek 2000, Král 2002, Zídek & Pokorný 2010).

Our recent field surveys on dung beetle communities inhabiting forest and meadow fragments in limestone areas in northern and central Vietnam led to the discovery of a new, unnamed *Synapsis* population in the Pu Luong Nature Reserve (NR), which clearly differs from the known species of the genus in morphology. We describe this *Synapsis* population as a new species. We also provide a redescription of the poorly known species *S. horaki* and a detailed key to the species of the genus *Synapsis* in Vietnam.

Materials and methods

Study area and sampling protocol. The field research was conducted in limestone karst ecosystems in the Pia Oac Nature Reserve (Cao Bang Province, northern Vietnam) and the Pu Luong Nature Reserve (Thanh Hoa Province, central Vietnam) from March to May over a two year period (2015–2016). We used 90 baited pitfall traps in total to collect dung beetles. The traps were placed in habitats with increasing land use intensity, comprising primary forests, secondary forests and meadows at an elevational range of 800–1250 m in both reserves. Each trap consisted of a 5-liter plastic bucket buried to its rim in the soil, filled with 2 liters of 70% ethanol, and baited with 300 grams of a fresh pig and buffalo dung (50 : 50 ratio) mixture. Beetles that fell in traps were removed after 72 hours of trap exposure and preserved in 70% ethanol until examination in the lab (Bui et al. 2018).

Comparative material of following species was studied in the NMPC: *Synapsis birmanica, S. brahmina, S. davidis, S. naxiorum, S. ovalis, S. ritsemae, S. simplex, S. strnadi, S. tridens, S. yama,* and *S. tmolus.*

Male genital morphology. The aedeagus was extracted through the abdominal apex using forceps and needles, and was then cleaned and softened in 5% KOH at 65ºC for one hour. Also the internal sac of the aedeagus was drawn out and heated again for 30 minutes for clearing. The aedeagus and its internal sac were placed in glycerin and photographed with a digital microscope (Keyence VHX-500F) (Bui et al. 2018).

Morphometrics. Measurements were taken with a digital caliper and from photographs taken with a digital microscope (Keyence VHX-500F). The following morphometric traits were measured:

BoL	body length from anterior margin of clypeus to posterior margin of elytra
BoW	maximum body width
HeadL	head length from anteriormost point of clypeus to posterior margin of head
HeadW	maximum head width
PronL	maximum pronotum length
PronW	maximum pronotum width
ElyL	elytra length from apex to base
MWoI123	maximum width of first three intervals (interstriae) from elytral suture
DP10,15	distance from puncture 10 (from base of elytra) to puncture 15 on first elytral stria
HoL	horn length from base to tip
PyL	maximum pygidium length
PyW	maximum pygidium width
ProTiL	protibia length
ProTiW	maximum protibia width
ProTiSL	protibial spur length
MesoTiL	mesotibia length
MesoTiW	maximum mesotibia width
1st MesoTiSL	1st mesotibial spur length (shortest spur)
2nd MesoTiSL	2nd mesotibial spur length (longest spur)
MetaTiL	metatibia length from proximal constriction to apex
MetaTiW	maximum metatibia width
MetaTiSL	metatibial spur length
MetaTaL	metatarsus length
MetaTa1L	metatarsomere 1 length
MetaTa1W	metatarsomere 1 width
MetaTa5W	metatarsomere 5 width
BoWeight	body weight after drying at 60ºC for 48 hours
DDC	distance between apices of clypeal denticles (teeth)
HyC	hypomeral cavity;
MeC	mesepisternal cavity
Gen	genae
MesoF	mesofemur at ventral side
MetaF	metafemur at ventral side
MetaTibrush	metatibial brush

Material examined. The type specimens are deposited in the following institution (curators in parenthesis):

NMPC	National Museum Prague, Czech Republic (Jiří Hájek);
PLNR	Pu Luong Nature Reserve, Thanh Hoa Province, Vietnam (Nguyễn BáTâm);
VNUF	Vietnam National University of Forestry, Vietnam (Bùi Văn Bắc).

Systematics

Synapsis puluongensis sp. nov.

(Figs 1A–F, 2A,C,E)

Type locality. Vietnam, Thanh Hoa Province, Puluong Nature Reserve, 20º28′54″N 105º14′31″E, 950 m a.s.l.

Type material. Holotype: ♂ ‘VIETNAM | THANH HOA Prov. | Pu Luong Nat. Reserve, near Ban Ba vill. | 20º28’54’’N 105º14’31’’E, 950 m | primary forest | 10.–25.iv.2016 | Van Bac Bui leg.’ (VNUF). Paratypes (five specimens): ♂, ‘VIETNAM | THANH HOA Prov. | Pu Luong Nat. Reserve, near Ban Ba vill. | 20º28’55’’N 105º14’29’’E, 958 m | primary forest | 10.–25.iv. 2016 | Van Bac Bui leg.’ (VNUF); ♀, ‘VIETNNAM | THANH HOA Prov. | Pu Luong Nat. Reserve, near Ban Ba vill. | 20º28’54’’N 105º14’29’’E, 954 m | primary forest | 10.–25.iv.2016 | Van Bien Nguyen leg.’ (VNUF); 3♀♀, ‘VIETNAM | THANH HOA Prov. | Pu Luong Nat. Reserve, near Ban Ba vill. | 20º28’56’’N 105º14’28’’E, 956 m | primary forest | 10.–25.iv.2016 | Van Bac Bui leg.’ (2 PLNR, 1 NMPC).

Diagnosis. Body length 17.2–18.5 mm, body width 10.4–11.5 mm; hypomeral cavities not covered by macrosetae; mesepisternal cavities absent; genae unexpanded; frons unarmed; anterolateral angles of pronotum not protruding; elytral striae strongly punctate; elytral intervals impunctate, convex and glossy, interval 2 near base not swollen; ventral sides of metafemora densely punctate.

Description of holotype (male). Body length 18.38 mm, body width 11.32 mm. Whole surface black, very shiny and glabrous. Margins of legs and pronotum with reddish-brown macrosetae.

Head broad (HeadL 3.67 mm, HeadW 7.44 mm), extremely rugose anteriorly; posterior part sparsely punctate; fine punctures surrounding eyes. Anterior margin of clypeus bidentate, V-shaped, flexed upwards, with few reddish setae. Distance between apices of clypeal denticles (DDC) 1.43 mm. Genae rectangular, quite distinctly separated from clypeus and frons by well-defined suture with sculptural punctures. Genae closely and evenly punctate, with scanty reddish macrosetae. Frons glabrous and very unevenly punctate. Area surrounding eyes bearing more closely spaced and coarser punctures than base. Frons unarmed, only slightly swollen. Antennae composed of 9 antennomeres. Antennomere I 1.34 mm in length, longer than antennomeres II–IV combined (1.25 mm in length). Antennomeres I and II darker, bearing more yellow macrosetae than remaining antennomeres.

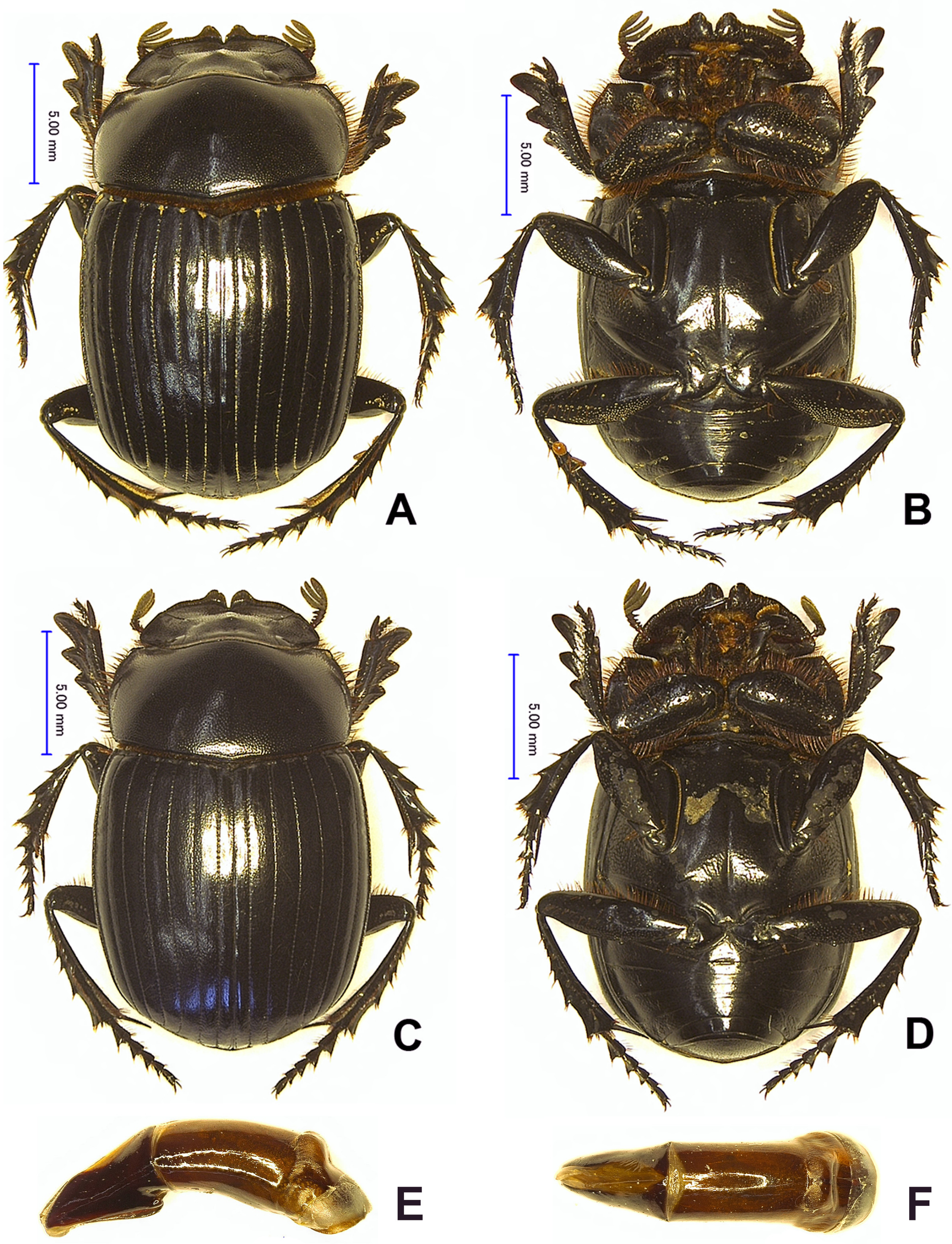

Fig. 1. *Synapsis puluongensis* sp. nov. A–B – male, holotype. C–D – female, paratype. E – aedeagus, lateral view. F – aedeagus, dorsal view.

Prothorax. Pronotum transverse (PronL 4.9 mm, PronW 10.08 mm), widest at anterior quarter, with two distinct lateral carinae at each side. Area between carinae black, matte, glabrous and not punctate. Outer margin of outer carina with dense reddish-brown macrosetae. Anterolateral angles short and not protruding. Punctures not evenly distributed, denser at sides. Only small area at anterior edge of pronotal collar microrugose. Hypomeral cavities present but shallow, sparsely punctate and not covered with macrosetae. Meso-metaventrum quite smooth, with a few scattered fine punctures at its anterior end, bearing posterior median groove and deep excavation near metacoxae.

Pterothorax. Elytra (ElyL 11.4 mm, MWoI123: 2.51 mm) convex, very shiny, deeply striate; elytral striae strongly, densely punctate (DP10, 15: 1.03 mm); intervals smooth and impunctate. Interval 2 near base not swollen.

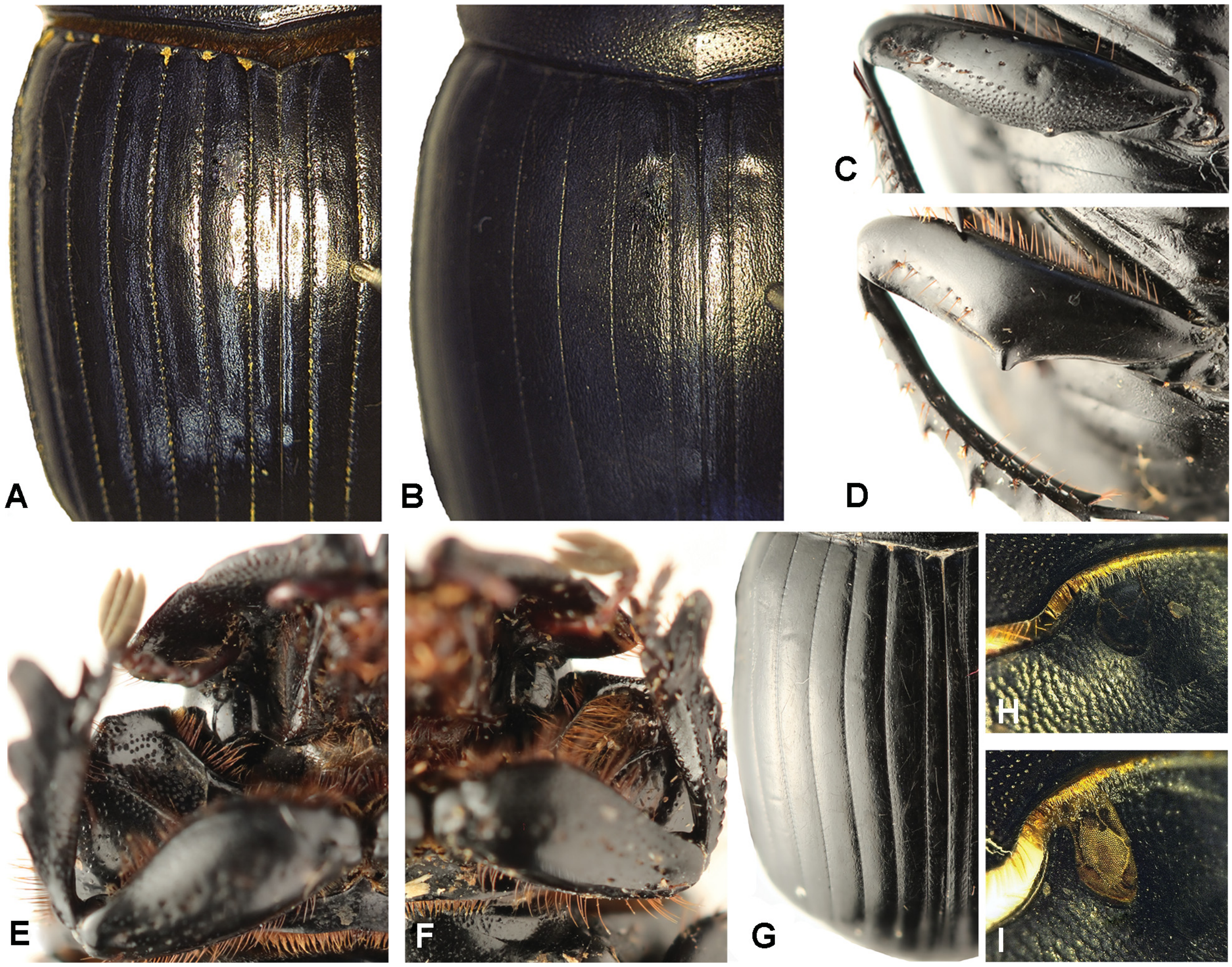

Fig. 2. Morphological details of *Synapsis* species. A–B – elytral surface: A – *S. puluongensis* sp. nov. with elytral striae strongly and densely punctate and interval 2 not swollen; B – *S. horaki* Zídek & Pokorný, 2010, with elytral striae impunctate and interval 2 swollen. C–D – metafemora: C – *S. puluongensis* sp. nov.; D – *S. yama* Gillet, 1911. E–F – setation of hypomeral cavities: E – *S. puluongensis* sp. nov.; F – *S. birmanica* Gillet, 1907. G – elytron of *S. naxiorum* Král & Rejsek, 2000 with weakly and sparsely punctate elytral striae and intervals weakly punctate. H–I – eye coloration in specimens of *S. horaki* Zídek & Pokorný, 2010: H – female; I – male.

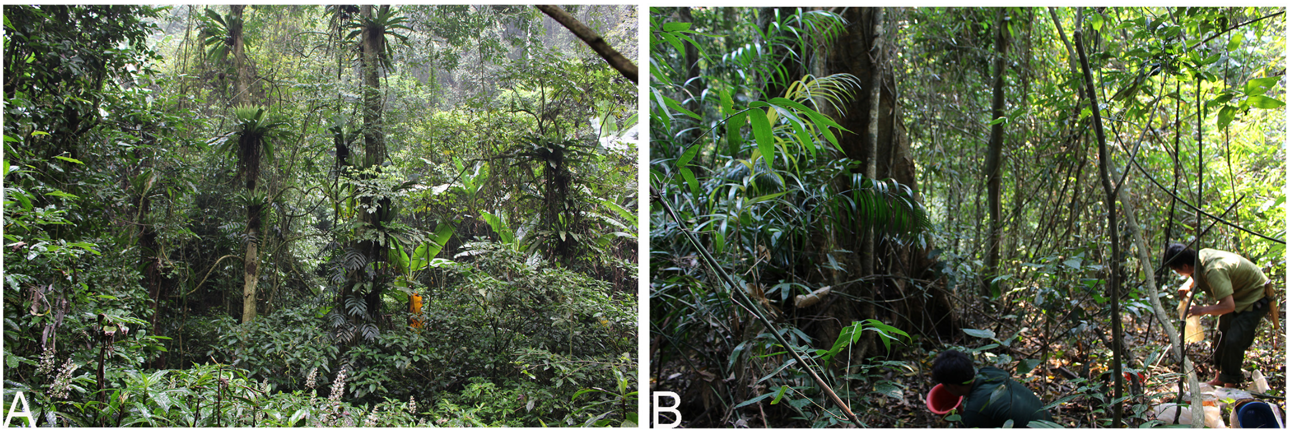

Fig. 3. Habitat of *Synapsis puluongensis* sp. nov. in Pu Luong Nature Reserve.

Mesepimeron and metepisternum flat, granulose and without macrosetae.

Legs. Protibia (ProTiL 3.30 mm, ProTiW 2.35 mm, ProTiSL 1.21 mm) tridentate, terminal tooth as long as protibial spur and nearly as long as protibial tarsus. Mesotibia (MesoTiL 3.34 mm, MesoTiW 1.33 mm, 1st MesoTiSL 2.09 mm, 2nd MesoTiSL 0.9 mm) and metatibia (MetaTiL 4.95 mm, MetaTiW 1.27 mm, MetaTiSL 1.55 mm) with red scanty macrosetae and slender spurs. Metatarsomeres nearly similar in size (MetaTaL 3.72 mm, MetaTa1L 1.08 mm, MetaTa1W 0.68 mm, MetaTa5W 0.32 mm).

Abdomen and pygidium. Abdominal ventrites opaque, sparsely punctate, and narrower at midline. Pygidium (PyL 2.46 mm, PyW 4.5 mm) feebly convex, densely and transversely punctate and scabrous.

Aedeagus (Figs 1E, F). Phallobase length 3.57 mm in lateral view, with strong swelling in middle of basal suture. Parameres length 2.19 mm (in lateral view), triangle-shaped. Phallobase and parameres forming angle > 130º.

Sexual dimorphism. Females differ from males in their weaker elytral striae, and meso- and metatrochanters with sparser reddish-brown macrosetae (absent in some specimens). Sexes also differ in the shape and strength of the metafemoral tooth, which is stronger in males. Compound eyes black in females but reddish brown in males.

Morphometrics. See Table 1.

Differential diagnosis. *Synapsis puluongensis* sp. nov. belongs to the *S. birmanica* group, as indicated by a combination of the following characters: hypomeral cavities present, genae unexpanded, frons unarmed, mesepisternal cavities absent, and upper longitudinal carina of male metatibia without brush of rusty setae. Species of the *S. birmanica* group may be clearly distinguished from those of *S. ovalis*, *S. brahmina* and *S. tmolus* groups by the presence of hypomeral cavities. The *S. ritsemae* group has expanded genae, in which it differs from the species of the *S. birmanica* group whose genae are unexpanded.

Synapsis puluongensis sp. nov. can be distinguished from other known species of the group by the following characters: in *S. puluongensis* the elytral interval 2 is not swollen near the base (swollen in *S. yama* from northern and central Vietnam and Laos, *S. horaki* from northern Vietnam, *S. dickinsoni* from northern Thailand: Phukieo, *S. ochii* from northern Thailand: Chiang Mai and in *S.*

Table 1. Morphometrics and morphology of *Synapsis puluongensis* sp. nov. and *S. horaki* Zídek & Pokorný, 2010 (in mm, except body weight in g)

	***Synapsis puluongensis* sp. nov.**			***Synapsis horaki***	
Character	Holotype	Male (n = 2)	Female (n = 4)	Male (n = 3)	Female (n = 1)
BoL	18.38	18.2	17.84 ± 0.59	18.72 ± 1.08	18.49
BoW	11.32	11.19	10.97 ± 0.53	11.73 ± 0.71	11.79
HeadL	3.67	3.82	3.77 ± 0.19	4.84 ± 0.46	5.21
HeadW	7.44	7.43	7.17 ± 0.34	8.02 ± 0.41	8.17
PronL	4.9	4.9	4.90 ± 0.26	4.93 ± 0.09	4.96
PronW	10.08	9.89	9.57 ± 0.56	9.97 ± 0.54	9.98
ElyL	11.4	11.24	10.97 ± 0.8	11.29 ± 0.74	11.61
MWoI123	2.51	2.51	2.48 ± 0.07	2.84 ± 0.2	2.86
DP10,15	1.03	1.04	0.98 ± 0.05	unclear	unclear
HoL	unarmed	unarmed	unarmed	unarmed	unarmed
PyL	2.46	2.44	2.36 ± 0.13	2.33 ± 0.12	2.24
PyW	4.5	4.42	4.28 ± 0.33	4.59 ± 0.41	4.66
ProTiL	3.3	3.28	3.20 ± 0.12	3.41 ± 0.24	3.25
ProTiW	2.35	2.35	2.28 ± 0.10	2.62 ± 0.23	2.68
ProTiSL	1.21	1.22	1.23 ± 0.18	1.5 ± 0.09	1.48
MesoTiL	3.34	3.45	3.54 ± 0.26	3.75 ± 0.21	3.72
MesoTiW	1.33	1.32	1.28 ± 0.16	1.42 ± 0.1	1.49
1st MesoTiSL	2.09	2.02	1.88 ± 0.24	2.26 ± 0.2	2.36
2nd MesoTiSL	0.9	0.94	0.95 ± 0.14	1.17 ± 0.09	1.18
MetaTiL	4.95	4.91	4.77 ± 0.21	4.89 ± 0.18	4.69
MetaTiW	1.27	1.25	1.22 ± 0.13	1.41 ± 0.07	1.39
MetaTiSL	1.55	1.5	1.49 ± 0.18	1.65 ± 0.06	1.71
MetaTaL	3.72	3.71	3.68 ± 0.25	3.92 ± 0.11	4.08
MetaTa1L	1.08	1.1	1.12 ± 0.07	1.24 ± 0.08	1.24
MetaTa1W	0.68	0.68	0.67 ± 0.08	0.77 ± 0.07	0.74
MetaTa5W	0.32	0.32	0.35 ± 0.03	0.39 ± 0.02	0.38
BoWeight	0.67432	0.67	0.63 ± 0.04	0.86 ± 0.03	0.89676
DDC	1.43	1.41	1.39 ± 0.11	1.45 ± 0.09	1.58
HyC	present	present	present	present	present
MeC	absent	absent	absent	absent	absent
Gen	unexpanded	unexpanded	unexpanded	unexpanded	unexpanded
MesoF	densely punctured	densely punctured	densely punctured	densely punctured	densely punctured
MetaF	densely punctured	densely punctured	densely punctured	densely punctured	densely punctured
MetaTibrush	absent	absent	absent	absent	absent

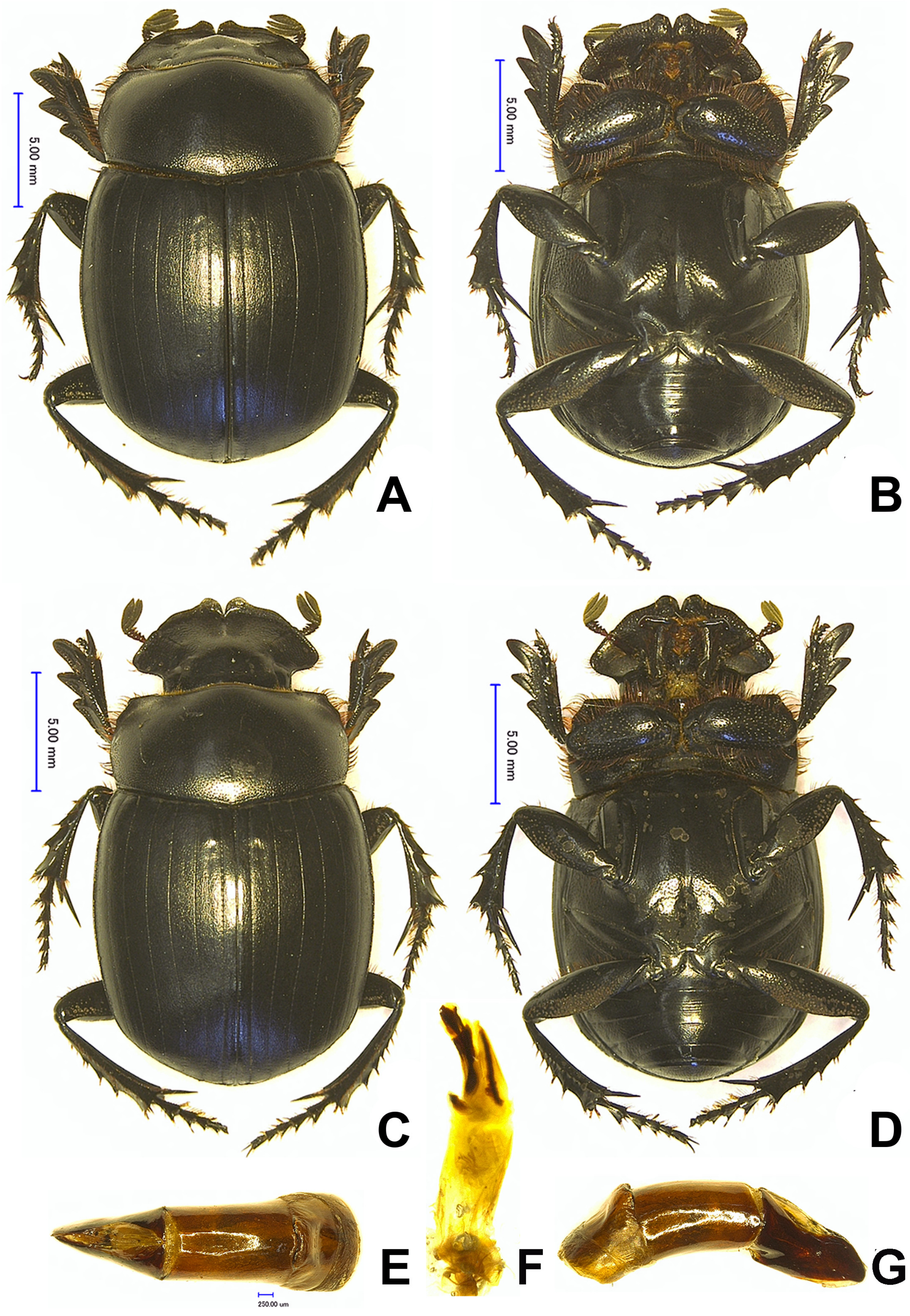

Fig. 4. *Synapsis horaki* Zídek & Pokorný, 2010: A – dorsal habitus, male. B – ventral habitus, male. C – dorsal habitus, female. D – ventral habitus, female. E – aedeagus, dorsal view. F – internal sac of aedeagus. G – aedeagus, lateral view.

masumotoi from Taiwan). Characters on the metafemora and elytral striae clearly differentiate *S. puluongensis* sp. nov. from the other species of the *S. birmanica* group recorded in Vietnam: both *S. puluongensis* sp. nov. and *S. horaki* have densely punctured metafemora on the ventral side, while *S. yama* has no punctures on the metafemur. In addition, *S. puluongensis* sp. nov. has coarse and closely spaced punctures on the elytral striae, which are absent or extremely weak in *S. horaki* (Figs 2A–D).

Synapsis puluongensis sp. nov. has hypomeral cavities without macrosetae, which distinguishes it from *S. birmanica* (hypomeral cavities are covered by a brush of rusty macrosetae). The new species has deep striae, whereas in *S. birmanica* the striae are feeble (Figs 2E–F).

Synapsis puluongensis sp. nov. is morphologically similar to *S. naxiorum* in its black and shiny dorsal side. However, the new species can be distinguished from *S. naxiorum* in having more punctures on the ventral side of the metafemora; elytral striae more densely punctate, intervals not punctate, and hypomeral cavities devoid of rusty setae (Figs 2A,G).

The entire surface of *S. puluongensis* sp. nov. is black and shiny, in contrast to the opaque surface of *S. punctata* from Myanmar and *S. roslihashimi* from Malaysia. In addition, *S. puluongensis* sp. nov. has convex intervals, whereas *S. roslihashimi* and *S. punctata* have flat or only weakly convex intervals. In *S. punctata* and *S. roslihashimi* all margins of intervals are punctate, whereas they are impunctate in the new species. The new species can also be distinguished from *S. punctata* and *S. roslihashimi* by the absence of hypomeral rusty macrosetae.

Etymology. The specific epithet *puluongensis* refers to the name of the type locality, Nature Reserve Puluong, Thanh Hoa Province, central Vietnam; adjective.

Biology. The new species was collected in primary forests on limestone bedrock. The primary forests are characterized by a complex structure with various storeys, comprising an upper storey with emergent trees more than 35 m tall, belonging to Dipterocarpaceae and Combretaceae, a dominant lower storey (various tree species from 15 to 30 m tall), and a brush layer on the forest floor containing various herbs (Urticaceae, Araceae, Begoniaceae), lianas and parasitic plants (Connaraceae, Fabaceae, Orchidaceae, Loranthaceae).

Synapsis horaki Zídek & Pokorný, 2010

(Figs 2B,H,I, 4A–G)

Synapsis horaki Zídek & Pokorný, 2010: 18, figs 12–15 (original description).

Type locality. Vietnam, Vinh Phuc Province, Tam Dao, 900 m a.s.l.

Type material examined. Holotype: ♂, '6–10.v.1990 | Tam Dao | Vinh Phu Distr. | Vietnam | 900 m | Jan Horák leg.' (NMPC).

Additional material examined. VIETNAM: Cao Bang Province: Pia Oac Nature Reserve, primary forest, baited pitfall trap, 5.–20.v.2016, 22°34′3.6″N, 105°53′3.3″E, 1223 m, 1 ♂, 22°34′1.4″N, 105°53′3.3″E, 1220 m, 1 ♂, 22°34′3.1″N, 105°53′4.7″E, 1220 m, 1 ♂, 22°34′3.1″N 105°53′4.4″E, 1213 m, 1 ♀, Bùi Văn Bắc leg. (all in VNUF).

Diagnosis. Hypomeral cavities present; surface sparsely punctate, and not covered by macrosetae. Mesepisternal surface flat and rugose. Genae unexpanded. Frons unarmed. Pronotal anterolateral angles not protruding. Elytral striae weak and indistinctly punctate; elytral interval 2 swollen near base. Ventral surface of femora densely punctate.

Description. Body length 17.5–20.1 mm, body width 10.8–12.6 mm. Colour: Dorsal surface black and glabrous. Ventral surface black on head and shiny black on thorax, abdomen and femora. Reddish brown macrosetae upon legs and pronotal margins. Mouthparts, maxillary palpi and tarsi reddish brown. Antennae brown; antennomeres IV–VI darker than other antennomeres.

Head nearly semicircular, 4.4–5.3 mm long, and 7.5–8.5 mm wide. Clypeal surface extremely rugose; apex strongly and deeply emarginated, V-shaped; distance between apices of clypeal denticles (DDC) 1.4–1.6 mm; anterior margin flexed upwards with few reddish setae. Genae rectangular, quite distinctly separated from clypeus and frons by well-defined suture; surface strongly rugose and weakly punctate; margins of anterolateral angles with dense reddish macrosetae. Frons unarmed, only slightly swollen; surface weakly rugose and punctate. Antennae with 9 antennomeres; length of antennomere I approx. 1.4 mm, equal in length to antennomeres II–VI combined; antennal club approx. 1.4 mm.

Prothorax. Pronotum transverse, 4.8–5.1 mm long, and 9.3–10.6 mm wide, widest at anterior quarter; pronotal disc almost indistinctly punctate, except for small weakly punctured areas near base and sides (at 30× magnification); anterolateral angles sharp and not protruding. Two lateral carinae on each side of pronotum clearly distinct; margin of outer carina with dense reddish brown macrosetae; area between carinae smooth. Hypomeral cavities present; surface of cavities weakly and sparsely punctate, and without macrosetae. Meso-metaventrum plate almost smooth, with posterior median weak groove, and with distinct excavation near metacoxae; surface of sides and anterior part sparsely and weakly punctate.

Pterothorax. Elytra 10.4–12.1 mm long, 10.8–12.6 mm wide, with weak and indistinctly punctured striae. Elytral intervals convex, smooth and impunctate (at 30× magnification); interval 2 swollen near base. Mesepimeron and metepisternum flat, granulose and without macrosetae.

Legs. Ventral surface of profemora strongly, coarsely and quite equally punctate; macrosetae upon profemoral margin reddish brown and long, denser in anterior margin. Protibia (ProTiL 3.2–3.6 mm, ProTiW 2.3–2.9 mm) with three broad and flat lateral teeth; protibial spurs (ProTiSL 1.4–1.6 mm) sharp, strongly curved outwards near apex, and equal in length to protibial tarsus. Ventral surface of mesofemora strongly and unequally punctate; punctures becoming denser on third posteior part. Mesotibia (MesoTiL 3.5–4 mm, MesoTiW 1.3–1.5 mm) with two sharp spurs (1st MesoTiSL 2.0–2.4 mm, 2nd MesoTiSL 1.1–1.3 mm). Ventral surface of metafemora strongly and unequally punctate; punctures denser on posterior half of metafemora. Metatibia (MetaTiL 4.7–5.1 mm, MetaTiW 1.3–1.5 mm) elongate and slightly curved. Metatarsus length 3.9–4.1 mm, with 5 metatarsomeres nearly similar in size.

Table 2 (on this and the opposite page). Morphological comparsions between the new species and its congeners compiled after Gillet (1911), Arrow (1931), Balthasar (1963), Masumoto (1973, 1996), Hanboonsong & Masumoto (1999), Král & Rejsek (2000), Král (2002), Ochi & Kon (2007), Ochi et al. (2008), Zídek & Pokorný (2010).

Character	***S. puluongensis* sp. nov.**	***S. yama***	***S. horaki***	***S. dickinsoni***	***S. ochii***	***S. naxiorum***
Color (dorsal view)	black, shiny	black, opaque	black, moderately glossy	black	black	black, shiny
BoL	17.2–18.5	27.0–29.0	17.5–24.0	26.0–28.5	26.0	18.0–29.0
BoW	10.7–11.5	??	10.8–13.1	??	??	??
Frons	unarmed	unarmed	unarmed	unarmed	unarmed	unarmed
Gen	unexpanded	unexpanded	unexpanded	unexpanded	unexpanded	unexpanded
HyC	present	present	present	present	present	present
Rusty setae covering HyC	absent	present (long and dense)	absent	present (long and dense)	present (long and dense)	present (long)
MeC	absent	absent	absent	absent	absent	absent
Elytral striae	deep	feeble	feeble	deep	feeble	deep
Punctures on elytral striae	strong and dense	impunctate	weak	weak	strong and dense	sparse
Interstriae shape	convex	flat	flat	weakly convex	flat	convex
Punctures on interstriae	absent	absent	absent	absent	absent	present
Second interstria near base	not swollen	swollen	swollen	swollen	swollen	not swollen
MetaF	densely punctate	impunctate	densely punctate	sparsely punctate	sparsely punctate	sparsely punctate
MetaTibrush (male)	absent	absent	absent	absent	absent	absent
Distribution	Central Vietnam: Thanh Hoa Province	N+C Vietnam (Tuyen Quang, Thanh Hoa), Laos	N. Vietnam: Vinh Phuc Prov., Cao Bang Prov.	Northern Thailand (Phukieo)	Northern Thailand (Chiang Mai)	China (Yunnan)

Character	***S. punctata***	***S. roslihashimi***	***S. birmanica***	***S. masumotoi***	***S. cambeforti***
Color (dorsal view)	opaque	black, opaque	black, opaque	black, opaque	black, Shiny
BoL	21.1	21.8–26.0	21.0-26.0	27.0–30.0	22.0–28.0
BoW	12.0	11.7–13.8	14.5	??	max. 14.6
Frons	unarmed	unarmed	unarmed	unarmed	armed (minute horn)
Gen	unexpanded	unexpanded	unexpanded	unexpanded	expanded
HyC	present	present	present	present	present
Rusty setae covering HyC	short and sparse	long and dense	long and dense	absent	??
MeC	absent	absent	absent	absent	absent
Elytral striae	??	deep	feeble	feeble	deep
Punctures on elytral striae	strong and dense	strong and dense	strong and dense	invisible	strong and dense
Interstriae shape	weakly convex	flat	flat	flat	flat
Punctures on interstriae	distinctly notched margin of interstriae	distinctly notched margin of interstriae	slightly notched margin of interstriae	absent	fine, sparse and scattered
Second interstria near base	not swollen	not swollen	not swollen	swollen	not swollen
MetaF	densely punctate	densely punctate	densely punctate	sparsely punctate	densely punctate
MetaTibrush (male)	absent	absent	absent	absent	absent
Distribution	Myanmar	Malaysia	China (Yunnan), Malaysia, Myanmar, Thailand	Taiwan	Brunei (Kalimantan)

Abdomen and pygidium. Abdominal ventrites opaque, indistinctly punctate, and narrower at midline. Pygidium 2.2–2.5 mm long, 4.0–4.8 mm wide; surface slightly convex, scabrous, and with mixture of punctures and rugosities.

Aedeagus. Phallobase length 3.4–3.6 mm (in lateral view); basal suture with strong swelling at middle. Parameres length 2.0–2.2 mm (in lateral view). Phallobase and parameres forming angle > 130°.

Sexual dimorphism. Based on an examination of the four specimens (3 males and 1 female), we did not find significant differences in morphological characters between both sexes, except for the colour of compound eyes, being black in the female but yellow in males (Figs 2H, I). This finding is consistent with the observed sexes of *S. puluongensis* sp. nov., raising the possibility of using this character to distinguish both sexes of these two species.

Biology. All four specimens were collected in the Pia Oac Nature Reserve. The habitat is primary forests at an elevation of 1220 m a.s.l. characterized by a forest canopy cover ranging from 76 to 95%. The percentage of exposed soil was 0–5%, with 6–25% herbaceous plant layer and leaf lit-

Table 2 (continued from previous page).

Character	***S. ritsemae***	***S. thoas*** = *S. sumatrensis*	***S. ovalis***	***S. strnadi***	***S. gilleti***
Color (dorsal view)	black	black	black, opaque	black	black, opaque
BoL	25.0	24.0	23.0–26.0	22.0–29.0	24.0
BoW	??	??	??	??	14.0
Frons	armed (minute horn)	armed (minute horn)	unarmed	unarmed	unarmed
Gen	expanded	strongly expanded	unexpanded	unexpanded	unexpanded
HyC	present	present	absent	absent	absent
Rusty setae covering HyC	??	present (long and dense)	absent	absent	??
MeC	absent	absent	present	present	present
Elytral striae	deep	deep	feeble	feeble	deep
Punctures on elytral striae	vague	distinct	irregular	irregular	distinct
Interstriae shape	flat	weakly convex	flat	flat	flat
Punctures on interstriae	fine, sparse and scattered	sparse	absent	absent	absent
Second interstria near base	not swollen	not swollen	not swollen	not swollen	not swollen
MetaF	??	weakly punctate	sparsely punctate	densely punctate	impunctate
MetaTibrush (male)	absent	absent	absent	absent	absent
Distribution	Borneo, Java, Sumatra (Indonesia)	Java, Sumatra (Indonesia)	Laos, Thailand, Vietnam	North Vietnam (Vinh Phuc, Lao Cai)	Bangladesh, India, Bhutan, Nepal

Character	***S. boonlongi***	***S. tridens*** = *S. yunnana*	***S. davidis***	***S. brahmina*** = *S. batesi*	***S. satoi***
Color (dorsal view)	black, not shiny	black, opaque	black, opaque	black, not shiny	black, opaque
BoL	26.0–27.0	28.0–34.0	28.0–33.0	28.0–30.0	29.5
BoW	??	17.0–21.0	??	17.0–18.0	16.3
Frons	unarmed	armed	armed	armed	armed
Gen	unexpanded	expanded	expanded	expanded	expanded
HyC	absent	absent	absent	absent	absent
Rusty setae covering HyC	??	absent	absent	absent	??
MeC	present	absent	absent	absent	absent
Elytral striae	deep	shallow	shallow	deep	deep
Punctures on elytral striae	weak, notching interstriae	weak	weak	weak	weak, indistinct
Interstriae shape	flat	flat	flat	slightly convex	slightly convex
Punctures on interstriae	present (very small)	absent	absent	absent	absent
Second interstria near base	??	not swollen	not swollen	not swollen	??
MetaF (ventral side)	??	impunctate	impunctate	impunctate	??
MetaTibrush (male)	absent	present	present	present	present
Distribution	Thailand	China, India, Laos, Myanmar, Thailand, northern Vietnam	China, Taiwan	Bhutan, Northeast India, Nepal, Pakistan	Laos-Myanmar border

Character	***S. simplex***	***S. tmolus***	***S. kiuchii***
Color (dorsal view)	black	black	black, shining
BoL	24.0–26.0	36.0–52.0	23.0–25.0
BoW	??	??	??
Frons	armed	armed	armed
Gen	unexpanded	unexpanded	unexpanded
HyC	absent	absent	absent
Rusty setae covering HyC	absent	absent	??
MeC	absent	absent	absent
Elytral striae	deep	deep	deep
Punctures on elytral striae	invisible	strong and close	invisible
Interstriae shape	weakly convex	weakly convex	weakly convex
Punctures on interstriae	absent	absent	absent
Second interstria near base	not swollen	not swollen	not swollen
MetaF (ventral side)	impunctate	impunctate	??
MetaTibrush (male)	present	present	present
Distribution	China (Yunnan), Laos, Myanmar, Thailand, Vietnam	Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan, China	Thailand

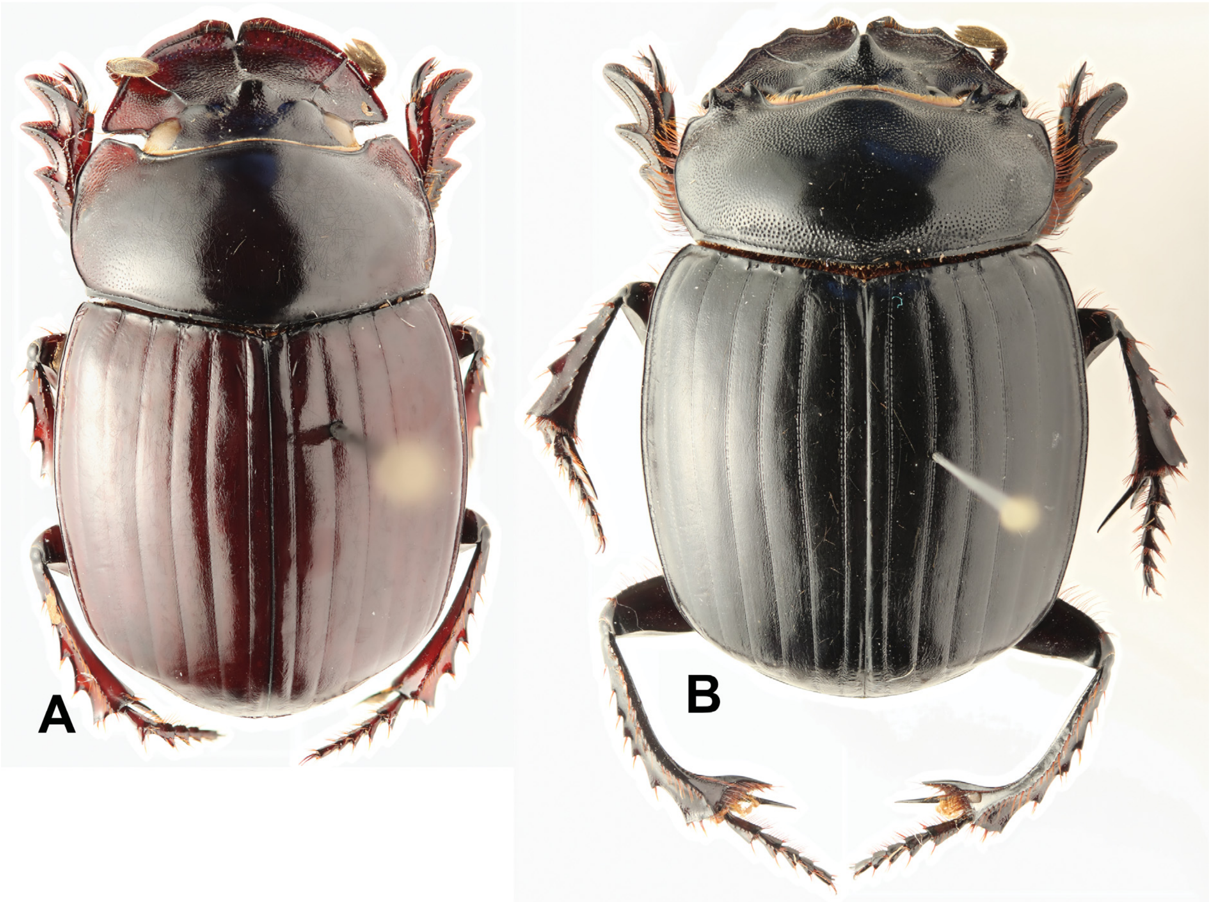

Fig 5. Dorsal habitus. A – *Synapsis simplex* Sharp, 1875. B – *S. tridens* Sharp, 1881

ter cover of 96–100%. The forests has a complex structure with various storeys. Dominant trees range from 20 to 30 m tall and belong mainly to two dominant families: Fagaceae (*Castanopsis* spp., *Lithocarpus* spp., *Castanea* spp.) and Lauraceae (*Litsea* spp., *Cinnamomum* spp., *Machilus* spp.), the herbaceous and parasitic plants comprised Poaceae, Asteraceae, Orchidaceae and Loranthaceae.

Remarks. So far, *Synapsis horaki* was known only from the holotype specimen collected in the Tam Dao National Park, Vinh Phuc Province, northern Vietnam. The herein presented specimens constitute a new record for the Cao Bang Province and the first known female. Morphometric measurements are summarized in the Table 1.

Synapsis tridens Sharp, 1881

Synapsis tridens Sharp, 1881: xcii (original description).

Type locality. India, Assam.

Material examined. VIETNAM: Cao Bang Province: Pia Oac Nature Reserve, primary forest, baited pitfall trap, 30.iv–15.v.2016, 22°34′3.1″N 105°53′3.6″E, 1227 m, 1 ♂, 22°33′59.7″N 105°52′48.5″E, 1165 m, 1 ♀, 22°34′3.1″N, 105°53′4.7″E, 1220 m, 1 ♂, 22°34′3.1″N 105°53′4.4″E, 1213 m, 1 ♀, Van Bac Bui leg. (all in VNFU). **Thanh Hoa Province:** Pu Luong Nature Reserve, primary forest, baited pitfall trap, 5.–25.iv.2016, 20°28′55.1″N 105°14′29.3″E, 958 m, 1 ♂, 20°28′54.7″N 105°14′30.9″E, 950 m, 1 ♂ 1 ♀, Bùi Văn Bắc leg. (VNUF).

Distribution. SW China, NE India, Laos, Myanmar, Thailand and N Vietnam (Zídek & Pokorný 2010).

Remarks. The aforementioned specimens represent additional records from Vietnam.

Discussion

Tropical forests on limestone bedrock in northern and central Vietnam are characterized by shallow soils. Perhaps these soil characteristics are not suitable for large *Synapsis* species which are known to tunnel deep nests for the storage of dung for feeding and breeding (Hanski & Cambefort 1991). *Synapsis puluongensis* sp. nov. and *S. horaki* were found exclusively in primary forests, and thus may be considered as indicator species for undisturbed forests. Specimens of the genus *Synapsis* were generally rare, comprising 10.45% of all coprine specimens found in primary forests.

The discovery of *S. puluongensis* sp. nov. increases the number of known species of *Synapsis* to 24, of which seven are now recorded from Vietnam. The Vietnamese species may be identified using the following key.

Key to species of *Synapsis* recorded from Vietnam

The key is based on the specimens examined by us in NMPC and VNUF as well as on literature data (Arrow 1931, Balthasar 1963, Král & Rejsek 2000, Král 2002, Hanboonsong & Masumoto 1999, Ochi & Kon 2007, Ochi et al. 2008, Zídek & Pokorný 2010).

1(6) Hypomeral cavities present (Figs 2E–F).
2(3) Elytral interval 2 near base not swollen (Fig. 2A). .... ***S. puluongensis* sp. nov.**

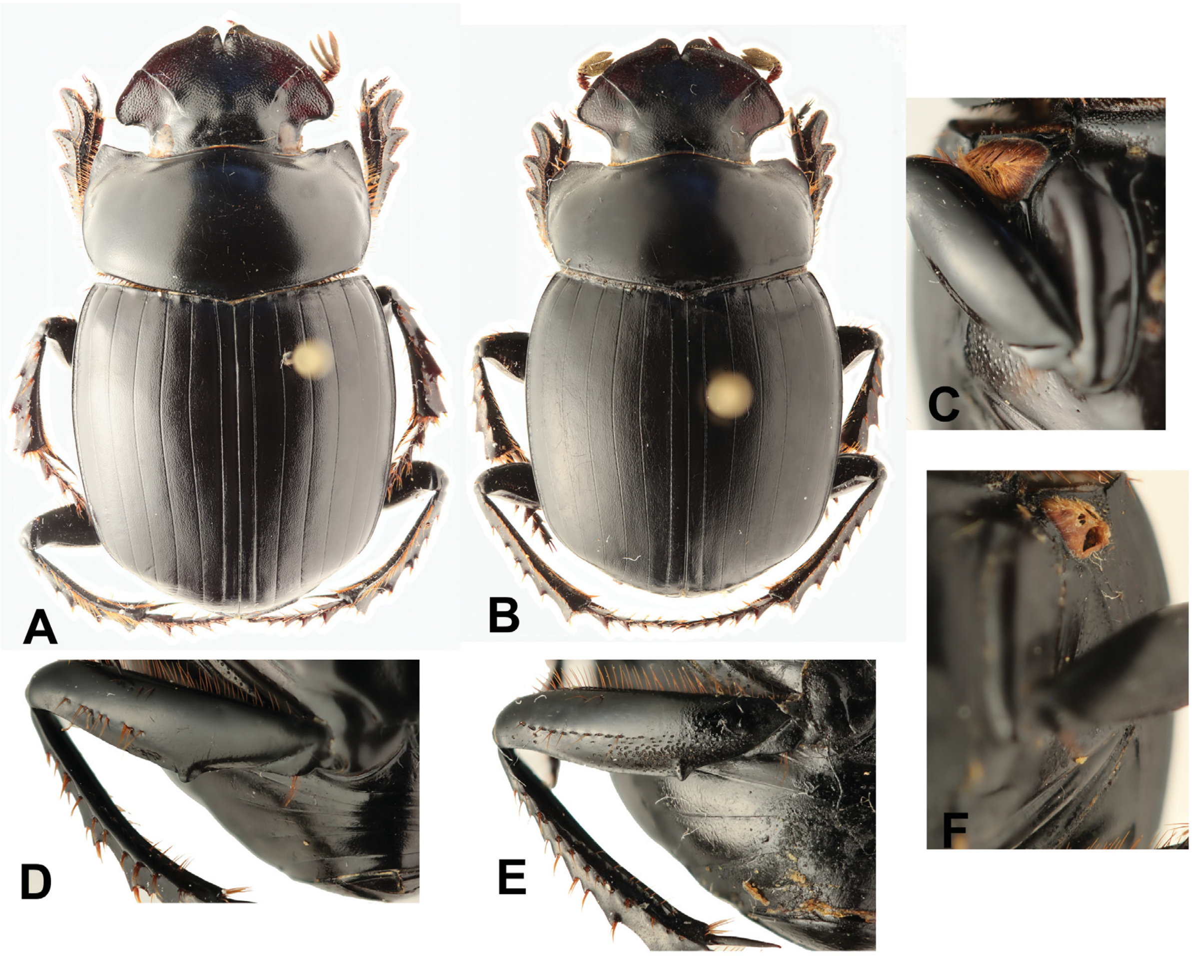

Fig. 6. Dorsal habitus, ventral surface of femora and mesepisternal cavities. A, C, D – *Synapsis ovalis* Boucomont, 1920; B, E, F – *S. strnadi* Král, 2002.

3(2) Elytral interval 2 near base swollen (Fig. 2B).

4(5) Metafemora in ventral view densely punctate, body length 17.5–24.0 mm. .... **S. horaki** Zídek & Pokorný, 2010

5(4) Metafemora in ventral view not punctate, body length 27.0–29.0 mm (Fig. 2D). .... **S. yama** Gillet, 1911

6(7) Hypomeral cavities absent.

7(10) Frons with minor horn or medial tubercle; mesepisternal cavities absent.

8(9) Genae not expanded, anterolateral angle of pronotum not dentate (Fig. 5A). .... **S. simplex** Sharp, 1875

9(8) Genae expanded; anterolateral angle of pronotum tridentate (Fig. 5B). .... **S. tridens** Sharp, 1881

10(11) Frons without minor horn or only with medial tubercle; mesepisternal cavities present and covered with red setae (Figs 6A–C, F).

11(12) Anterolateral angles of pronotum nearly rectangular (90°). Lateral angles of genae obtuse, rounded. Metafemora in ventral view sparsely punctate (Figs 6A, D). .... **S. ovalis** Boucomont, 1920

12(11) Anterolateral angles of pronotum about 135°. Lateral angles of genae rather sharp, metafemora in ventral view densely punctate (Figs 6B, E). .... **S. strnadi** Král, 2002

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GENERAL DISCUSSION

This thesis investigated the impact of anthropogenic land-use change (LUC) on dung beetle (DB) communities through describing changes in the community structure and morphological traits of DB communities across the gradient of tropical forest conversion. It is well known that DB communities differ between land-use types (Davis et al., 2001; Vulinec, 2002; Shahabuddin et al., 2005; Quintero & Roslin, 2005; Vulinec et al., 2006; Gardner et al., 2008; Hayes et al., 2009; Boonrotpong et al., 2012; Audino et al., 2014; Beiroz et al., 2017; Costa, et al., 2017) but conclusions from taxonomic studies remain controversial. Earlier studies were mostly based on taxonomy. However, due to fundamental differences in the taxonomic composition of DB communities between continents, countries and even regions, the nomenclatural approach focusing on species identity made the generalization of results difficult and led to a loss of ecological generality (Fukami et al., 2005; Mc Gill et al., 2006). Instead species traits reflect their environmental adaptations through natural selection across species borders and accordingly have direct fitness consequences. More recent studies have adopted a trait-based approach to describe patterns of community change resulting from habitat transformation, highlighting that the observed responses were due to the identity and dominance patterns of trait composition rather than species richness or abundance (Violle et al., 2007; Laughlin et al., 2012; Gagic et al., 2015; Griffiths et al., 2016; Raine et al., 2018). Particularly, body size has shown consistent patterns in responses to habitat change. For example, the abundances of large-bodied forest species of three groups: birds, beetles and ants significantly declined following the forest conversion to oil palms (Senior et al., 2013), because the decreased availability of food resources hampered the great energy requirement of large-bodied species (Damuth, 1981; Henle et al., 2004). We followed this modern trait approach in addition to the traditional taxonomic approach to relate various morphological traits of DB communities to changing environmental conditions imposed by different land-uses, and in addition, we linked these with one of the most important ecosystem functions, dung removal rate. As indicated in Chapter 2, we found significant shifts of specific morphological traits associated with the dispersal capacity and foraging behaviour of DB across land-use types, reflecting their adaptations to the changing environments. The shape of pronotum and elytra in addition to body length and biomass turned out to be key morphological traits, strongly associated with dung removal rate.

By investigating two tropical, high-elevation karst ecosystems in north-eastern and north-central Vietnam, it turned out that the DB communities of these ecosystems harbour unique patterns of community responses to LUC, with both abundance and species richness being significantly higher in meadows compared to forests (Chapter 1). Three formally described new species, one new country record and rare species of a large-body size and many potentially new small-bodied species were recorded from these karst ecosystems (Chapter 3, 4). These results provide strong evidence for the assumption that tropical karst ecosystems host a high level of endemism. A significant difference in the species composition of DB between the two karst ecosystems further confirmed this assumption (Chapters 1).

Finally, we were able to assess the conservation value of the old (>35 years) 2nd Forests for DB by comparing the community attributes and structure of DB communities between 2nd Forests and 1st Forests throughout both NR. Our results showed that the old 2nd Forests could provide refuge for some 1st Forest species but did not provide a substitute for 1st Forests (Chapter 1).

Structure of DB communities in different land-use types of karst ecosystems

Changes in the composition structure of DB between land-use types within non-karst ecosystems of SE-Asia were described by Boonrotpong et al. (2004) and Shahabuddin et al. (2005). Yet, DB communities inhabiting karst ecosystems have received little attention. For the first time we assessed the effects of LUC on the karst DB communities in northern and central Vietnam. Our study indicated significant differences in community structure between land-uses, and a separation between the two karst ecosystems was by far broader than expected (Chapter 1). It seems likely that, the karst ecosystems possess differing terrains and variable climatic conditions across space (Clements et al., 2006), and this spatial configuration supports a heterogeneous ecological selection across spatially separated karst ecosystems, leading a high variation in community structure (Zhou & Ning, 2017). In addition, the incidences of stochastic events, degrees of isolation and human impacts, which differ across space, may affect patterns of community dynamics in responses to LUC to varying degrees.

In complementation of the studies of Boonrotpong et al. (2004) and Shahabuddin et al. (2005) which focussed on the evaluation of the overall impact of local LUC on community composition, we determined in this thesis potential environmental factors driving the structure of the two similar communities of 1st Forests and 2nd Forests. Among the seven examined environmental variables including leaf litter cover (LLC), leaf litter thickness (LLT), soil clay content (Clay), diameter of shrub crown (Di.s), forest canopy cover (Fc), cover of ground vegetation (GV) and diameter of trees (Di.t), the two latter revealed to significantly affect the forest community structure. The cover of ground vegetation turned out to provide ideal perches for the abundant and small-bodied tunnelers to locate food resources, while large trees seems shelter and offer an abundant food source for many mammals, and therefore affect the distribution of their close associations (e.g., large-bodied DB). Leaf litter is a typical physical barrier on the forest floor that was showed to significantly affect the nesting activities of many DB species, as a thick litter layer may exert a high resistance to dung-ball rolling for small rollers (Nichols et al., 2013). However, due to few small rollers inhabiting the karst forests, leaf litter is unlikely to be the factor structuring the forest DB communities.

When detecting patterns of community attributes in responses to LUC across the two karst ecosystems, we found a consistently higher abundance and species richness in meadows than in forests. This finding is in stark contrast to those found in Central and South America (Harvey et al., 2006; Gardner et al., 2008; Braga et al., 2013), therefore confirming the uniqueness of DB fauna of the karst ecosystems. A high abundance and species richness in the meadow sites was due to the increasing number of small-bodied tunnelling beetles which are by far abundant and species-rich in the typical composition structure of SE-Asian DB. The dominance of small-bodied DB communities in meadows reflected the adaptations of morphological traits to the environments (Chapter 2).

Diversity of dung beetles in tropical karst ecosystems

The DB fauna of SE-Asian karst ecosystems turned out to be highly diverse with around 50 species recorded in each investigated nature reserve in comparison to other non-karst ecosystems (Hayes et al., 2009; Boonrotpong et al., 2004; Shahabuddin et al., 2005). Our results on DB support the notion of Schilthuizen et al. (2004) and Clements et al. (2006) that SE-Asian karst ecosystems harbour a high species diversity. Three formally described new large-bodied species, including *Copris caobangensis* Bui, Dumack and Bonkowski, 2018; *Copris sonensis* Bui, Dumack and Bonkowski, 2018 and *Synapsis puluongensis* Bui & Bonkowski, 2018, were recorded from these ecosystems. The high number of new species described and high species turnover between both NR indicate the existence of endemic species in DB, as shown for other organisms in these ecosystems (Ng, 1991; Ng et al., 1996; Schilthuizen et al., 2005; Clements et al., 2008). It was surprising that the two surveyed karst ecosystems, being essentially similar in topology, climate and vegetation structure, and separated by only 380 km, had only 24% and 21% of the total meadow species and forest species, respectively, in common. Our findings correspond with studies on the flora or snail fauna of karst ecosystems (Wikramanayake et al., 2000; Clements et al., 2006), reporting that no single hill harboured more than 20% similar plant species from karst ecosystems in Malaysia, or recorded an overlap of only 35% between snail species among intensively surveyed karst sites only 150 km part, in northern Vietnam. This can possibly be explained by the exceptionally karst abiotic characteristics of karst ecosystems, such as alkaline soil conditions, thin soil layers and comparatively steep and isolated mountains that likely restrict gene flow between population and promote allopatric speciation.

Land use change selected for distinct dung beetle species with altered morphological traits forming distinct clusters of traits adapted to the environment at the community level

Based on a cluster analysis (Chapter 2) we identified three distinct clusters of morphological traits, turned out to reflect their adaptations to the environments. For example, trait cluster A comprised seven species of large body length and biomass, being absent or rare in meadows but common in forests. Most DB of meadows were grouped in trait cluster C, and comprised DB species of small body length and biomass, nearly semicircular elytra and long metatarsi. It seems likely that the convergence of small body length, together with elongated metatarsi for climbing and nearly semicircular elytra reflect morphological traits that confer a competitive advantage for these DB to locate food from perches in high ground vegetation (Howden & Nealis, 1978; Peck & Forsyth, 1982; Larsen et al., 2008). Given the observation of South African DB that the wingless species typically possess a more rounded body than equivalent-sized and winged species (Chown et al., 1998), the nearly semicircular elytra of SE Asian DB could also reflect DB species of poor dispersal.

Overall, the results strongly support the hypothesis that the observed clustering of morphological traits reflects selective processes on DB species in responses to LUC. This supports recent calls for the increased use of trait-based approaches to assess the influence of LUC on invertebrate communities (Mc Gill et al., 2006; Gagic et al., 2015; Griffiths et al., 2016; Raine et al., 2018), as traits hold information about community structure and functioning. With the correct methods, traits can be well defined and are easily measured on continuous scales in comparison to species identity. By applying a new approach combining co-inertia (RLQ) analysis and fourth-corner methods, allowed us for the first time to relate environmental variables directly to specific morphological traits of DB species.

Are large-bodied dung beetles vulnerable to forest conversion in karst ecosystems?

Large-bodied DB are highly sensitive to forest degradation, showing a serious decline in species richness, abundance and biomass, and eventually functional loss in highly degraded tropical forests of South America (Larsen et al., 2005), however, studies on large DB communities of SE-Asian karst ecosystems were lacking. Here we considered whether and which harsh environmental factors of karst ecosystems affect community attributes of large-bodied DB communities.

Our study demonstrated an impoverishment of the total species richness of large DB in karst meadows across both NR with the complete absence of *Synapsis* spp. and some *Copris* spp.. While, abundance and biomass exhibited unclear patterns in responses to LUC across space, with both being significantly higher in meadows of Piaoac but overall very impoverished in meadows of Puluong, compared to forests. It has been shown that large DB are closely associated with the composition and density of large mammals (Slade et al., 2011; Culot et al., 2013). This is because large DB have larger food requirements for their brood masses during the breeding season than small species (Howden & Nealis, 1978; Hanski & Cambefort, 2014). Accordingly, the availability of large mammalian excrements in karst ecosystems may primarily affect the distribution of large DB species. Further vegetation structure may influence large DB (Halffter & Arellano, 2002; Nichols et al., 2008; Gardner et al., 2008). Under non-shaded conditions, the bodies of large DB may be vulnerable to heating up above the maximum tolerated temperature of 42°C (Verdu et al., 2006). The decreased canopy cover in meadows could be detrimental to many DB species. However, most large DB are nocturnal beetles with a good dispersal capacity, suggesting that vegetation cover is less important than dung resources. In general, the tropical forests have a more species-rich fauna of large mammals than meadows, because many large mammals, such as primates, boars and the Sumatran serow, do not favour open areas where lack well-connected habitat networks. Thus, the karst forests in general have more species-rich large DB than meadows.

However, meadows in Piaoac were intensively grazed by cattle throughout the year, and dung resources of large mammals (e.g., cows, buffalos) were significantly higher in these meadows than in the forests with the impoverishment of large mammal fauna in terms of biomass and abundance as a consequence of animal hunting and limestone quarrying (Tran & Le, 2000). This supported a higher abundance and biomass of large DB in meadows of Pioac than forests. In contrast, the meadow sites of Puluong were located in protected areas with livestock grazing forbidden, and accordingly had little mammalian dung resources, leading to impoverished communities of large DB.

Overall, our study indicates the high sensitivity of large-bodied DB to shifts in large mammal communities following forest conversion in the tropics. As the conversion of forests to meadows within conservation areas may lead to a reduction in the density and composition of large mammals whose extreme vulnerabilities to a lack of large and well-connected habitat networks (Sieber et al., 2015), this has ripple effects on the closely associated communities of large-bodied DB.

In terms of the correlation of the abundance, biomass and species richness of DB, our findings were in correspondence with studies on the DB communities of Borneo (Malaysia) (Slade et al., 2011), but contrast to studies on the DB communities of South America (Larsen et al., 2005) reporting that biomass and abundance were strongly correlated with species richness. These differences are apparently due to changes in the species composition, species richness, abundance and biomass of particular DB species or even functional groups across continent. This again emphasizes the potential dangers of drawing broad conclusions about community responses to habitat change based on taxonomic information.

Body size/mass more than abundance determined dung removal rate

Our study confirmed a positive correlation between the body length and biomass of DB communities and dung removal rate in correspondence with Braga et al. (2013), Nervo et al. (2014), Tixier et al. (2015) and Frank et al. (2017). In addition, when evaluating the relative importance of body mass/length and abundance for their contributions to dung removal rate, we proved that body length and biomass more than abundance determined the capacity of dung removal. Despite having the highest abundance of DB in the meadow sites of Puluong, these communities showed a very low amount of dung removal. In contrast, forests had a high rate of dung removal by DB, despite a low abundance of DB.

Accordingly, the conversion of forests to meadows in conservation areas of kart ecosystems may lead to a reduction in large-bodied DB, with negative effects on the dung removal capacity of DB.

Is the capacity of dung removal of DB associated with the shape of traits?

The capacity of dung removal by DB is mostly described by a positive correlation of body length and/or body mass and dung removal rate (Nervo et al., 2014; Tixier et al., 2015; Frank et al., 2017). Our analysis of various morphological trait values quantified within a single functional group and measured on continuous scales allowed a much more detailed analysis on the role of specific morphological traits in the dung removal process. As indicated in Chapter 2, dung removal rate was positively correlated with pronotal aspect ratio and elytral aspect ratio, while the shape of mesotibia, metatibia and head did not correlate with this ecosystem function. A possible explanation expressed in Chapter 2 is that when tunnelling DB species dig their tunnels under dung piles, the pronotal shape rather than head shape and the robustness of mesotibia and metatibia plays an important role for pushing dung balls from these dung piles into the tunnels. Tunnelling DB species with a broader pronotum can move a larger amount of soil from tunnels as well as collect a larger amount of dung, hence have a competitive advantage over those species with a relatively longer pronotum. In the karst ecosystems where unevenly distributed and scare dung resources are common, also the elytral shape, being associated with the dispersal capacity of DB, appears crucial. The DB species with high dispersal capacity, characterized by elongated elytra, may be favoured in locating and occupying food resources. Although a few recent studies have showed that the elytra of beetles can influence aerodynamic performance and vertical force production in flight, and in addition the rotation angle and wing locking systems of elytra indirectly affect the ability to fly (Sun & Bhushan, 2012; Johansson et al., 2012), the role of elytral shape (elytral length-width ratio) in flight is not yet examined. It is very likely that DB species with an elongated body (i.e., typically possessing elongated elytra) takes advantages of their movements not only on the forest floor but also in tunnels, particularly in soils with high clay content, and therefore these beetles can rapidly occupy scare dung resources in karst forests.

In conclusion we identified the pronotal aspect ratio and elytral aspect ratio in addition to body length and body mass as being positively associated with dung removal rate. These morphological traits may become important bio-indicators of dung removal capacity when examining the impact of anthropogenic LUC on this key ecosystem function.

The conservation value of old secondary forests for dung beetles

Although the conversion of tropical 1st Forests to anthropogenic intensive agricultural land certainly leads to dramatic changes in the species composition and structure of DB, there are still uncertainties about the conservation value of old 2nd forests regrown on abandoned arable land following forest clearing some decades ago. Our data obtained from the two spatially separated NR showed no significant difference in species richness, abundance and biomass between old (>35 years) 2nd Forests and the reference (i.e., 1st Forests). This indicates a potential biodiversity value of these old 2nd Forests in comparison to young (<20 years) 2nd Forests that harboured a very low abundance, species richness or biomass (Klein, 1989; Boonrotpong et al., 2004; Shahabuddin et al., 2005; Gardner et al., 2008). Potentially these old 2nd Forests can provide refuge for many 1st Forest species (Chapter 1). Nevertheless, the old 2nd Forests did not provide a complete substitute for 1st Forests, as the NMDS result revealed a significant difference in composition structure between these two forest types throughout both NR (Chapter 1). The irreversible changes in the community composition of DB communities, particularly in the tunnelers group, hence lead to potential changes in ecosystem functions of DB.

Dung beetles as potential indicators of LUC in tropical karst ecosystems

Dung beetles have been broadly seen as ideal bio-indicators of habitat transformation in none-karst ecosystems, because they are highly sensitive to environmental changes, widely distributed and easily sampled (Halffter & Favila, 1993; McGeoch et al., 2002; Nichols et al., 2007; Gardner et al., 2008). However, due to the distinct species composition of DB in karst ecosystems, it is still unclear whether the karst DB communities are good indicators of habitat change. In this study, we evaluated the impacts of forest conversion in the SE-Asian tropical karst ecosystems using DB as bio-indicators, combining various measures of community composition, species richness, abundance, biomass, functional diversity and morphological traits. We found significant shifts in these community attributes and structure across the conversion of forests to meadows throughout the two karst ecosystems. Further, we used the indicator value analysis (IndVal) to identity the species characteristic for specific land-uses. Our initial results revealed that, although most species revealed clear local land-use preferences and accordingly were considered as potential indicator species of local LUC, few species showed land-use preferences at the regional scale. Hence, the indicator species of DB in karst ecosystems are unlikely to be applicable in the regional scale.

Taxonomic studies on dung beetles in SE-Asia

SE-Asian DB were taxonomically revised by Paulian (1945), Balthasar (1963) and Ochi (1992), but the classification system used in these publications is now outdated. For example, 40%–60% of the total recorded DB species in Sabah (Malaysia), Babe National Park (Vietnam) and Lore Lindu National Park (Indonesia) remained unidentified (Davis et al., 2001; Shahabuddin et al., 2005; Hayes et al., 2009). In this thesis, we established the two thoroughly illustrated identification keys to all worldwide members of the genus *Synapsis* Bates, 1868 and all Vietnamese members of the genus *Copris* Geoffroy, 1762. The genus *Synnapsis* comprises remarkably large-bodied species, and most *Synapsis* species are tropical forest specialists of SE-Asia. Hence, *Synapsis* spp. provide important ecosystem services (e.g., dung removal, secondary seed dispersal), and are potential bio-indicator species of disturbed forests. The genus *Copris* is relatively abundant and widely distributed across various habitats, and therefore they can be used in evaluating the impacts of habitat change on biodiversity. Thus, the two identification keys established in this thesis may be useful for further studies on the taxonomy and ecology of SE-Asian DB. Yet, there is still a lack of taxonomic knowledge of other genera, particularly in the abundant genus *Onthophagus* Latreille, 1802. The local treatments of the genus *Onthophagus* occurring in the Malay Peninsula, Sulawesi, New Guinea and Indo-china (Krikken & Huijbregts, 2008, 2009, 2012, 2013 &2017; Ochi et al., 2009; Tarasov et al., 2010) cannot resolve this critical issue as SE-Asian *Onthophagus* spp. are very diverse and locally restricted (Krikken & Huijbregts, 2008, 2009, 2012). Further, the existing local keys are including different diagnoses, and accordingly may lead to erroneous and inconsistent identifications between different regions. These are posing major challenges for the nomenclatural approach, and suggesting that the use of other approaches (e.g., trait-based approaches) in addition to the traditional taxonomic approach is critically needed in examining the human impacts on the SE-Asian DB communities.

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SUBPUBLICATIONS AND RECORD OF ACHIEVEMENT

Chapter 1 – Influence of land use change on dung beetle communities in tropical karst ecosystems of Vietnam

1. (*) **Bui VB** & Bonkowski M (2019). (in prep.) Influence of land use change on dung beetle communities in high tropical karst ecosystems of Vietnam

Chapter 2 – Influence of land use change on morphological traits and key ecosystem functions of dung beetles in tropical limestone ecosystems in South East Asia.

2. (*) **Bui VB** & Bonkowski M (2019). (in revision). Morphological traits reflect dung beetle response to land use changes in tropical limestone karst ecosystems

Chapter 3 – A review of the genus *Copris* Geoffroy (Coleoptera: Scarabaeidae)

3. **(*#)** **Bui VB**, Dumack K & Bonkowski M (2018). Two new species and one new record for the genus *Copris* (Coleoptera: Scarabaeidae: Scarabaeinae) from Vietnam with a key to Vietnamese species. European Journal of Entomology 115, 167–191. Doi: 10.14411/eje.2018.016.
4. **(*)** **Bui VB** & Bonkowski M (2019). (in prep.) *Copris* (*Paracopris*) Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae) from Asia with description of a new species, and redescription of *Copris* (*Paracopris*) *punctulatus*

Chapter 4 – A review of the genus Synapsis Bates (Coleoptera: Scarabaeidae)

5. **(*)** **Bui VB** & Bonkowski M (2019). (in prep.) An illustrated key and diagnoses of beetle species in the genus *Synapsis* Bates (Coleoptera: Scarabaeidae)
6. **(*)** **Bui VB** & Bonkowski M (2018). Synapsis puluongensis sp. nov. and redescription of Synapsis horaki (Coleoptera: Scarabaeidae), with a key to Vietnamese species. Acta Entomologica Musei Nationalis Pragae 58 (2), 407– 418. Doi: 10.2478/aemnp-2018-0032.

(*) The study was designed and planned together with Prof. Dr. Michael Bonkowski. All results described in this paper/manuscript were carried out by the author, if not stated otherwise. The paper/manuscript was written by the author under the guidance and correction of Prof. Dr. Michael Bonkowski, if not stated otherwise.

(#) Molecular analyses were performed with the guidance of the co-author Dr. Dumack.

ERKLÄRUNG GEMÄß § 4 ABSATZ 1 PUNKT 9 DER PRÜFUNGSORDNUNG

Ich versichere, dass ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit – einschließlich Tabellen, Karten und Abbildungen –, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie – abgesehen von unten angegebenen Teilpublikationen – noch nicht veröffentlicht worden ist, sowie, dass ich eine solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde. Die Bestimmungen der Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Prof. Dr. Michael Bonkowski betreut worden.

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VAN BAC BUI

Cologne, 14.5.2019