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High diversity of *Cetiocyon* beetles (Coleoptera: Hydrophilidae) along an elevational gradient on Mt. Wilhelm, New Guinea, with new records from the Bird's Head Peninsula

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Abstract. A major component of the "Our Planet Reviewed – Papua New Guinea" project was to evaluate insect diversity along an elevational gradient on Mt. Wilhelm (Madang Province, Papua New Guinea), the fourth highest peak in New Guinea. Flight intercept traps were installed at eight sites separated by approximately 500 m in elevation from 200 m a.s.l. to 3700 m a.s.l. Here we focus on the water scavenger beetle genus *Cetiocyon* (Coleoptera: Hydrophilidae) collected as part of this project. *Cetiocyon* species are uniform in much of their external morphology, but diagnostic characters are found in the male genitalia. Our aim was to test the hypothesis that local species diversity was high, and that *Cetiocyon* species diversity is elevationally structured. A small amount of additional material from western New Guinea (Bird's Head Peninsula: Arfak Mts.) was also examined. Ten new species are described, seven from Mt. Wilhelm *Cetiocyon paweli* **sp.n.**, *C. depilis* **sp.n.**, *C. onyx* **sp.n.**, *C. augai* **sp.n.**, *C. ibiscanus* **sp.n.**, *C. mogianus* **sp.n.**, and *C. gemellus* **sp.n.**, and three from the Arfak Mountains: *C. jakli* **sp.n.**, *C. colossus* **sp.n.**, and *C. hamifer* **sp.n.**. Twelve *Cetiocyon* species were found on the slopes of Mt. Wilhelm, most of which were only found at one or two neighboring elevations. The largest diversity of species was found at intermediate elevations (1200–1700 m). We successfully sequenced the 3' end of mitochondrial *cox1* gene for 10 species, which we used along with morphological characteristics to infer a species level phylogeny and examine the effect of elevation on species diversity. Interspecific genetic distances were significantly lower at higher elevations on Mt. Wilhelm, and our phylogenetic reconstruction suggests that *Cetiocyon* ancestrally inhabited low or intermediate elevations. As the result of recent research eighteen *Cetiocyon* species are currently known form New Guinea. An updated identification key to all New Guinean species is included, along with photographs and illustrations of relevant morphological characters.

Key words. Megasternini, new species, diversity, altitude, phylogeny, systematics, New Guinea.

1. Introduction

New Guinea is the second largest island on Earth, covering an area of nearly 800,000 km^2. The island, situated in the equatorial zone, is largely covered by tropical rainforest. Due to its highly variable topology, including mountain ranges reaching up to 4,800 m in elevation and its sheer size, it contains a wide spectrum of climatic and vegetation zones, ranging from seasonal savannah areas in the south to lowland rainforests further north to alpine areas on the highest summits (Johns 1982). New Guinea is a relatively young geological formation. Initially it

was most likely an archipelago of islands of different ages, with the majority of present-day New Guinea apparently formed in the last 10 million years as a result of the collision between the Pacific and the Australian tectonic plates. This collision led to the formation of today's mountain ranges within the last ca. 8 million years (Quarles van Ufford & Cloos 2005; Baldwin et al. 2012; Novotný & Toko 2014; Toussaint et al. 2014).

The immense biodiversity and high endemism in New Guinea is in large part due to this complex geological history, proximity to large source areas such as Australia and SE Asia, and the diverse climatic conditions and vegetation types found across the island. Miller (1996) estimated that the number of New Guinean insect species might be as high as 300,000, clearly most of which remain undescribed. Although more recent estimates are lower (Miller 2007), extremely high numbers of species have been documented for the few groups that have been studied in detail. Forty species had been described from New Guinea by 1982 in the weevil genus *Trigonopterus* Fauvel, 1862 (Riedel 2010), but recent detailed studies found more than 300 species of the genus on the island (Riedel 2010; Tänzler et al. 2012; Riedel et al. 2013) with very high local diversity (Riedel et al. 2010), and there might be more than 1,000 species of this genus alone in New Guinea. Prior to 1998, just two New Guinean species of the diving beetle genus *Exocelina* Broun, 1886 had been described (Balke 1998). Today, there are more than 90 New Guinean species of *Exocelina* (Shaverdo et al. 2016). Moreover, radiation within this genus has occurred largely in the last 5 million years, as a consequence of the formation of high mountain ranges on the island (Toussaint et al. 2014).

Studies of most insect groups in New Guinea are still in the 'early phase', as *Trigonopterus* and *Exocelina* were prior to the 1980s–1990s, where only a handful of species were described based on largely opportunistically-collected material. Inventories to collect taxa in a more systematic fashion have only been organized more recently, and were originally focused on large-scale studies of tropical forest ecology and biodiversity (e.g., Richards & Gamui 2011). However, material accumulated during these projects also allows for a more thorough taxonomic treatment of many insect groups. The most recent international project "Our Planet Reviewed – Papua New Guinea" focused on an inventory of insects along an elevational gradient on the slopes of Mt. Wilhelm, the fourth highest peak in New Guinea (Leponce et al. 2016). Material collected during this project is at the core of this study.

Water scavenger beetles (Hydrophilidae) comprise ca. 2,900 known species. Most hydrophilids are aquatic, but the vast majority (ca. 900 species) from the subfamily Sphaeridiinae are terrestrial, inhabiting forest leaf litter and other habitats with decaying organic matter (Short & Fikáček 2011, 2013). The New Guinean hydrophilid fauna was treated by Hebauer (2001) with later additions by Hebauer (2004, 2006), Komarek (2009), Fikáček & Short (2010), Gentili (2014) and Nasserzadeh & Komarek (2017). It currently comprises 209 species in total, of which 109 species belong to the Sphaeridiinae (of which 107 species are terrestrial). Flight intercept traps installed on the slopes of Mt. Wilhelm during the "Our Planet Reviewed – Papua New Guinea" project collected a huge number of hydrophilid beetles. A preliminary sorting to morphospecies of the first part of the material indicated a surprisingly high diversity. The vast majority of specimens belong to the tribe Megasternini of the Sphaeridiinae, and many species are likely to be undescribed. Moreover, due to the high number of specimens to be sorted, this morphospecies sorting was done without examining male genitalia. The actual species diversity is therefore likely to be underestimated to some extent.

Prior to further sorting, we decided to perform a detailed treatment of the megasternine genus *Cetiocyon* Hansen, 1990, in order to (1) test the hypothesis of high local species diversity, (2) estimate the accuracy of our morphospecies sorting, and (3) test the quality of the material for potential DNA based studies. The selection of *Cetiocyon* was based on the fact that the genus is easily recognizable from other Megasternini by its large size (and was hence easy to sort even from samples not treated in detail yet), it was recently reviewed by Fikáček & Short (2010), and it is known to be very uniform externally but with diagnostic differences in male genitalia. Results of this case study are presented in this paper, along with new findings concerning the same genus based on a small amount of material from the Bird's Head Peninsula in the western part of New Guinea.

2. Material and methods

2.1. Sampling

The majority of the specimens presented in this paper were collected during the "Our Planet Reviewed – Papua New Guinea" international project (Leponce et al. 2016), and were provided to us by the IBISCA (Investigating the Biodiversity of Soil and Canopy Arthropods) expert network. All *Cetiocyon* specimens from this project were collected in flight intercept traps (FITs): in total 180 FITs (1.2 m × 2 m = 2.4 m^2) were installed during the sampling period from the middle of October to the beginning of December 2012, with each trap running for 16 days. Collecting trays were filled with a low concentration water-NaCl solution and the specimens were collected every second day and transferred to 96% ethanol. Traps were installed at eight plots (each with 20 traps) on Mount Wilhelm (Madang Province, Papua New Guinea). Each plot was situated at a different elevation: 200 m (mixed alluvium forest), 700 m and 1,200 m (mixed evergreen forest), 1,700 m (lower montane forest), 2,200 m and 2,700 m (mixed lower montane forest with *Nothofagus*), 3,200 m (upper montane forest) and

Table 1. List of morphological characters used for the phylogenetic analysis. Characters marked by * were newly introduced. 'FS2010' refers to Fikáček & Short (2010), from where other characters were adopted.

1	**Head punctures:** (0) not surrounded with porose area; (1) surrounded with porose area. [FS2010: char. 3]
2	**Anterolateral lobes of mentum:** (0) absent; (1) present. [FS2010: char. 4]
3	**Proportions of first club antennomere:** (0) as long as wide; (1) slightly elongate (1.2–1.3×); (2) very elongate (1.5× or more). [FS2010: char. 5, adapted]
4	**Length of pedicel relative to antennomere 3:** (0) as long as antennomere 3; (1) much longer than antennomere 3. [FS2010: char. 6]
5	**Ultimate antennomere:** (0) elongate; (1) not elongate. [FS2010: char. 7]
6	**Antennal grooves:** (0) absent; (1) present. [FS2010: char. 10]
7	**Size of antennal grooves:** (0) extremelly small; (1) moderately large. [FS2010: char. 11]
8	**Shape of antennal grooves:** (0) rounded; (1) angular. [FS2010: char. 12]
9	**Pronotal punctures:** (0) not surrounded by porose area; (1) surrounded by porose area. [FS2010: char. 13]
10	**Shape of posterior corners of pronotum:** (0) rounded; (1) angulate. [FS2010: char. 14]
11	**Punctures of elytral intervals:** (0) not surrounded by porose area; (1) surrounded by porose area. [FS2010: char. 16]
12	**Shape of mesoventral elevation:** (0) narrow posteriorly; (1) wide posteriorly. [FS2010: char. 17]
13	**Relation of mesoventral plate to anterior metaventral margin:** (0) overlapping metaventrite margin; (1) not overlapping metaventrite margin. [FS2010: char. 18]
14	**Mesal extension of postcoxal ridge:** (0) reaching medially; (1) not reaching medially. [FS2010: char. 19, rephrased]
15	**Anterolateral ridge of metaventrite:** (0) absent; (1) present. [FS2010: char. 20]
16*	**Shape of protrochanter (both sexes):** (0) not projecting; (1) projecting.
17	**Tuft of hairs on male protrochanter:** (0) absent; (1) present. [FS2010: char. 21]
18	**Tuft of hairs on male mesotrochanter:** (0) absent; (1) present. [FS2010: char. 22]
19	**Tuft of hairs on male metatrochanter:** (0) absent; (1) present. [FS2010: char. 23]
20	**Tibial grooves on femora:** (0) absent; (1) present. [FS2010: char. 26]
21*	**Tuft of hair on abdominal apex:** (0) absent; (1) present.
22	**Width of median process of male sternite 8:** (0) wide; (1) narrow; (2) narrow but much wider at apex. [FS2010: char. 27]
23	**Shape of median portion of male sternite 9:** (0) V-shaped; (1) U-shaped; (2) tongue-shaped. [FS2010: char. 28]
24	**Shape of lateral sturts of male sternite 9:** (0) arcuate; (1) sinuate. [FS2010: char. 29]
25	**Shape of median lobe:** (0) nearly parallel-sided; (1) wide, narrowing apicad. [FS2010: char. 30]
26	**Shape of apex of median lobe:** (0) entire; (1) bilobate. [FS2010: char. 31]
27	**Lateral projections of median lobe:** (0) absent; (1) present. [FS2010: char. 32]
28	**Anteriad-directed lobes of lateral projections of median lobe:** (0) absent; (1) present. [FS2010: char. 33]
29*	**Manubrium:** (0) absent; (1) present.
30	**Manubrium asymmetrical:** (0) no; (1) yes. [FS2010: char. 34, adapted]
31*	**Shape of the end of parameres:** (0) rotated; (1) not rotated.
32*	**Proportion of parameres relative to phallobase:** (0) parameres longer; (1) parameres as long as phallobase.
33*	**Proportion of median lobe length relative to parameres length:** (0) as long as or longer; (1) much shorter.
34*	**Ventral hooks on parameres:** (0) absent; (1) present.
35*	**Dorsal tooth at apex of parameres:** (0) absent; (1) present.

3,700 m (subalpine forest). Two additional plots were situated at 120 m and 175 m in the lowland plain north of Mt. Wilhelm near the village of Wanang. Collected material was sorted to principal taxonomic groups directly at the Wanang Conservation Centre by local parataxonomists and students supervised by a group of taxonomists. Detailed sorting of "other Coleoptera" samples (i.e. all beetles except scarabs, weevils and bark beetles) into families was done at the University of South Bohemia by C. Wardhaugh. For more details on the collection of samples and processing protocols see Leponce et al. (2016).

In addition to the material from Mt. Wilhelm, we also examined a small amount of material of *Cetiocyon* collected randomly by amateurs from the Bird's Head Peninsula in the western part of New Guinea (West Papua). Since very limited sampling had previously been carried out in western New Guinea (Fikáček & Short 2010), and the material included species that are probably closely related to those discovered at Mt. Wilhelm, we treated this material here as well.

2.2. Morphological studies

We examined about 150 specimens from the genus *Cetiocyon* for this study, including type material of most of the previously described species. All specimens were dissected, and in the case of males, genitalia were placed in glycol in micro vials below the beetle. Abdominal parts were usually mounted below or next to the beetle, or placed in micro vials.

Photographs of male genitalia were taken using a Canon D-550 digital camera with Canon MP-E65mm f/2.8 1–5× macrolens, multiple layers were combined using Helicon Focus software. Beetle habitus images were taken using a Leica M205C stereo microscope with a Leica DFC495 camera, and combined by Leica Application Suite 4.9.0 software. All photos were subsequently adapted in Adobe Photoshop 7.0. Drawings were traced from photographs taken in the same way.

Specimens for SEM analysis were partly prepared using a method modified from that of Kanturski et al. (2015, 2017). Samples were mounted on aluminium stubs

Table 2. List of gene fragments which we tried to amplify for the 36 *Cetiocyon* samples from Mt. Wilhelm elevational transect, indicating used forward and reverse primers and the number of successful amplifications (= s.a.).

Gene fragment	Forward primer	Reverse primer	# s.a.
Barcoding *cox1*	LCO1490 GGTCAACAAATCATAAAGATATTGG (Folmer et al. 1994)	HCO2198 TAAACTTCAGGGTGACCAAAAAATCA (Folmer et al. 1994)	2
Pat-jerry *cox1*	stev_jerryF CAACATYTATTYTGATTYTTTGG (Timmermans et al. 2010)	stev_patR GCACTAWTCTGCCATATTAGA (Timmermans et al. 2010)	4
Pat-jerry *cox1* internal 5'	Jerry CAACATTTATTTTGATTTTTTGG (Simon et. al. 1994)	Tom ACRTAATGAAARTGGGCTACWA (Ribera et al. 2010)	22
Pat-jerry *cox1* internal 3'	Chy TWGTAGCCCAYTTTCATTAYGT (Ribera et al. 2010)	Pat TCCAATGCACTAATCTGCCATATTA (Simon et. al. 1994)	3
28S rDNA	NLF184-21 ACCCGCTGAAYTT-AAGCATAT (Van der Auwera et al. 1994)	LS1041R TACGGACRTCCATCAGGGTTTCCCCTGACTTC (Maddison 2008)	0

with double-sided adhesive carbon tape and sputter-coated in a Pelco SC-6 sputter coater (Ted Pella Inc., Redding, CA, USA). Specimens were imaged at the Department of Biology and Environmental Protection of University od Silesia in Katowice using a Phenom XL field emission scanning electron microscope (Phenom-World B.V., Eindhoven, The Netherlands) at 10 and 15 kV accelerating voltage with a secondary electron detector (ESD).

Morphological terminology follows Komarek (2004), Fikáček (2010) and Fikáček & Short (2010). Descriptions of the new species are prepared in the same format as in Fikáček & Short (2010), with only the most important characters indicated. The complete morphological description of *Cetiocyon hanseni* Hebauer, 2001 was provided by Fikáček & Short (2010).

Label data are cited verbatim for all specimens presented in the paper. Specimens from which DNA was extracted contain a green label with relevant codes and details about the isolation process. Sex is indicated for all dissected specimens.

Morphological characters for phylogenetic analyses were prepared in Nexus Data Editor (Page 2001). We adopted the data matrix by Fikáček & Short (2010) which was adapted as follows: all new species were included, 8 new characters (16, 21, 29, 31, 32, 33, 34, 35) were included and 7 originally used characters were excluded (1, 2, 8, 9, 15, 24, 25); the final matrix contains 35 characters. New characters include newly discovered characters (shape of protrochanters, tuft of hairs on abdominal apex) and cover the aedeagus morphology in more detail. The excluded characters were either quantitative characters (body size and convexity), or characters that we evaluated as difficult to code after examining a more diverse set of material (prosternal ridge and emargination, impression of elytral series, sculpture of trochanters). *Cetiocyon goliathus* (Huijbregts, 1984) was included despite its male-specific characters being unknown. Outgroup taxa were also adopted from Fikáček & Short (2010). The list of characters and their states is provided in Table 1, and the character matrix is in Supplementary Table S1.

2.3. DNA sequencing

DNA was isolated from 36 *Cetiocyon* specimens (31 males and 5 females) from Mt. Wilhelm; males were assigned to 10 species based on the morphology of the genitalia. Genomic DNA was extracted from whole specimens (excluding the abdomen) using a Qiagen Blood and Tissue Kit following the manufacturer's instructions. We first attempted to amplify two fragments of the protein-coding mitochondrial cytochrome oxidase 1 (*cox1*) and the nuclear gene for large ribosomal subunit (28S), but with very limited success. Subsequently we focused on the 3' *cox1* fragment using the routinely used internal primers. Used primers are listed in Table 2. The PCR conditions were as follows: barcoding *cox1*: initialization at 94°C for 3 min, denaturation at 94°C for 30 s, annealing at 47°C for 30 s, elongation at 72°C for 1 min (last three steps for 40 cycles), final elongation at 72°C for 10 min; other *cox1* fragments: initialization at 95°C for 3 min, denaturation at 95°C for 45 s, annealing at 50°C for 45 s, elongation at 72°C for 1 min 30 s (last three steps for 35 cycles), final elongation at 72°C for 8 min; 28S: initialization at 98°C for 30 s, denaturation at 98°C for 10 s, annealing at 54°C for 30 s, elongation at 72°C for 1 min (last three steps for 35 cycles), final elongation at 72°C for 8 min. Sequencing was done using a sequencer 3130 and 3130xl Genetic Analyzer (Applied Biosystems) with BigDye®Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Forward and reverse sequences were aligned and the consensus sequences edited in BioEdit 7.1.9 software (Hall 1999). Sequences were submitted to GenBank under accession numbers MH142697–MH142718 (see Supplementary Table S2 for details).

2.4. Analyses of phylogeny and genetic diversity

We performed four separate phylogenetic analyses: (1) parsimony analysis of morphological characters; (2) maximum likelihood analysis of *cox1* data; (3) Bayesian ana-

lysis of *cox1* data, and (4) Bayesian analysis of combined *cox1* + morphological data.

Parsimony analysis of morphological data was performed using the TNT software (Goloboff et al. 2008) using the Traditional Search approach (1,000 replicates, 50 trees saved per replicate, TBR as swapping algorithm). Characters were mapped on the majority consensus tree using WinClada (Nixon 2002). The data matrix in Nexus format is available in the zip file uploaded to the Zenodo data archive under doi 10.5281/zenodo.1212736 (see also Electronic Supplement 1 of online version of this article).

Cox1 sequences were aligned using the ClustalW algorithm (Thomson et al. 1994) in BioEdit (Hall 1999). Maximum likelihood analysis of molecular sequences and the analysis of intra- and interspecific genetic distances were conducted using MEGA 7.0 software (Kumar et al. 2015). Bayesian analyses (that of *cox1* data and that combining morphology + molecules) were conducted in MrBayes 3.2.1 (Huelsenbeck & Ronquist 2001); sequences were partitioned by codon positions, with substitution models set according to the analysis performed in PartitionFinder (Lanfear et al. 2012). For combined analysis, we used the consensus sequence for the particular species in case multiple specimens for the species were available. The analyses were performed using four chains with 10,000,000 generations, sampling the chain every 100 generations; stationarity in MCM chains was determined using Tracer 1.5.0 (Rambaut et al. 2014), and burn-in was set appropriately (10%).

We examined the effect of elevation on the diversity of *Cetiocyon* in two ways: (1) by mapping elevation on the trees resulting from the phylogenetic analyses using Winclada, and (2) by examining the relationships between elevation and interspecific genetic distances irrespective of the phylogeny. For elevation mapping, we summarized the occurrence from this study, Fikáček & Short (2010) and Hebauer (2001) (see Supplementary Table S2) and subdivided New Guinean *Cetiocyon* species into four categories: lowland species (i.e. those occurring below 1,200 m a.s.l.), and species never recorded below 1,200 m, 1,700 m and 2,200 m. By examining the relationships between elevation and interspecific genetic distances, we tested (1) whether interspecific distances are generally lower at higher elevations on Mt. Wilhelm as expected from the very recent origin of New Guinean high elevation habitats, and (2) whether species from nearby elevations are generally more closely related than those from very different elevations. We filtered interspecific distances from the output of the genetic distance analysis in MEGA and counted the mean elevation and difference between elevations for each pair of specimens. We excluded pairs with elevation differences of > 1,000 m for testing the correlation between interspecific distance and elevation (to exclude distances e.g. between specimens from 200 m and 2,700 m for which mean elevation makes no sense). For performing correlations between interspecific distances and elevational differences, all distances were used. The order of the regression was tested by Aikake Information Criterion (AIC) using an R script. P-values and final graphic output was generated using PAST software (Hammer et al. 2001).

2.5. Specimen depositories

Examined specimens are deposited in the following institutions: **IECA** – Institute of Entomology, Biology Centre ASCR, České Budějovice, Czech Republic; **IRSNB** – Institute Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **KSEM** – University of Kansas, Lawrence, USA; **MNHN** – Muséum National d'Histoire Naturelle, Paris; **NMPC** – National Museum, Prague, Czech Republic; **ZSM** – Zoologische Staatssammlung, München, Germany.

3. Taxonomy

New Guinean *Cetiocyon* species are rather similar to each other in external morphology (Figs. 1, 2), and can be reliably identified only for males using the morphology of the genitalia and the presence/absence of hair tufts on the trochanters. Few additional diagnostic characters are present in both sexes (relative length of antennal pedicel, proportions of antennomere 7, and presence/absence of porose areas around punctures on the head, pronotum, and elytra, modified protrochanters), but usually do not allow for positive species identification if males are not available. External characters may be compared in Table 3, which can also be used for a rough identification of females. Some of the diagnostic characters described by Fikáček & Short (2010) were verified and corrected (e.g., hair tufts on male trochanters of *Cetiocyon papuensis* (d'Orchymont, 1924)). Because males of *C. goliathus* are currently unknown, this species was excluded from the following key.

In the species treatment, first we treat the new species found on Mt. Wilhelm [sections 3.2–3.8], then new species from the Bird´s Head Peninsula [sections 3.9–3.11], and finally we list examined specimens of described species [sections 3.12–3.16].

3.1. Key to males of *Cetiocyon* species of New Guinea

1 Antennomere 7 (= basal segment of club) at most as long as wide; pedicel slightly longer than antennomere 3 (Fig. 37); porose areas around dorsal punctuation absent (Figs. 2, 42) **2**

1' Antennomere 7 (= basal segment of club) longer than wide (sometimes only slightly); pedicel usually ca. as long as antennomere 3 (Figs. 38, 39); porose areas around dorsal punctuation present or absent (Figs. 42, 43) **6**

Table. 3. Compilation of the most important external characters of all New Guinean *Cetiocyon* species.

species name	antennal characters		hair tufts on male trochanters			projection on pro-trochanters	porose areas around punctures			body length (mm)
	antenno-mere 7	pedicel (compared to anten-nomere 3)	pro-trochanter	meso-trochanter	meta-trochanter		on head	on pronotum	on elytra	
Cetiocyon depilis	as long as wide	slightly longer	no	no	no	no	no	no	no	4.7 – 5.4
Cetiocyon hanseni	as long as wide	slightly longer	no	no	no	no	no	no	no	4.3 – 5.2
Cetiocyon papuensis	as long as wide	slightly longer	yes (small)	yes	no	no	no	no	no	4.5 – 5.2
Cetiocyon paweli	as long as wide	slightly longer	yes (huge)	yes	no	no	no	no	no	4.8 – 5.3
Cetiocyon ibiscanus	as long as wide	slightly longer	yes (huge)	yes	no	no	no	no	no	5.9
Cetiocyon mogianus	slightly longer	slightly longer	yes (medium)	yes	no	no	no	no	no	5.1 – 5.5
Cetiocyon loksai	slightly longer	as long as	yes (medium)	yes	no	no	no	no	no	5.0 – 5.8
Cetiocyon hamifer	much longer	as long as	yes (huge)	yes	no	no	no	no	no	6.0 – 6.1
Cetiocyon jakli	slightly longer	as long as	yes (huge)	yes	no	no	yes	yes	yes	5.2 – 5.6
Cetiocyon traipela	much longer	as long as	yes (medium)	yes	yes	no	no	no	no	7.4 – 8.0
Cetiocyon onyx	much longer	as long as	yes (small)	yes	yes	no	no	no	no	6.2 – 7.1
Cetiocyon gemellus	much longer	as long as	yes (medium)	yes	yes	no	yes	no	no	7.4
Cetiocyon colossus	slightly longer	as long as	yes (medium)	yes	yes	no	yes	no	no	8.7
Cetiocyon augai	much longer	as long as	no	yes	yes	no	yes	yes	yes	5.3 – 5.9
Cetiocyon riedeli	slightly longer	as long as	no	yes	yes	no	yes	yes	yes	5.4 – 6.0
Cetiocyon hebaueri	slightly longer	as long as	no	yes	no	yes	yes	yes	no	5.8 – 6.9
Cetiocyon cribripunctatus	slightly longer	as long as	no	yes	no	yes	yes	yes	yes	5.0 – 5.5
Cetiocyon goliathus	much longer	as long as	?	?	?	?	yes	yes	yes	7.2

2 Pro- and mesotrochanters without tuft of long yellowish setae (e.g., as in Figs. 20, 21) **3**

2' Pro- and mesotrochanters with tuft of long yellowish setae (e.g., as in Figs. 22–24) **4**

3 Body length 4.7–5.4 mm; median lobe much shorter than parameres, wide basally, strongly tapering in apical third (Fig. 6) ..... ***C. depilis* sp.n.**

3' Body length 4.3–5.2 mm; median lobe as long as parameres, narrow, indistinctly narrowing from base to apex (Fig. 5) ..... ***C. hanseni* Hebauer, 2001**

4 Protrochanter with tuft of long yellowish setae large (Figs. 23, 24) **5**

4' Protrochanter with tuft of long yellowish setae very small (Fig. 22), aedeagus as in Fig. 7 ..... ***C. papuensis* (d'Orchymont, 1924)**

5 Median lobe both much shorter than and ca. as wide as parameres; phallobase with asymmetrical manubrium (Fig. 4) ..... ***C. paweli* sp.n.**

5' Median lobe both ca. as long as and much wider than parameres; phallobase without manubrium (Fig. 14) ..... ***C. ibiscanus* sp.n.**

6 Protrochanters with tuft of long yellowish setae (Figs. 25–32); porose areas around dorsal punctuations absent or present (Figs. 42, 43) **7**

6' Protrochanters without tuft of long yellowish setae (Figs. 33–36); porose areas around dorsal punctuation always present, at least on head and pronotum, but usually also on the elytra (Fig. 43) **14**

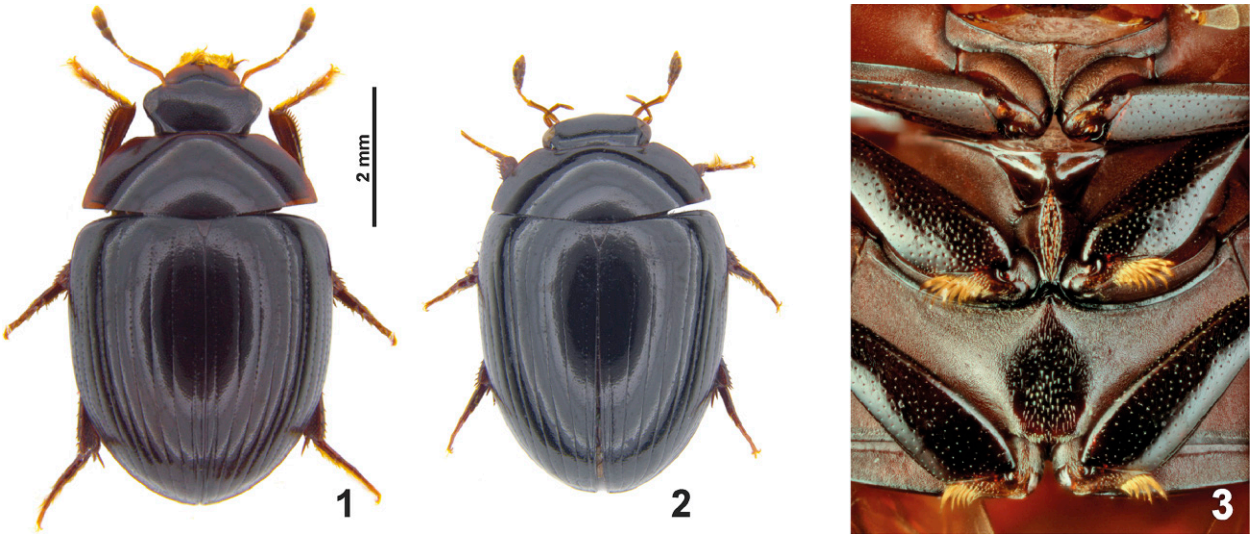
7 Metatrochanters with tuft of long yellowish setae (Figs. 3, 48), body size relatively large, usually not smaller than 6 mm **8**

7' Metatrochanters without tuft of long yellowish setae; body size relatively small, usually not larger than 6 mm **11**

8 Median lobe much shorter than parameres, with lateral lobes (Fig. 10); dorsal punctuation on head without porose areas (Fig. 42) **9**

8' Median lobe ca. as long as parameres; simple, without any lateral lobes (Figs. 15–17); dorsal punctuation on head surrounded by porose areas (Fig. 43) **10**

9 Body length ≥ 7.4 mm; each protrochanter with medium-size tuft of long yellowish setae (Fig. 29); lat-



Figs. 1–3. Dorsal (1, 2) and ventral (3) habitus of *Cetiocyon* from Mt. Wilhelm altitudinal transsect. **1**, **3**: *C. augai* sp.n. collected at 1700–2200 m. **2**: *C. depilis* sp.n. collected at 1200 m.

eral portions of median lobe without lateral finger-like projections directed anteriorly; apex of median lobe distinctly protruding vertically in lateral view (Fikáček & Short 2010: figs. 34–36) ..... ***C. traipela* Fikáček & Short, 2010**

9' Body length ≤ 7.1 mm; protrochanter tuft of long yellowish setae small (Fig. 30); lateral portions of median lobe with lateral finger-like projections directed anteriorly; apex of median lobe distinctly protruding dorsally in lateral view (Fig. 10) ..... ***C. onyx* sp.n.**

10 Last abdominal ventrite weakly emarginated at apex (Fig. 40); apex of parameres with dorsal tooth in lateral view (Fig. 17a); median lobe widest in the middle (Fig. 16) ..... ***C. colossus* sp.n.**

10' Last abdominal ventrite not emarginate at apex (Fig. 41); apex of parameres without dorsal tooth in lateral view (Fig. 17b), median lobe widest near the base (Fig. 15) ..... ***C. gemellus* sp.n.**

11 Porose areas around dorsal punctures on head, pronotum, and elytra absent (Fig. 42) **12**

11' Porose areas around dorsal punctures on head, pronotum, and elytra present (Fig. 43); genitalia as in Fig. 18 ..... ***C. jakli* sp.n.**

12 Median lobe widest in the middle, apex of parameres without a large hook directed mesally (Figs. 8, 9) **13**

12' Median lobe more or less parallel-sided; apex of parameres with a large hook directed mesally (Fig. 19) ..... ***C. hamifer* sp.n.**

13 Median lobe more slender, apex of parameres without dorsal tooth in lateral view (Fig. 8), pedicel ca. as long as antennomere 3 (Fig. 39) ..... ***C. loksai* Hebauer, 2001**

13' Median lobe very wide in the middle; apex of parameres with small dorsal tooth in lateral view (Fig. 9); pedicel longer than antennomere 3 (Fig. 38) ..... ***C. mogianus* sp.n.**

14 Metatrochanter with tuft of long yellowish setae (Figs. 3, 48), protrochanter without small projection (tooth) on anterior margin in the place of contact with femur (Figs. 33, 34) **15**

14' Metatrochanter without tuft of long yellowish setae; each protrochanter with small projection (tooth) on anterior margin in the place of contact with femur (Figs. 35, 36) **16**

15 Apex of the median lobe narrowly triangular; median lobe lateral projections small not jutting out anteriad (Fig. 11) ..... ***C. augai* sp.n.**

15' Apex of the median lobe rounded; median lobe with large lateral projections (Fig. 12) ..... ***C. riedeli* Fikáček & Short, 2010**

16 Protrochanteral projection (tooth) very distinct and long (Fig. 36); median portion of median lobe narrow, anteriorly-directed projections of lateral lobes large, finger-like (Fig. 13) ..... ***C. cribripunctatus* Fikáček & Short, 2010**

16' Protrochanteral projection (tooth) small (Fig. 35); median portion of median lobe wide, anteriorly-directed projections of lateral lobes small and wide (Fikáček & Short 2010: figs. 40–42) ..... ***C. hebaueri* Fikáček & Short, 2010**

3.2. *Cetiocyon paweli* sp.n.

Figs. 4, 24

Type locality: Papua New Guinea, Madang province, E slope of Mt. Wilhelm, Memeku, 1200 m, 5°43′15.2″S 145°16′10.1″E.

Type material: Holotype: ♂ (NMPC), 'PAPUA NEW GUINEA: Madang | E slope of Mt. Wilhelm, 1200 m | -5.720873833 145.2694702 | 4–6.xi.2012; Ibisca Nuigini | Project FIT-MW1200-J-6/8-d11 | P1565 Vial: 17360' [DNA extraction: MF1765]. — Paratypes (2 spec.): 1 ♂ (IECA): PAPUA NEW GUINEA: Madang, E slope of Mt. Wilhelm, 1200 m, -5.720873833 145.2694702, 3–5.xi.2012, Ibisca Niugini Project, FIT-MW1200-M-5/8-d10, P1588 Vial: 17327 [DNA extraction: MF1786]; 1 ♂ (ZSM): Ibisca Ni-

ugini, PNG, Mount Wilhelm 1200m, -5.720873833 145.2694702, 28–30.x.2012, MW1200/P1601 Vial 17313.

Diagnosis. Males of *C. paweli* can be easily distinguished from other New Guinean *Cetiocyon* by the combination of their simple aedeagus with narrow short median lobe, tufts of hairs present on pro- and mesotrochanters, and absence of porose areas around dorsal punctation. In genital morphology, *C. paweli* resembles *C. hanseni*, from which it differs by having median lobe shorter than parameres, apices of parameres expanded apically, basal part of phallobase with asymmetrical manubrium, and by the presence of tufts of hairs on male trochanters. Externally, *C. paweli* is identical to *C. ibiscanus* from which it can be distinguished only by the aedeagus morphology (compare Figs. 4 and 14), and very similar to *C. hamifer*, *C. loksai*, and *C. mogianus*, from which it differs in genital morphology and proportions of antennomeres 2 and 7 (see Table 3).
Description. ***Measurements***. Body length 4.8–5.3 mm (holotype: 5.3 mm); body width 3.3 mm (holotype: 3.3 mm). Eyes separated by 4.2× width of one eye. Length of aedeagus of holotype 2.9 mm. Body convexity index (length : height) 2.4. ***Morphology***. Ground punctures on head and pronotum, and interval punctures of elytra without porose areas. Pedicel slightly longer than antennomere 3; antennomere 7 ca. as long as wide. Elytral series distinctly impressed except anteromesally. Male pro- and mesotrochanters each with tuft of long yellowish setae, metatrochanters bare; tuft of setae on protrochanters large (Fig. 24). In remaining characters fully conforming to the description of *C. hanseni* in Fikáček & Short (2010). ***Male genitalia and postabdominal sclerites***. Phallobase with asymmetrical manubrium. Parameres with lateral margins almost parallel-sided, wide at the apex. Median lobe shorter than parameres; narrow, distinctly narrowing from base to apex; with lack of any lateral projections; apex not divided; gonopore subapical. Sternite 8 with median projection narrow at base and much wider apex. Median portion of sternite 9 V-shaped, lateral struts arcuate.
Variation. None observed in the examined specimens.
Etymology. We dedicate the new species to Paweł Jałoszyński (The Museum of Natural History, Wroclaw University, Poland) as thanks for his support of the first author and his SYNTHESYS project during which this study was conducted.
Distribution. Known only from the type locality.

3.3. *Cetiocyon depilis* sp.n.

Figs. 2, 6, 20, 42

Type locality: Papua New Guinea, Madang province, E slope of Mt. Wilhelm, Memeku, 1200 m, 5°43′15.2″S 145°16′10.1″E.

Type material: Holotype: ♂ (NMPC), 'PAPUA NEW GUINEA: Madang | E slope of Mt. Wilhelm, 1200 m | -5.720873833 145.2694702 | 9–11.xi.2012; Ibisca Niugini | Project FIT-MW1200-S-8/8-d18 | P1639 Vial: 17020' [DNA extraction: MF1785]. — Paratypes (2 spec.): 1 ♂ (IECA): PAPUA NEW GUINEA: Madang, E slope of Mt. Wilhelm, 1200 m, -5.720873833 145.2694702, 31.x.–2.xi.2012, Ibisca Niugini Project, FIT-MW1200-I-4/8-d07, P1555 Vial: 17354 [DNA extraction: MF1763]; 1 ♂ (ZSM): PAPUA NEW GUINEA: Madang, E slope of Mt. Wilhelm, 1200 m, -5.720873833 145.2694702, 4.–6.xi.2012, Ibisca Niugini Project, FIT-MW1200-I-6/8-d11, P1557 Vial: 17200.

Diagnosis. Males of *C. depilis* can be easily distinguished from other New Guinean *Cetiocyon* by the combination of their rather narrow aedeagus with simple, basally wide and apically tapering median lobe and parameres with expanded apices, hairless pro-, meso-, and metatrochanters, and absence of porose areas around dorsal punctation. The species is unique in genital morphology and cannot be confused with any other species (Fig. 6). Externally, males of *C. depilis* are identical to *C. hanseni* only (Table 3), from which it can be only distinguished by the aedeagus morphology.
Description. ***Measurements***. Body length 4.7–5.4 mm (holotype: 5.4 mm); body width 3.3–3.4 mm (holotype: 3.4 mm). Eyes separated by 4.3× width of one eye. Length of aedeagus of holotype 3.2 mm. Body convexity index (length : height) 2.3. ***Morphology***. Ground punctures on head and pronotum, and interval punctures of elytra without porose areas. Pedicel slightly longer than antennomere 3; antennomere 7 ca. as long as wide. Median portion of prosternum with very distinct median keel. Elytral series distinctly impressed except anteromesally. Male trochanters without tufts of long yellowish setae. In remaining characters fully conforming to the description of *C. hanseni* in Fikáček & Short (2010). ***Male genitalia and postabdominal sclerites***. Phallobase symmetrical basally. Parameres with lateral margins almost parallel-sided, expanded apically, apex widely rounded. Median lobe shorter than parameres; wide basally, strongly tapering in apical third, without any lateral projections; apex not divided; gonopore apical. Sternite 8 with median projection narrow at base and much wider at apex. Median portion of sternite 9 V-shaped, lateral struts arcuate.
Variation. None observed in the examined specimens.
Etymology. The species name is derived from the Latin *depilis* (= hairless), referring to the hairless trochanters of this species. Adjective.
Distribution. Known only from the type locality.

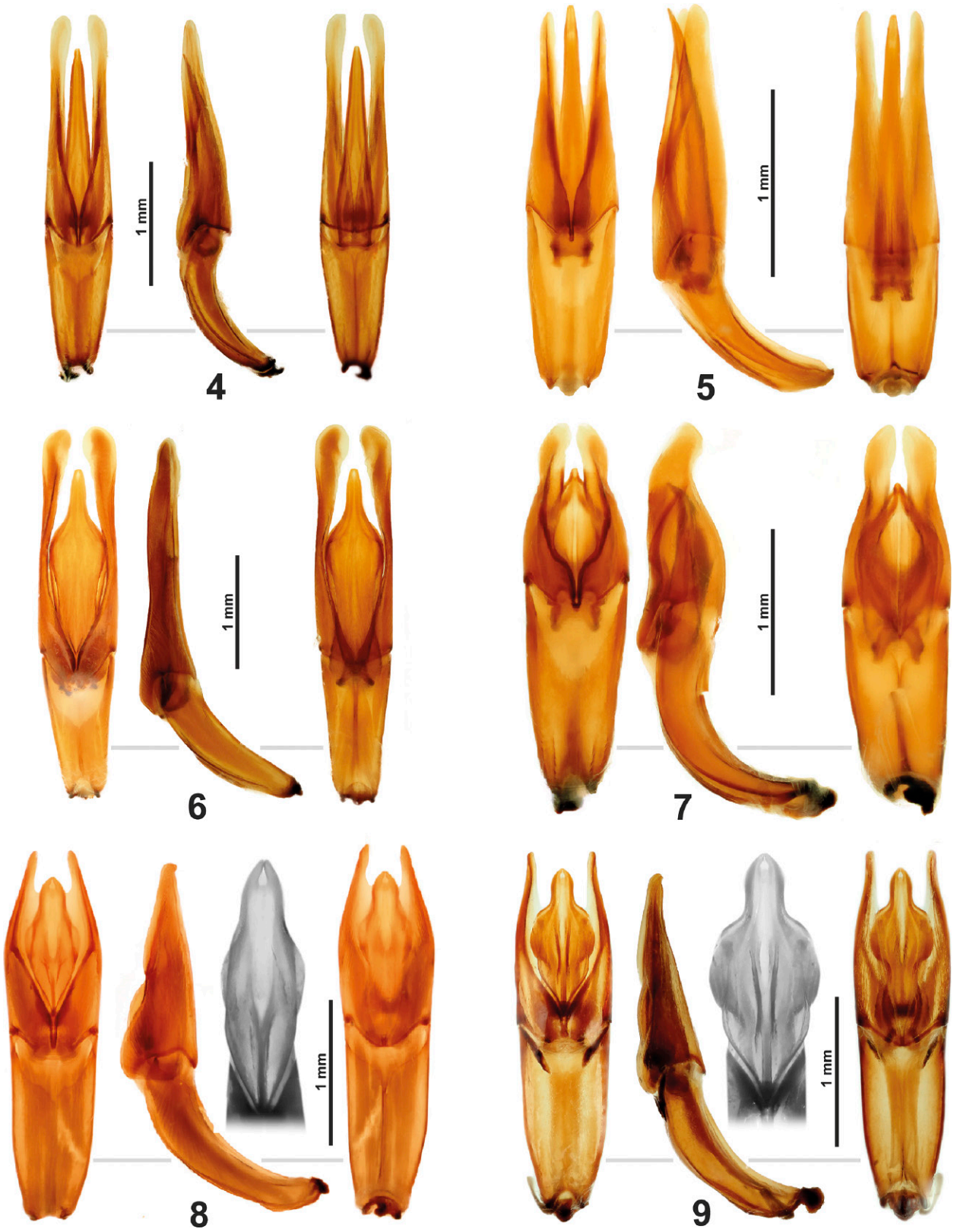
3.4. *Cetiocyon mogianus* sp.n.

Figs. 9, 25, 38

Type locality: Papua New Guinea, Madang province, E slope of Mt. Wilhelm, Memeku, 1200 m, 5°43′15.2″S 145°16′10.1″E.

Type material: Holotype: ♂ (NMPC), 'PAPUA NEW GUINEA: Madang | E slope of Mt. Wilhelm, 1200 m | -5.720873833 145.2694702 | 6–8.xi.2012; Ibisca Niugini | Project; FIT-MW1200-J-7/8-d13 | P1566 Vial: 17078, [DNA extraction: MF1784].— Paratype (1 spec.): 1 ♂ (ZSM): Ibisca Niugini PNG, Mount Wilhelm, 1200 m, -5.720873833 145.2694702, 8.–10.xi.2012, MW1200/P1567 Vial: 16988.

Additional material examined: 1 ♀ (IECA): 'PAPUA NEW GUINEA: Madang | E slope of Mt. Wilhelm, 1200 m | -5.720873833 145.2694702 | 4–6.xi.2012; Ibisca Niugini | Project; FIT-MW1200-J-6/8-d11 | P1565 Vial: 17360' [female associated with males, not included into the type series].



Figs. 4–9. Male genitalia of *Cetiocyon* species found in Mt. Wilhelm elevational transect (color photos: dorsal, lateral, and ventral views; greyscale photos: details of median lobe, dorsal view). **4**: *C. paweli* sp.n. **5**: *C. hanseni*. **6**: *C. depilis* sp.n.; **7**: *C. papuensis*. **8**: *C. loksai*. **9**: *C. mogianus* sp.n.

Diagnosis. Externally, males of *C. mogianus* are very similar to *C. paweli*, *C. ibiscanus*, *C. hamifer*, and *C. loksai* by the combination of dorsal punctation without porose areas and male pro- and mesotrochanters each bearing a tuft of yellowish setae; in contrast to all these species (and in fact all other *Cetiocyon*), it is however

characterised by antennae characters: pedicel is longer than antennomere 3 while antennomere 7 is slightly elongate (Table 3, Fig. 38). In genital morphology, *C. mogianus* is similar to *C. loksai* and *C. jakli*, from which it differs by widely swollen median portion of the median lobe (compare Figs. 8, 9, and 18).

Description. ***Measurements***. Body length 5.1–5.5 mm (holotype: 5.1 mm); body width 3.1–3.8 mm (holotype: 3.1 mm). Eyes separated by 5.2× width of one eye. Length of aedeagus of holotype 2.4 mm. Body convexity index (length : height) 2.5. ***Morphology***. Ground punctures on head and pronotum, and interval punctures of elytra without porose areas. Pedicel slightly longer than antennomere 3; antennomere 7 slightly elongate, ca. 1.2× as long as wide. Elytral series distinctly impressed except anteromesally. Male pro- and mesotrochanters each with tuft of long yellowish setae; metatrochanters bare; tuft of setae on protrochanters medium-sized. In remaining characters fully conforming to the description of *C. hanseni* (see Fikáček & Short 2010). ***Male genitalia and postabdominal sclerites***. Phallobase with moderately large, nearly symmetrical manubrium. Parameres slightly bent outwards apically; slightly curved at apex in lateral view. Median lobe shorter than parameres; moderately wide basally, largely expanded in central part, with rather small lateral lobes in anterior part of the expansion, apical part narrow, parallel-sided; apex bilobate, gonopore subapical. Sternite 8 with median projection narrow basally and much wider at apex. Median portion of sternite 9 V-shaped, lateral struts arcuate.

Variation. None observed in the examined specimens.

Etymology. The species is dedicated to Martin Mogia, paraecologist at the Binatang Research Centre, Madang, New Guinea, and Team Leader of the Wanang unit, who participated in collecting and processing of the material in which this new species was discovered.

Distribution. Known only from the type locality.

3.5. *Cetiocyon onyx* sp.n.

Figs. 10, 30

Type locality: Papua New Guinea, Madang province, E slope of Mt. Wilhelm, Bananumbo, 1700 m, 5°45′33.4″S 145°14′08.2″E.

Type material: Holotype: ♂ (NMPC), 'PAPUA NEW GUINEA: Madang | E slope of Mt. Wilhelm, 1700 m | 5.759269238 145.235611 | 6.–8.xi.2012; Ibisca Niugini | Project; FIT-MW1700-I-7/8-d1 | P1948 Vial: 15384' [DNA extraction: MF1782]. — Paratypes (5 spec.): 1 ♂ (IECA): PAPUA NEW GUINEA: Madang, E slope of Mt. Wilhelm, 1700 m, -5.759269238 145.235611, 31.x.–2.xi.2012, Ibisca Niugini Project, FIT-MW1700-I-4/8-d07, P1945 Vial: 2419 [DNA extraction: MF1781]; 1 ♂ (NMPC): same locality data but 8.–10.xi.2012, FIT-MW1700-I-8/8-d15, P1945, Vial: 4111; 1 ♂ (ZSM): Ibisca Niugini PNG, Mount Wilhelm, 1700 m, -5.759269238 145.235611, 8.–10.xi.2012, MW1700/P1917 Vial: 16414; 1 ♂ (ZSM): same label data but 25.–27.x.2012, MW1700/P1915 Vial: 02485; 1 ♂ (ZSM): same locality data but 6.–8.xi.2012, FIT-MW1700-J-7/8-d13, Plot 10, P1956 Vial: 02339.

Diagnosis. Males of *C. onyx* can be easily distinguished from other New Guinean *Cetiocyon* by the combination of the morphology of their aedeagus, in which they resemble only *C. riedeli* and *C. hebaueri*; *C. onyx* differs from *C. riedeli* by narrowly parallel-sided and apically rounded apex of the median lobe (triangular and pointed apically in *C. riedeli*); it differs from *C. hebaueri* by longer and narrower apex of the median lobe and much smaller lateral projections of the median lobe. Externally, *C. onyx* is identical to *C. traipela* from which it can be only distinguished by genital morphology, and very similar to *C. gemellus* and *C. colossus*, from which it differs in genital morphology (compare Figs. 10, 15–16) and absence of porose areas around dorsal punctuation on the head. Moreover, *C. onyx* is slightly smaller than all above species (see Table 3).

Description. ***Measurements***. Body length 6.2–7.1 mm (holotype: 7.0 mm); body width 4.1–4.4 mm (holotype: 4.3 mm). Eyes separated by 5.8× width of one eye. Length of aedeagus of holotype 3.5 mm. Body convexity index (length : height): 2.7. ***Morphology***. Ground punctures on head and pronotum, and interval punctures of elytra without porose areas. Pedicel as long as antennomere 3; antennomere 7 elongate, ca. 1.6× as long as wide. Elytral series distinctly impressed except anteromesally. Male pro-, meso-, and metatrochanters each with tuft of long yellowish setae; tuft of setae on protrochanters small. In remaining characters fully conforming to the description of *C. hanseni* in Fikáček & Short (2010). ***Male genitalia and postabdominal sclerites***. Phallobase with large asymmetrical manubrium. Parameres narrowly spatulate apically. Median lobe shorter than parameres; wide basally, with anteriad directed finger-like lateral projections and small dorsal submedian projections; medial lobe constricted just below lateral projections; apex of median lobe bilobate; apex of median lobe distinctly protruding dorsally in lateral view; gonopore subapical. Sternite 8 with median projection narrow at base and much wider apically. Median portion of sternite 9 V-shaped, lateral struts arcuate.

Variation. None observed in the examined specimens.

Etymology. The species name refers to the black colouration of this species. Noun in apposition.

Distribution. Known only from the type locality.

3.6. *Cetiocyon augai* sp.n.

Figs. 1, 3, 11, 33, 43, 46

Type locality: Papua New Guinea, Madang province, E slope of Mt. Wilhelm, Sinopas, 2200 m, 5°45′39.7″S 145°11′09.7″E.

Type material: Holotype: ♂ (NMPC), 'PAPUA NEW GUINEA: Madang | E slope of Mt. Wilhelm, 2200 m | -5.75897789 145.1860657 | 29–31.x.2012; Ibisca Niugini | Project; FIT-MW2200-T-7/8-d14 | P2426 Vial: 15735' [DNA extraction: MF1760]. — Paratypes (4 spec.): 1 ♂ (IECA): PAPUA NEW GUINEA: Madang, E slope of Mt. Wilhelm, 1700 m, 5.759269238 145.235611, 25.–27.x.2012, Ibisca Niugini Project, FIT-MW1700-J-1/8-d01, P1950, vial 2484 [DNA extraction: MF1779]; 1 ♂ (NMPC): PAPUA NEW GUINEA: Madang, E slope of Mt. Wilhelm, 2200 m, -5.75897789 145.60657, 30.x.–1.xi.2012, Ibisca Niugini Project, FIT-MW2200-I-8/8-d15, P2339, vial 16349; 1 ♂ (ZSM): Ibisca Niugini PNG, Mount Wilhelm, 2200 m, 28.–

Figs. 10–13. Male genitalia of *Cetiocyon* species found in Mt. Wilhelm elevational transect (dorsal, lateral, and ventral view). **10**: *C. onyx* sp.n. **11**: *C. augai* sp.n. **12**: *C. riedeli.* **13**: *C. cribipunctatus*.

30.x.2012, -5.75897798 145.1860657, MW2200/P2274, vial 07024; 1 ♂ (ZSM): same collecting data but MW2200, P2290 Vial: 07167.

Diagnosis. *Cetiocyon augai* externally corresponds to *C. riedeli*, *C. cribipunctatus*, *C. jakli*, and *C. goliathus* by the presence of porose areas around dorsal punctation on head, pronotum, and elytra. *Cetiocyon augai* appears identical to *C. riedeli*, however it can be still distinguished from *C. cribipunctatus* and *C. jakli* by male metatrochanters each with a tuft of yellowish hairs (present only on pro- and mesotrochanters or mesotrochanters only in the above species) (see Table 3). Currently the only way to distinguish *C. augai* from *C. goliathus* (with males undescribed) is the body length of 5.3–5.9 mm in *C. augai* versus 7.2 mm in *C. goliathus*. *Cetiocyon augai* is easy to recognize by the examination of male genitalia – its aedeagus resembles that of *C. hebaueri* and *C. riedeli* and differs from them by the narrowly triangular apex of the median lobe with small lateral projections not jutting out anteriad (rounded at apex and small lateral projections jutting out anteriad in *C. hebaueri*, with large lateral projections in *C. riedeli*).

Description. ***Measurements***. Body length 5.3–5.9 mm (holotype: 5.8 mm); body width 3.5–4.0 mm (holotype: 3.8 mm). Eyes separated by 6.6× width of one eye. Length of aedeagus of holotype 2.3 mm. Body convexity index (length : height): 2.6. ***Morphology***. Ground punctures on head and pronotum, and interval punctures of elytra with porose areas. Pedicel as long as antennomere 3; antennomere 7 elongate, ca. 1.5× as long as wide. Elytral series distinctly impressed except anteromesally. Male protrochanters bare; meso- and metatrochanters each with tuft of long yellowish setae. In remaining characters fully conforming to the description of *C. hanseni* in Fikáček & Short (2010). ***Male genitalia and postabdominal sclerites***. Phallobase with large asymmetrical manubrium. Parameres spatulate, vertically oriented, arcuate in dorsal view, sinuate in lateral view. Median lobe shorter than parameres; wide basally, with small lateral lobes and anteriad directed finger-like lateral projections; medial lobe constricted just below lateral projections; apex of median lobe bilobate; gonopore subapical. Sternite 8 with narrow median projection. Median portion of sternite 9 V-shaped, lateral struts arcuate.

Variation. None observed in the examined specimens.

Etymology. The species is dedicated to John Auga, Deputy Director of the Binatang Research Centre, Madang, New Guinea, and the Paraecologist Team Leader

at the same station, who participated on collecting and processing of the material in which this new species was discovered.

Distribution. Known only from the slope of Mt. Wilhelm.

3.7. *Cetiocyon ibiscanus* sp.n.

Figs. 14, 23, 37

Type locality: Papua New Guinea, Madang province, E slope of Mt. Wilhelm, Oromongu, 700 m, 5°43′55.06″S 145°15′7.80″E.

Type material: Holotype: ♂ (NMPC), 'PAPUA NEW GUINEA: Madang | E slope of Mt. Wilhelm, 700 m | -5.731960773 145.2521667 | 1.–3.xi.2012; Ibisca Niugini | Project; FIT-MW700-O-4/8-d08 | P1213 Vial: 16236' [DNA extraction: MF1767].

Diagnosis. Males can be easily distinguished from other New Guinean *Cetiocyon* by characteristic massive aedeagus, tufts of hairs present on pro- and mesotrochanters, and absence of porose areas around dorsal punctation. In genital morphology, *C. ibiscanus* cannot be confused with any other species (Fig. 14). Externally, *C. ibiscanus* appears identical to *C. paweli* from which it can be only distinguished by aedeagus morphology (compare Figs. 4 and 14), and very similar to *C. hamifer*, *C. loksai*, and *C. mogianus*, from which it differs in genital morphology (compare Figs. 8, 9 and 19) and proportions of antennomeres 2 and 7 (see Table 3).

Description. ***Measurements***. Body length (holotype only) 5.9 mm; body width (holotype only) 3.8 mm. Eyes separated by 6.0× width of one eye. Length of aedeagus of holotype 3.4 mm. Body convexity index (length : height) 2.7. ***Morphology***. Ground punctures on head and pronotum, and interval punctures of elytra without porose areas. Pedicel slightly longer than antennomere 3; antennomere 7 ca. as long as wide. Elytral series distinctly impressed including anteromesally. Male pro- and mesotrochanters each with tuft of long yellowish setae, metatrochanters bare; tuft of setae on protrochanters huge. In remaining characters fully conforming to the description of *C. hanseni* in Fikáček & Short (2010). ***Male genitalia and postabdominal sclerites***. Phallobase asymmetrical basally. Parameres spatulate, vertically oriented, nearly parallel-sided in dorsal view. Median lobe almost as long as parameres; very wide and parallel-sided throughout, triangularly narrowing apically, lateral projections absent; apex not divided apicaly; gonopore subapical. Sternite 8 with median projection narrow at base and much wider at apex. Median portion of sternite 9 V-shaped, lateral struts arcuate.

Variation. Only a single specimen examined.

Etymology. The name of the new species is derived from the acronym of the IBISCA project (Investigating the Biodiversity of Soil and Canopy Arthropods), from which most of the new *Cetiocyon* species described in this study were collected. Adjective.

Distribution. Known only from the type locality.

3.8. *Cetiocyon gemellus* sp.n.

Figs. 15, 17b, 31, 39, 41

Type locality: Papua New Guinea, Madang province, E slope of Mt. Wilhelm, Bananumbo, 1700 m, 5°45′33.4″S 145°14′08.2″E.

Type material: Holotype: ♂ (ZSM), 'Ibisca Niugini, PNG | 26–28.x.2012 | Mount Wilhelm 1700m | -5.759269238 145.235611 | MW1700/P1958 Vial 05576'.

Additional material examined: 1 ♀ (NMPC): same data as the holotype [female associated with males, not included into the type series].

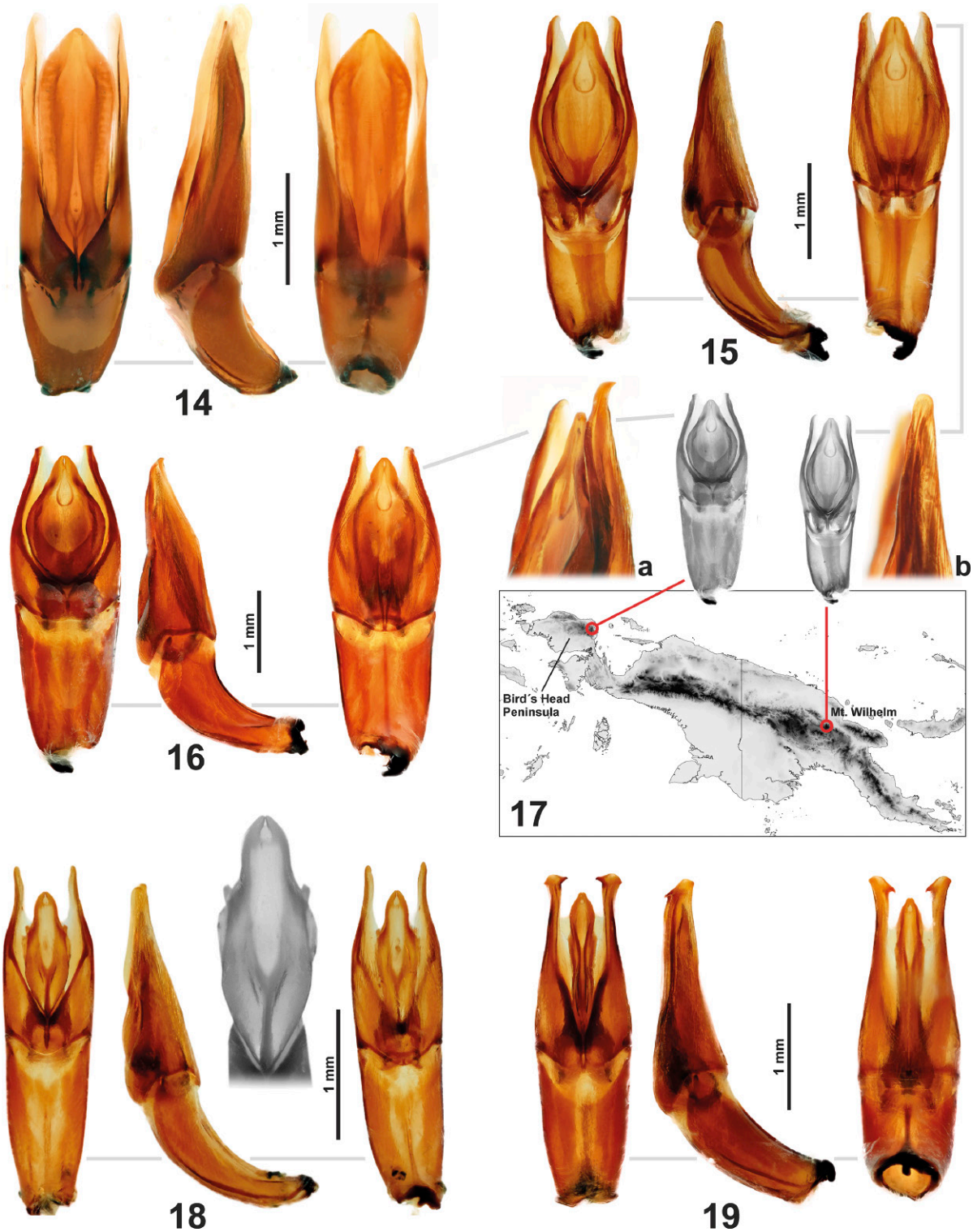
Diagnosis. In external and genital morphology, *C. gemellus* is very similar to *C. colossus*; both species can be distinguished from all other species by presence of porose areas around dorsal punctation only on the head (see Table 3). They are also characteristic by large body length (over 7 mm, similar as in *C. traipela* and *C. goliathus*) and all male trochanters with tufts of yellowish setae (in this they are similar to *C. traipela* and *C. onyx*). *Cetiocyon gemellus* may be distinguished from *C. colossus* by details of the genital morphology and the shape of male abdominal ventrite 5. The aedeagus of *C. gemellus* is slightly narrower, with more elongated parameres and median lobe (generally broader and with shorter parameres and median lobe in *C. colossus*), and the parameral apex is rounded in lateral view (with small tooth-like projection dorsally in *C. colossus*) (compare Figs. 15–17). Abdominal ventrite 5 is simply arcuate on posterior margin in male *C. gemellus*, but deeply sinuate in *C. colossus* (compare Figs. 40 and 41).

Description. ***Measurements***. Body length (holotype only) 7.4 mm; body width (holotype only) 4.3 mm. Eyes separated by 5.9× width of one eye. Length of aedeagus of holotype 3.5 mm. Body convexity index (length : height) 2.1. ***Morphology***. Ground punctures on head with porose areas, those on pronotum and interval punctures of elytra without porose areas. Pedicel as long as antennomere 3; antennomere 7 elongate, ca. 1.5× as long as wide. Elytral series distinctly impressed except anteromesally. Male pro-, meso-, and metatrochanters each with tuft of long yellowish setae; tuft of setae on protrochanters medium-sized. In remaining characters fully conforming to the description of *C. hanseni* in Fikáček & Short (2010). ***Male genitalia and postabdominal sclerites***. Phallobase with large asymmetrical manubrium. Parameres narrowly spatulate apically, vertically oriented, simply rounded at apex in lateral view. Median lobe almost as long as parameres; simple, wide basally, widest ca. at midlength, then gradually tapering toward apex; apex bilobate; gonopore subapical. Sternite 8 with narrow median projection. Median portion of sternite 9 V-shaped, lateral struts sinuate.

Variation. Only one specimen was examined.

Etymology. The Latin *gemellus* (= twin) refers to the strong resemblance of this new species to *C. colossus* sp.n., both in external and genital morphology. Noun in apposition.

Distribution. Known only from the type locality.



Figs. 14–19. Male genitalia of *Cetiocyon* species from Mt. Wilhelm elevational transect (14, 15) and from Bird's Head Peninsula (16, 18, 19). **14**: *C. ibiscanus* sp.n. **15**: *C. gemellus* sp.n. **16**: *C. colossus* sp.n. **17**: distribution and comparison of aedeagal morphology of *C. colossus* and *C. gemellus* (localities, aedeagi in same relative size and detail of parameres in ventrolateral view). **18**: *C. jakli* sp.n. **19**: *C. hamifer* sp.n.

3.9. *Cetiocyon colossus* sp.n.

Figs. 16, 17a, 32, 40

Type locality: Indonesia, West Papua, Manokwari district, Arfak Mountains, surroundings of Maibri village, 1570 m [GPS ca. 1°03.5′S 133°54.1′E].

Type material: Holotype: ♂ (NMPC), 'INDONESIA: West Papua | Arfak Mts., Manokwari district | Maibri vill. env., 1570 m | 6–19. xii.2012, S. Jákl leg.'.

Diagnosis. *Cetiocyon colossus* is very similar to *C. gemellus* in external and genital morphology. For details

and diagnostic characters of both species, see under *C. gemellus*.

Description. ***Measurements***. Body length (holotype only) 8.7 mm; body width (holotype only) 5.3 mm. Eyes separated by 6.8 × width of one eye. Length of aedeagus of holotype 3.9 mm. Body convexity index (length : height) 2.2. ***Morphology***. Ground punctures on head with porose areas, those on pronotum and interval punctures of elytra without porose areas. Pedicel as long as antennomere 3; antennomere 7 elongate, ca. 1.3 × as long as wide. Elytral series distinctly impressed except anteromesally. Male pro-, meso-, and metatrochanters each with tuft of long yellowish setae, tuft of setae on protrochanters small. In remaining characters fully conforming to the description of *C. hanseni* in Fikáček & Short (2010). ***Male genitalia and postabdominal sclerites***. Phallobase with large asymmetrical manubrium. Parameres narrowly spatulate apically, vertically oriented, apex with a small dorsal tooth in lateral view. Median lobe almost as long as parameres; simple, wide basally, widest near midlength, then gradually tapering toward apex; apex bilobate; gonopore subapical. Sternite 8 with narrow median projection. Median portion of sternite 9 V-shaped, lateral struts sinuate.

Variation. Only a single specimen was examined.

Etymology. The species name is derived from Latin *colossus* (= large statue), and refers to the body size of this species, which is the largest of the hitherto known species of *Cetiocyon*. Noun in apposition.

Distribution. Known only from the type locality.

3.10. *Cetiocyon jakli* sp.n.

Figs. 18, 28

Type locality: Indonesia, West Papua, Manokwari district, Arfak Mountains, surrounding of the Maibri village, 1570 m [GPS ca. 1°03.5′S 133°54.1′E].

Type material: Holotype: ♂ (NMPC), 'Indonesia: West Papua | Arfak Mts., Manokwari district | Maibri vill. env., 1570 m | 6–19.12.2012, S. Jákl leg.'. — Paratypes (2 spec.): 2 ♂♂ (NMPC, ZSM): same label data as holotype.

Additional specimens examined: 11 ♀♀ (NMPC, ZSM, MNHN, IRSNB): same label data as the holotype [females associated with males, not included into the type series].

Diagnosis. Males of *C. jakli* can be easily distinguished from other New Guinean *Cetiocyon* by aedeagus morphology, tufts of hairs present only on pro- and mesotrochanters, and presence of porose areas around dorsal punctation. In aedeagus morphology, *C. jakli* resembles *C. loksai* and *C. mogianus* from both of which it is easy to distinguish by the presence of anteriad-directed lateral finger-like projections (compare Figs. 8, 9 and 18). Externally, it corresponds to *C. cribipunctatus*, *C. augai*, *C. riedeli*, and *C. goliathus* by the presence of porose areas around dorsal punctation on head, pronotum, and elytra. However, C. *jakli* differs from those species in combination of tufts of hairs on trochanters. Currently the only way to distinguish *C. jakli* from *C. goliathus* (with males undescribed) is the body length 5.2–5.6 mm in *C. jakli* versus 7.2 mm in *C. goliathus*.

Description. ***Measurements***. Body length 5.2–5.6 mm (holotype: 5.4 mm); body width 3.3–3.4 mm (holotype: 3.4 mm). Eyes separated by 5.3 × width of one eye. Length of aedeagus of holotype 2.7 mm. Body convexity index (length : height) 2.4. ***Morphology***. Ground punctures on head and pronotum, and interval punctures of elytra with porose areas, but those on pronotum and elytra very small and hard to see. Pedicel as long as antennomere 3; antennomere 7 elongate, ca. 1.2 × as long as wide. Elytral series distinctly impressed except anteromesally. Male pro- and mesotrochanters each with tuft of long yellowish setae; metatrochanters bare; tuft of setae on protrochanters huge. In remaining characters fully conforming to the description of *C. hanseni* in Fikáček & Short (2010). ***Male genitalia and postabdominal sclerites***. Phallobase with small asymmetrical manubrium. Parameres slightly bent outwards apically. Median lobe shorter than parameres; moderately wide basally, with small lateral lobes and small anteriad directed finger-like lateral projections; apex of median lobe bilobate; gonopore subapical. Sternite 8 with median projection narrow basally and much wider at apex. Median portion of sternite 9 V-shaped, lateral struts arcuate.

Variation. None observed in the examined specimens.

Etymology. The new species is dedicated to the Czech entomologist Stanislav Jákl during whose trip to western New Guinea this new species was collected.

Distribution. Known only from the type locality.

3.11. *Cetiocyon hamifer* sp.n.

Figs. 19, 27

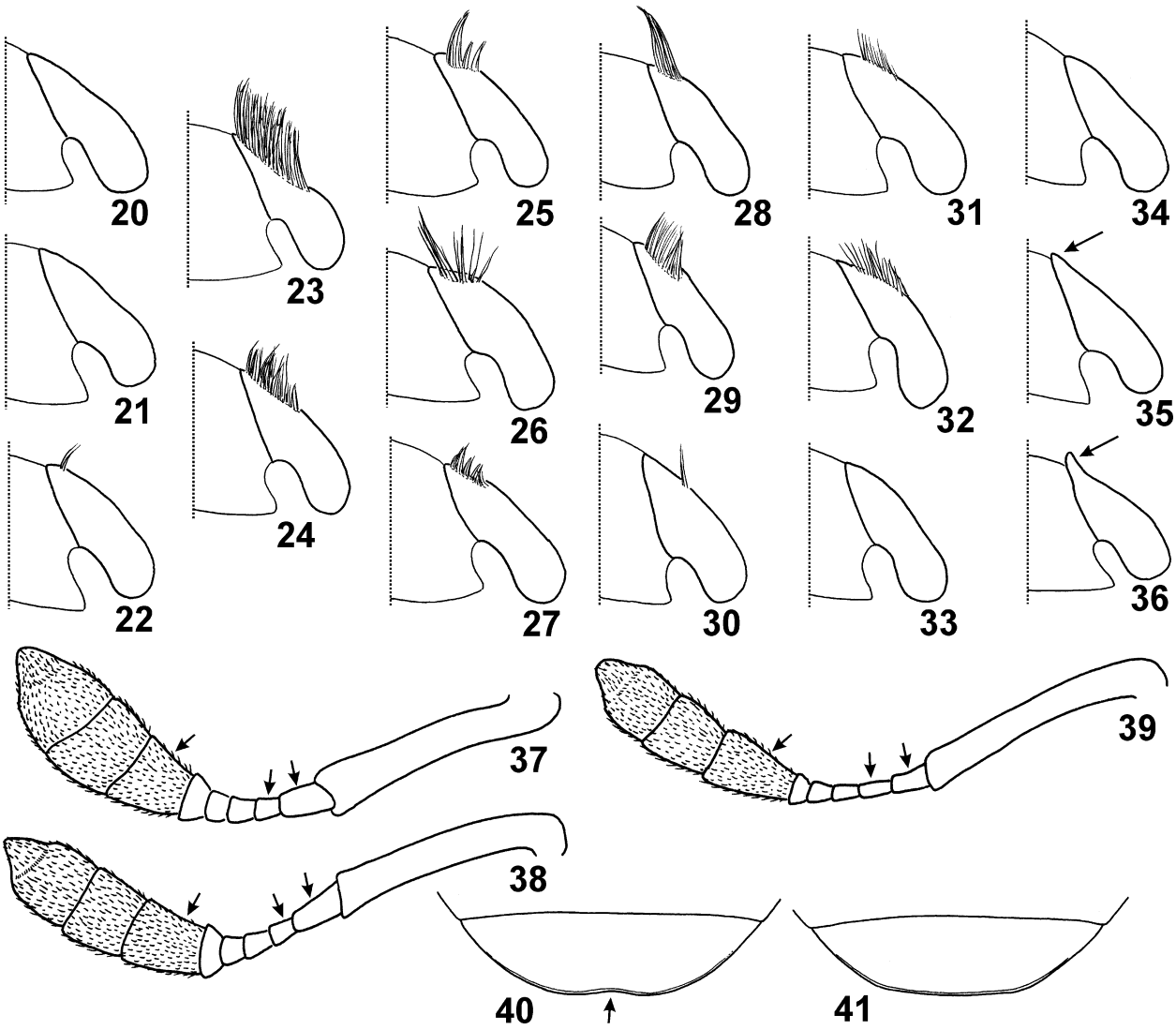
Type locality: Indonesia, West Papua, Manokwari district, Arfak Mountains, Maibri village environment, 1570 m [GPS ca. 1°03.5′S 133°54.1′E].

Type material: Holotype: ♂ (NMPC), 'INDONESIA: West Papua | Arfak Mts., Manokwari district | Maibri vill. env., 1570 m | 6–19.xii.2012, S. Jákl leg.'. — Paratype: 1 ♂ (ZSM): same label data as the holotype.

Additional material examined: 2 ♀♀ (NMPC): same label data as the holotype [females associated with males, not included into the type series].

Diagnosis. Males of *C. hamifer* can be easily distinguished from all other New Guinean *Cetiocyon* by parameres with a large hook-like process at apices (Fig. 19). Externally, *C. hamifer* is identical to *C. loksai* from which it can only be distinguished by the aedeagus morphology, and very similar to *C. mogianus*, *C. paweli*, and *C. ibiscanus*, from which it externally differs in antennal morphology (pedicel as long as antennomere 3, and antennomere 7 distinctly longer than wide) (see Table 3).

Description. ***Measurements***. Body length 6.0–6.1 mm (holotype: 6.1 mm); body width 4.0–4.1 mm (holotype: 4.1 mm). Eyes separated by 6.8 × width of one eye. Length of aedeagus of holotype 3.1 mm. Body convexity index (length : height): 2.5. ***Morphology***. Ground,



Figs. 20–41. Morphological details of New Guinean *Cetiocyon* species: male protrochanters (20–36, ventral view), antenna (37–39) and male abdominal ventrite 5 (40, 41). **20**: *C. depilis* sp.n. **21**: *C. hanseni*. **22**: *C. papuensis*. **23**, **37**: *C. ibiscanus* sp.n. **24**: *C. paweli* sp.n. **25**, **38**: *C. mogianus* sp.n. **26**: *C. loksai*. **27**: *C. hamifer* sp.n. **28**: *C. jakli* sp.n. **29**: *C. traipela*. **30**: *C. onyx* sp.n. **31**, **39**, **41**: *C. gemellus* sp.n. **32**, **40**: *C. colossus* sp.n. **33**: *C. augai* sp.n. **34**: *C. riedeli* sp.n. **35**: *C. hebaueri*. **36**: *C. cribripunctatus*. — ***Arrows*** point to anterior projection of protrochanter (35, 36), antennomeres which relative length is species-specific (37–39) and weak emargination of abdominal ventrite 5 (40).

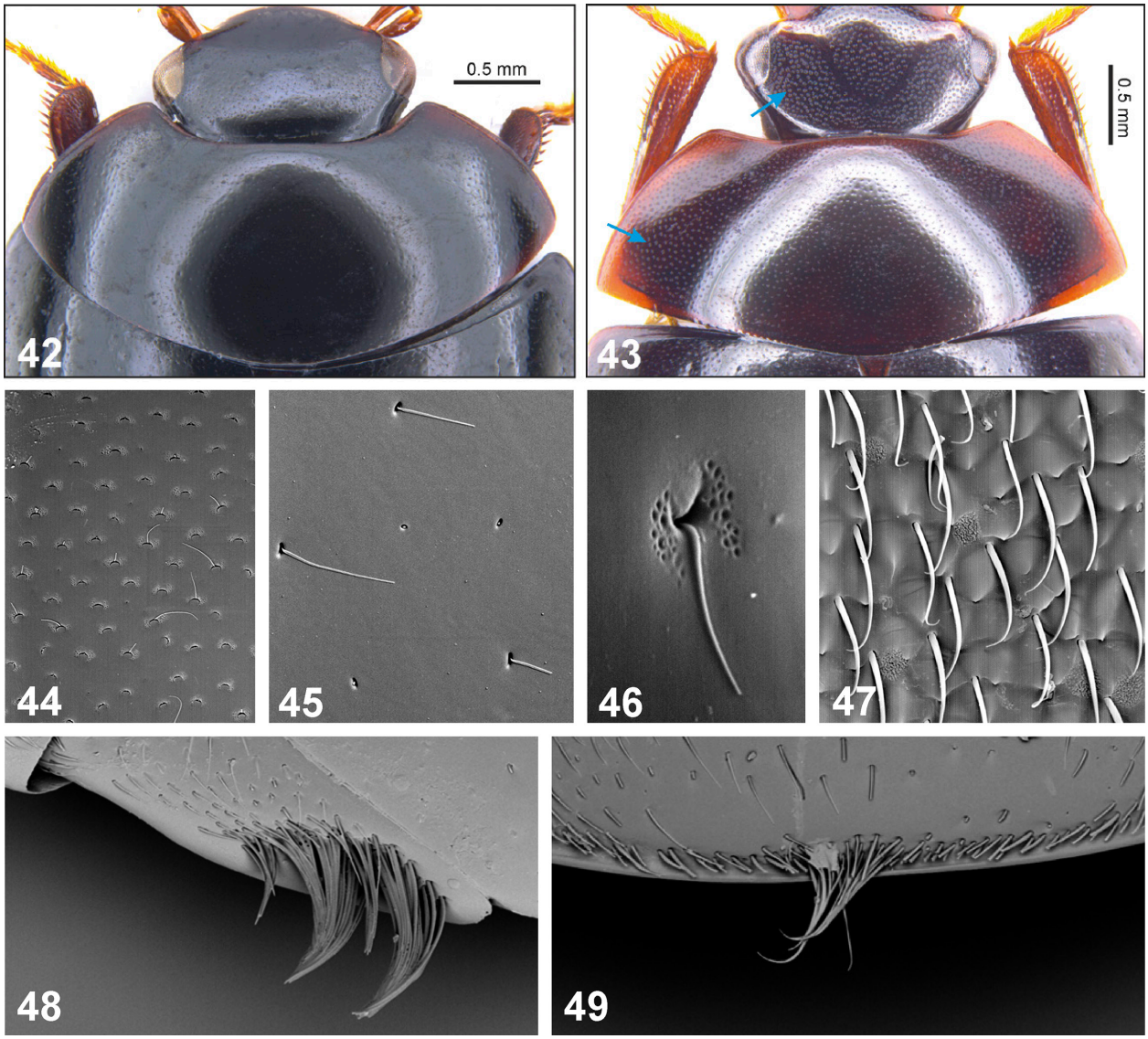
punctures on head and pronotum, and interval punctures of elytra without porose areas. Pedicel as long as antennomere 3; antennomere 7 elongate, ca. 1.5× as long as wide. Elytral series distinctly impressed except anteromesally. Male pro- and mesotrochanters each with tuft of long yellowish setae; metatrochanters bare; tuft of setae on protrochanters huge. In remaining characters fully conforming to the description of *C. hanseni* (see Fikáček & Short 2010). ***Male genitalia and postabdominal sclerites***. Phallobase slightly asymmetrical, with small manubrium. Parameres slightly bent outwards, slightly widened apically, with a large hook directed mesally. Median lobe shorter than parameres; narrow basally; with large lateral lobes; apex of median lobe bilobate; gonopore subapical. Sternite 8 with median process narrow basally and much wider at apex. Median portion of sternite 9 V-shaped, lateral struts arcuate.

Variation. None observed in the examined specimens.
Etymology. The species name is derived from the Latin word *hamus* (= hook or spike) and the ending *-fer* (= bearing); it refers to the hook-like process on the tip of each paramere.
Distribution. Known only from the type locality.

3.12. *Cetiocyon hanseni* Hebauer, 2001

Figs. 5, 21, 45

Material examined: ***Mt. Wilhelm transect*: 120 m**: 1 ♂ (NMPC): 20–22.xi.2012, FIT-WAN-R-2/8-d04 (P0685, vial 3974) [DNA voucher MF1756]; 1 ♂ (NMPC): 24–26.xi.2012, FIT-WAN-P-4/8-d08 (P0671, vial 17649) [DNA voucher MF1772]; 1 ♂, 1 ♀ (IECA): 20–22.xi.2012, FIT-WAN-N-2/8-d04 (P0653, vial 22265) [male: DNA voucher MF1770]; 1 ♂, 1 ♀ (NMPC): 24–26.xi.2012, FIT-WAN-O-4/8-d08 (P0646, vial 17658) [male: DNA voucher



Figs. 42–49. Morphological characters of New Guinean *Cetiocyon*. **42**, **43**: dorsal view of head and pronotum: **42** with punctation not surrounded by porose areas, **43** with punctation surrounded by porose areas (e.g. in areas highlighted by arrows). **44–46**: punctation of the dorsal body surface: **44** pronotal punctation surrounded by porose areas,; **45** elytral punctation without porose areas, **46** detail of elytral puncture surrounded by porose area. **47**: detail of surface of abdominal ventrite with disc-like fields. **48**: tuft of hairs on male metatrochanter. **49**: tuft of hairs on the apex of 5th abdominal ventrite. Species illustrated: **42**: *C. depilis* sp.n.; **43**, **46**: *C. augai* sp.n.; **44, 47–49**: *C. riedeli*; **45**: *C. hanseni*.

MF1773]; 1 ♀ (NMPC): 18–20.xi.2012, FIT-WAN-H-1/8-d01 (P0604, vial 22331) [DNA voucher MF1757]; 1 ♀ (NMPC): 26–28.xi.2012, FIT-WAN-N-5/8-d10 (P0656, vial 22303); 1 ♀ (NMPC): 20–22.xi.2012, FIT-WAN-K-2/8-d04 (P0629, vial 22254); 1 ♀ (ZSM): 20–24.xi.2012, FIT-WAN-C-3/8-d05 (P0566, vial 17538); 1 ♀ (ZSM): 22–24.xi.2012, FIT-WAN-M-3/8-d06 (P0646, vial 16546); 1 ♀ (ZSM): 22–24.xi.2012, FIT-WAN-N-3/8-d06 (P0654, vial 16574); 1 ♀ (ZSM): 22–24.xi.2012, FIT-WAN-N-3/8-d06 (P0654, vial 16574) [DNA voucher MF1771]; 1 ♀ (IECA): 18–20.xi.2012, FIT-WAN-E-1/8-d01 (P0663, vial 3884). **200 m**: 1 ♂ (IRSNB): 8–10.xi.2012, FIT-MW200-B-8/8-d15 (P0723, vial 14369) [molecular voucher MF1758]; 1 ♂ (MNHN): 3–5.xi.2012, FIT-MW200-Q-5/8-d10 (P0840, vial 9663) [molecular voucher MF1774]; 1 ♀ (ZSM): 7–9.xi.2012, MW0200 (P0866, vial 7444); 1 ♀ (ZSM): 25-27.x.2012, MW0200 (P0740, vial 14341). **700 m**: 1 ♂ (ZSM): 4–6.x.2012, FIT-MW700-B-6/8-d11 (P1111, vial 7281); 1 ♂ (NMPC): 2–4.xi.2012, FIT-MW700-F-5/8-d09 (P1142, vial 16019) [DNA voucher MF1766]; 1 ♂ (NMPC): 3–5.xi.2012, FIT-MW700-C-4/8-d07 (P1117, vial 15664) [DNA voucher MF1769].

Other regions: **INDONESIA**: **West Papua**: 1 ♂ (NMPC): Arfak Mts., Manokwari District, Maibri village env., 1570 m, 6–19.xii.2012, lgt. S. Jákl [the locality of this specimen is actually very likely much lower in the Mokwam valley, possibly at ca. 1°0′35″S 133°54′19″E at altitudes around 500 m; S. Jákl & J. Hájek, pers. comm.] **PAPUA NEW GUINEA**: **Eastern Highlands**: 1 ♂ (KSEM): Herovana village, Crater Mountain Research Area, 15–19.vii.2001, lgt. Bradler, Jarvis & Svenson [DNA voucher MF1670]. **Madang**: 1 ♂, 1 ♀ (IRSNB): Canopy Mission, Baiteta, at light, 4.vi.1996, lgt. O. Missa (AR7); 3 ♂♂, 1 ♀ (IRSNB, NMPC): same label data but 17.v.1995 (M1); 1 ♀ (IRSNB): same data but 9.iv.1995 (AR3); 1 ♀ (IRSNB): same data but 2.vii.1995 (AR27); 1 ♀ (IRSNB): same data but 3.vii.1996 (AR60); 1 ♀ (IRSNB): same data but 18.vi.1996 (XP); 1 ♀ (IRSNB): 24.iii.1993 (T2).

3.13. *Cetiocyon cribripunctatus* Fikáček & Short, 2010

Figs. 13, 36

Material examined: ***Mt. Wilhelm transect***: **2700 m**: 1 ♂ (NMPC): 17–19.x.2012, FIT-MW2700-M-1/8-d02 (P2754, vial 14154); 1 ♂ (NMPC): 30.x.–1.xi.2012, FIT-MW2700-A-8/8-d15 (P2665, vial 14196); 1 ♂ (NMPC): 30.x.–1.xi.2012, FIT-MW2700-E-8-8-d15 (P2697, vial 14145) [DNA voucher MF1762]; 1 ♂, 1 ♀ (NMPC): 18–20.x.2012, FIT-MW2700-D-2/8-d03 (P2683, vial 14340) [DNA voucher MF1778]; 1 ♂ (IRSNB): 18–20.x.2012, FIT-MW2700-H-2/8-d03 (P2715, vial 14109) [DNA voucher MF1775]; 1 ♂ (MNHN): 24–26.x.2012, FIT-MW2700-D-5/8-d09 (P2686, vial 6488) [DNA voucher MF1759]; 1 ♂ (IECA): 26–28.x.2012, FIT-MW2700-G-6/8-d11 (P2711, vial 5960) [DNA voucher MF1776];1 ♂ (ZSM): 23–25.x.2012, MW2700 (P2773, vial 6406); 1 ♀ (IECA): 30.x.–1.xi.2012, FIT-MW2700-D-8/8-d15 (P2689, vial 14128); 1 ♀ (ZSM): 25–27.x.2012, MW2700 (P2774, vial 14716); 2 ♀♀ (ZSM): 16–18.x.2012, MW2700 (P2690, vial 6598); 1 ♀ (ZSM): 31.x.–2.xi.2012, MW2700 (P2809, vial 8575); 1 ♀ (ZSM): 20–22.x.2012, MW2700 (P2684, vial 8569); 1 ♀ (ZSM): 25–27.x.2012, MW2700 (P2798, vial 14248); 1 ♀ (ZSM): 24–28.x.2012, MW2700 (P2670, vial 8567); 1 ♀ (ZSM): 31.x.–2.x.2012, MW2700 (P2793, vial 6543); 2 ♀♀ (MNHN): 16–18.x.2012, FIT-MW2700-H-1/8-d01 (P2714, vial 6386); 1 ♀ (MNHN): 27–29.x.2012, FIT-MW2700-O-6/8-d12 (P2775, vial 14217); 1 ♀ (IRSNB): 27–29.x.2012, FIT-MW2700-Q-6/8-d12 (P2791, vial 14207) [DNA voucher MF1777]; 1 ♀ (IECA): 24–26.x.2012, FIT-MW2700-H-5/8-d09 (P2718, vial 6576); 1 ♀ (IECA): 30.x.–1.xi.2012, FIT-MW2700-H-4/8-d07 (P2717, vial 14147); 1 ♀ (NMPC): 27.x.–29.xi.2012, FIT-MW2700-N-1/8-d02 (P2762, vial 14153); 1 ♀ (NMPC): 6–8.x.2012, FIT-MW2700-J-2/8-d03 (P2731, vial 14335).

3.14. *Cetiocyon loksai* Hebauer, 2001

Figs. 8, 26

Material examined: ***Mt. Wilhelm transsect***: **1200 m**: 1 ♂ (NMPC): 26–28.x.2012, FIT-MW1200-S-1/8-d02 (P1632, vial 18777); 1 ♂ (ZSM): 3–5.x.2012, FIT-MW1200-M-5/8-d10 (P1588, vial 17327) [DNA voucher MF1787]; 11 ♀♀ (NMPC, IECA, MNHN, IRSNB): 6–8.xi.2012, FIT-MW1200-J-7/8-d13 (P1566, vial 17078); 3 ♀♀ (ZSM): 8–10.xi.2012, FIT-MW1200 (P1567, vial 16988); 1 ♀ (ZSM): 1-3.xi.2012, FIT-MW1200 (P1635, vial 16968); 1 ♀ (ZSM): 3–5.xi.2012, FIT-MW1200 (P1572, vial 18837); 1 ♀ (NMPC): 3–5.xi.2012, FIT-MW1200-N-5/8-d10 (P1596, vial 18812); 2 ♀♀ (NMPC): 4–6.xi.2012, FIT-MW1200-J-6/8-d11 (P1565, vial 17360); 2 ♀♀ (NMPC): 26–28.xi.2012, FIT-MW1200-S-1/8-d02 (P1632, vial 18777). **1700 m**: 1 ♂ (NMPC): 7–9.x.2012, FIT-MW1700-K-7/8-d14 (P1964, vial 5645) [DNA voucher MF1783]; 1 ♂ (ZSM): 26–28.x.2012, MW1700 (P1958, vial 5576); 2 ♀♀ (ZSM): 4–6.xi.2012, FIT-MW1700-I-6/8-d11 (P1947, vial 4011); 1 ♀ (NMPC): 7–9.xi.2012, FIT-MW1700-L-7/8-d11 (P1972, vial 6695).

3.15. *Cetiocyon papuensis* (Orchymont, 1924)

Figs. 7, 22

Material examined: **Mt. Wilhelm transect**: **700 m**: 2 ♂♂ (NMPC, ZSM): 3–5.x.2012, FIT-MW700-K-5/8-d10 (P1182, vial 16083) [DNA vouchers MF1755, MF1768].

3.16. *Cetiocyon riedeli* Fikáček & Short, 2010

Figs. 12, 34, 44, 47–49

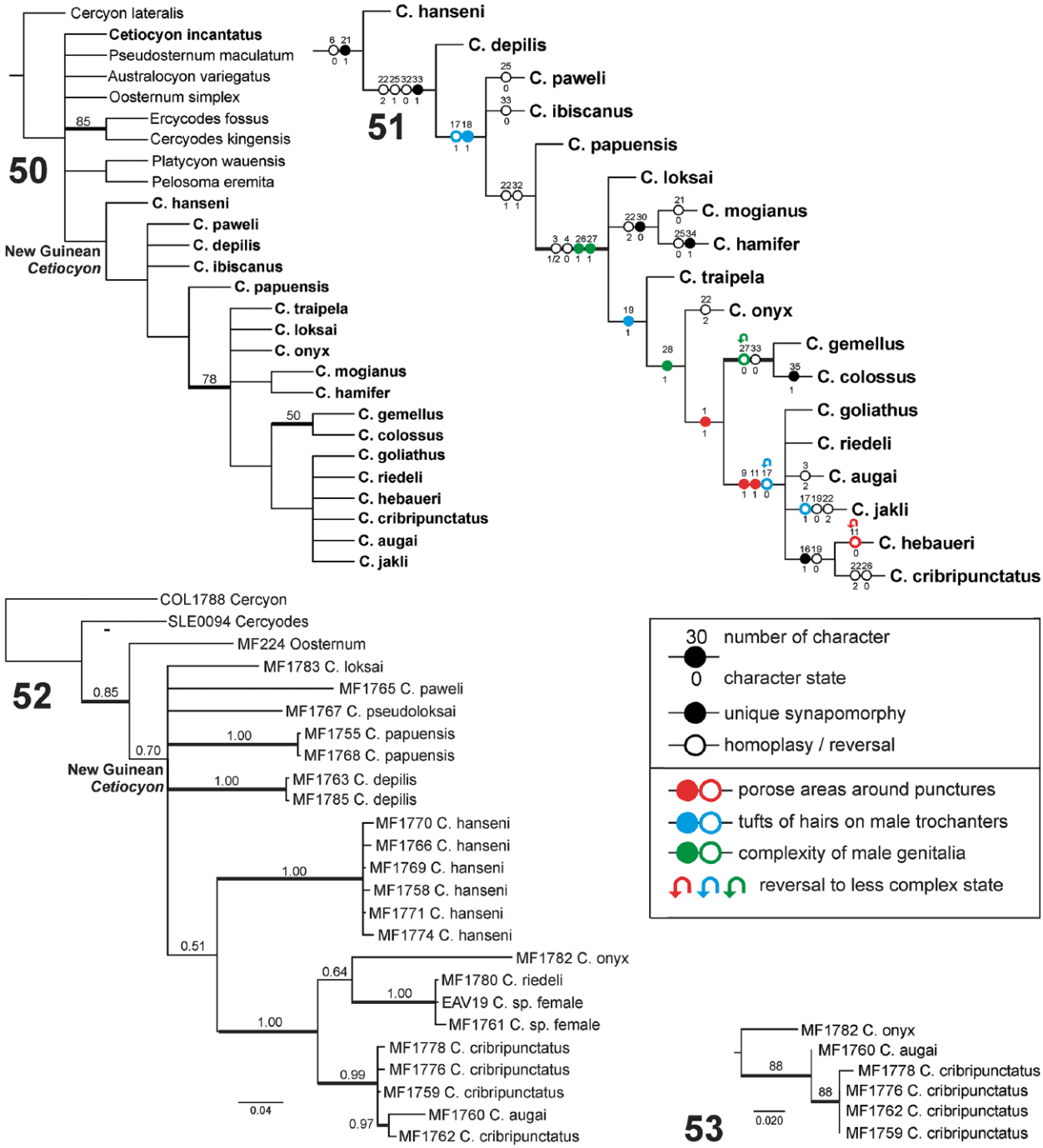
Material examined: ***Mt. Wilhelm transect***: **1700 m**: 1 ♂ (NMPC): 3–5.x.2012, FIT-MW1700-K-5/8-d02 (P1962, vial 5687) [DNA voucher MF1780]; 1 ♂ (NMPC): 6–8.x.2012, FIT-MW1700-B-7/8-d02 (P1892, vial 2361); 2 ♂♂ (ZSM): 26–28.x.2012, MW1700 (P1958, vial 5576); 1 ♂ (ZSM): 25–27.x.2012, MW1700 (P1886, vial 7540); 1 ♂ (IECA): 27–29.x.2012, MW1700 (P1943, vial 4017); 1 ♂ (ZSM): 30.x.2012, MW1700 (P1960, vial 06632).

4. Results of data analyses

Morphological phylogenetic analysis. The maximum parsimony analysis based on morphological characters resulted in 973 equally long most parsimonious trees of a length of 79 steps. The strict consensus tree (Fig. 50) indicates the monophyly of the New Guinean *Cetiocyon*, the position of *C. hanseni* as sister taxon to all remaining species, early-branching position of *C. depilis*, *C. paweli* and *C. ibiscanus*; sister relationships of *C. mogianus* + *C. hamifer* and *C. gemellus* + *C. colossus*, monophyly of the clade comprising species with porose punctures on the head and monophyly of the clade comprising species with porose punctures on the pronotum and/or elytra. In the majority consensus tree (Fig. 51), *C. hebaueri* + *C. cribripunctatus* are revealed as sister species. However, most clades are only weakly supported. The results are largely compatible with those of Fikáček & Short (2010), with two important differences: the Suriname *C. incantatus* is never revealed as deeply nested within New Guinean *Cetiocyon* (it is part of the basal polytomy and its relationship to New Guinean *Cetiocyon* remains unclear), and *C. loksai* + *C. goliathus* + *C. traipela* are never revealed as forming monophylum or at least as closely related species.

PCR amplification (see Table 2 and Supplementary Table S3)**.** We failed to amplify the 28S fragment for any of the 36 samples of Mt. Wilhelm *Cetiocyon* tested, and the success rate was also very low for the complete fragments of both traditionally used *cox1* markers (barcoding one and sJerry/sPat one) and for one of the shorter internal *cox1* fragment (Chy/Pat). The amplification was more successful for the 361 bp fragment of Jerry/Tom, in which we got positive results in 22 of the 36 tested specimens (61%). This fragment was sequenced and used for further analyses.

***Cox1* phylogeny.** HKY+I was selected as substitution model for first and second codon position, HKY+G for the third codon position. The Bayesian analysis of the *cox1* fragment (Fig. 52; contains only 10 *Cetiocyon* species) found support for a clade consisting of the New Guinean *Cetiocyon*, and strongly supported monophyly of the included high-altitude species (*C. onyx*, *C. riedeli*, *C. cribripunctatus* and *C. augai*). *Cetiocyon hanseni* was revealed as sister to that high-altitude clade (instead of being sister to all other species), but with weak support. *Cetiocyon papuensis* is placed in the 'basal' unresolved cluster, together with *C. paweli*, *C. mogianus* and *C. depilis*. Maximum likelihood analysis corresponds to the Bayesian in clustering the high-altitude species into a single clade, with the difference that *C. papuensis* is also placed into



Figs. 50–53. Results of the phylogenetic analyses based on morphology and *cox1* sequences. **50**: strict consensus of 970 most parsimonious trees resulting from the analysis of morphological characters. **51**: majority rule consensus of most parsimonious trees resulting from the morphological analysis, with mapped characters. **52**: Bayesian tree of *cox1* sequences. **53**: topology of the terminal part of the tree as revealed by maximum likelihood analysis of *cox1* sequences. Branch support ≤ 50 indicated above respective branch (bootstraps for maximum parsimony and maximum likelihood, posterior probability for Bayesian inference); clades with at least moderate support are highlighted by thicker line.

that clade, sister to *C. riedeli* (with weak support). *Cetiocyon paweli* and *C. depilis* form a clade sister to remaining *Cetiocyon* species (weakly supported). The only specimen of *C. augai* analysed is nested inside of *C. cribripunctatus* in the Bayesian analysis, whereas both species are separated in the maximum likelihood analysis (Fig. 53).

Combined morphology + molecules phylogenetic analysis. The Bayesian analysis based on mixed data (Supplementary Figure S4) revealed a tree which closely corresponds to that based on morphology, with *C. hanseni* and *C. papuensis* as early branching taxa sister to all remaining species; the only difference from morphological analysis is the weakly supported clade formed by *C. depilis* + *C. paweli* + *C. ibiscanus*.

Genetic distances (Table 4, Supplementary Table S3)**.** We sequenced representatives of 10 of 12 *Cetiocyon*

Table. 4. Summary of the intraspecific and mean interspecific generic distances estimated using maximum composite likelihood model as implemented in MEGA7. See Supplementary Table S4 for genetic distances between all specimens analysed. 'n/a' indicates species in which single specimen was sequenced and intraspecific distance could not be calculated.

Intraspecific distances	Species	Mean interspecific distances									
			1	2	3	4	5	6	7	8	9
0.000	*C. depilis*	**1**									
n/a	*C. paweli*	**2**	0.071								
0.000–0.017	*C. hanseni*	**3**	0.084	0.145							
n/a	*C. ibiscanus*	**4**	0.070	0.088	0.075						
n/a	*C. loksai*	**5**	0.089	0.088	0.073	0.061					
0.000	*C. riedeli*	**6**	0.107	0.128	0.089	0.098	0.098				
0.000	*C. papuensis*	**7**	0.078	0.098	0.108	0.096	0.107	0.042			
n/a	*C. onyx*	**8**	0.098	0.116	0.097	0.098	0.098	0.060	0.086		
n/a	*C. augai*	**9**	0.118	0.127	0.080	0.079	0.088	0.061	0.069	0.051	
0.000–0.008	*C. cribripunctatus*	**10**	0.110	0.120	0.092	0.090	0.090	0.072	0.072	0.072	0.019

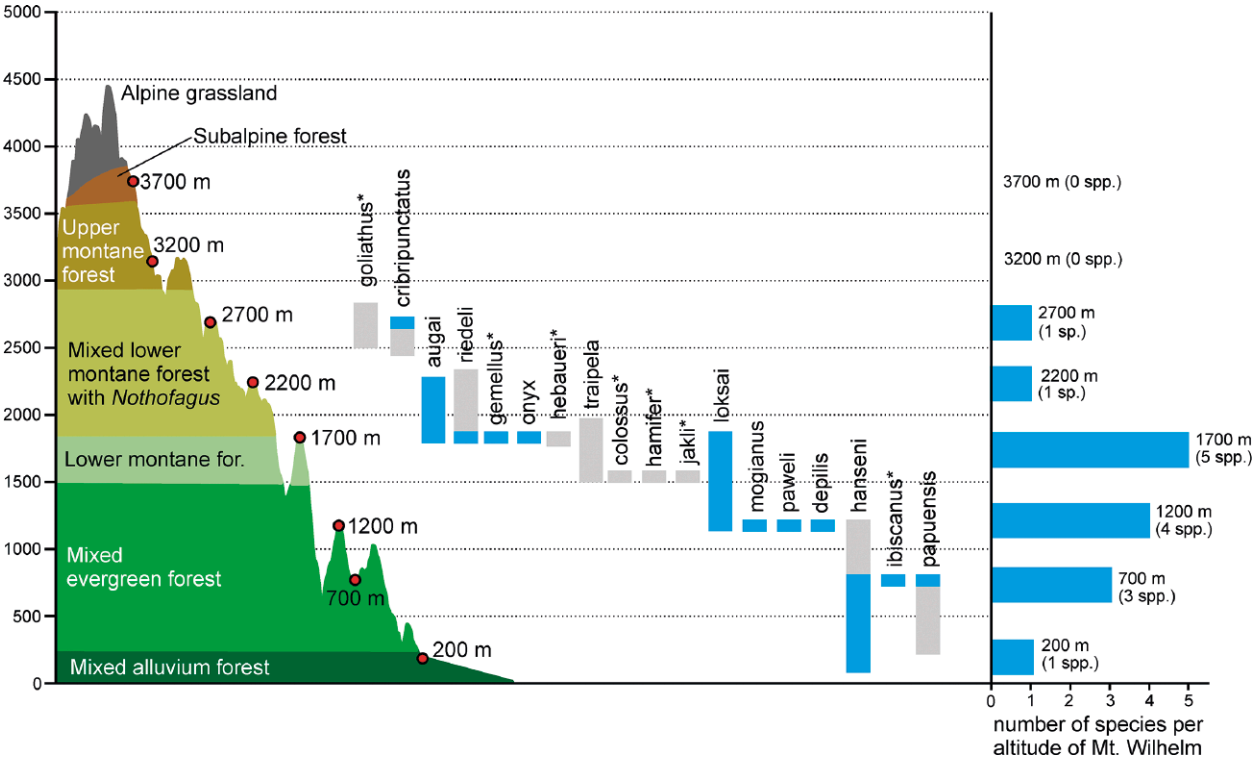
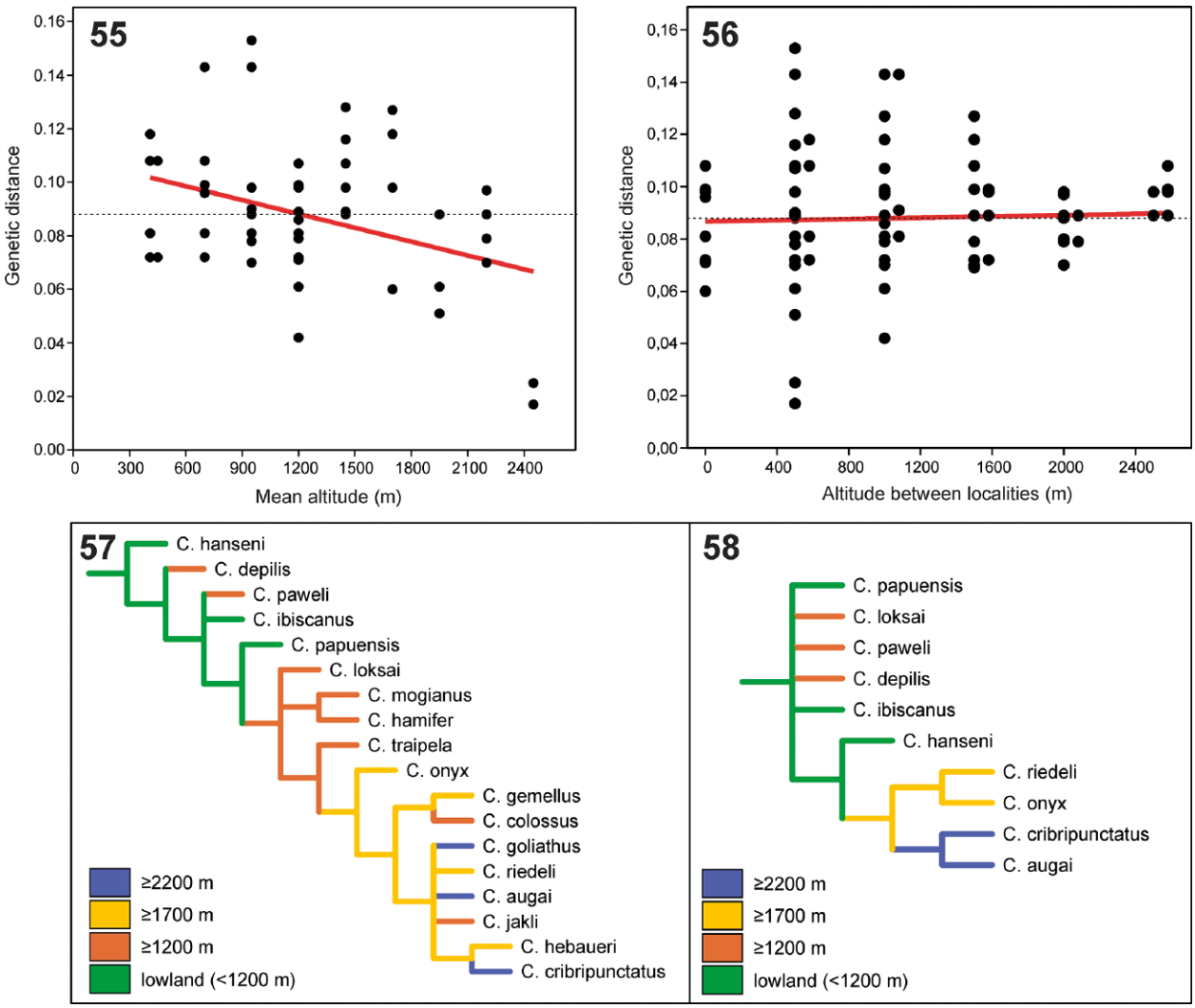


Fig. 54. Altitudinal distribution of New Guinean *Cetiocyon* species (blue color highlights species occurring in Mt. Wilhelm transect, grey bars indicate data from other parts of New Guinea, species known from a single collecting event are marked by an asterisk). Left part shows the altitudinal profile of the Mt. Wilhelm transect with collecting sites (red points) and vegetation types indicated.

species found on the Mt. Wilhelm transect, but multiple specimens were sequenced in five species only. The intraspecific genetic distances in these species vary from 0 to 1.7 %. Mean interspecific distances vary from 4.2–14.5% in most species (the maximal value is between lowland species *C. hanseni* and *C. paweli*). The mean genetic distance is extremely low between *C. cribripunctatus* and *C. augai* (ranging between 1.7–2.5%, mean 1.9%), reaching the value found intraspecifically in *C. hanseni*.

Effect of altitude. AIC criterion indicated that linear regression is the best-fitting model for both interspecific distances *vs.* mean elevation and *vs.* elevation difference. Mean elevation was negatively correlated with interspecific genetic distances ($p < 0.001$, $R^2 = 0.1608$) which are on average lower at higher elevations (Fig. 55). The negative correlation remains significant ($p < 0.005$, $R^2 = 0.0989$) even when the interspecific distances between *C. cribripunctatus* and *C. augai* (i.e. the 'outliers' in the bottom right) are excluded, and is hence not drawn by the extremely small distance between these two species only. On the other hand, no effect of elevational difference on interspecific distances was found ($p = 0.578$, $R^2 = 0.0015$), i.e. species living in nearby elevations are in general not more closely related than those living at more distant elevations. The regression curve (i.e. expected mean distance for each elevation difference) moreover closely corresponds to the mean value for the whole data-



Figs. 55–58. Relationships of genetic distances and species-level phylogeny versus altitude in *Cetiocyon* beetles in New Guinea. **55**: interspecific genetic distances in relation to the altitude. **56**: interspecific genetic distances in relation to the altitudinal difference between localities of both species. **57**, **58**: altitudinal distribution of the species mapped on the tree topology resulting from maximum parsimony analysis of morphological characters (57) and Bayesian analysis of *cox1* sequences (58). — Red line: linear regression; dotted line: mean genetic distance of the whole dataset.

set (Fig. 56). The interspecific distances show the highest variance in case of neighbouring elevations (i.e. altitude between localities = 500 m) as they contain the extremely low distances between some species from neighbouring high altitudes (e.g., *C. cribripunctatus* and *C. augai*) as well as the very high genetic distances revealed for some species (e.g., *C. hanseni* and *C. paweli*) at neighbouring lowland elevations. When the elevational distribution of the species is mapped on the phylogenetic trees, low elevations (up to 1,200 m) are always reconstructed as ancestral for *Cetiocyon*, irrespective of the different topologies revealed by different analyses (Figs. 57–58, see also Supplementary Figs. S1–S4). One transition to elevations over 1,700 m is reconstructed in most analyses. Only the topology resulting from maximum likelihood analysis of *cox1* data indicates two independent transitions to higher elevations (in *C. riedeli* separately from *C. onyx*, *C. augai* and *C. cribripunctatus*) due to the deeply nested position of lowland *C. papuensis*.

5. Discussion

5.1. Elevation and species diversity

Studies on the distribution of insects along elevational gradients often bring contrasting results. The topic was summarized by McCoy (1990) who indicated that there is a complex interplay of local and global factors which influence the differences in insect species richness along elevation gradients. Hence, any data collected along elevational gradients reflect a combined effect of regional peculiarities and general elevational phenomena (Körner 2007). Investigations of tropical insect biodiversity along elevational gradients were recently conducted e.g. in Borneo (Chen et al. 2009), New Britain (Richards & Gamui 2011) and in Queensland (e.g. Ashton et al. 2011). In Papua New Guinea, it was examined in canopy-inhabiting beetles (Allison et al. 1993), phytophagous insects

on *Ficus* trees (Novotny et al. 2005; Volf et al. 2017), Hemiptera (Le Cesne et al. 2015), Formicidae (Lucky et al. 2011a,b), Tettigoniidae (Naskrecki 2011) and Odonata (Gassmann & Richards 2011). Three contrasting effects of elevation were found in these studies: **(1)** species richness declining with increasing elevation; **(2)** species richness increasing with increasing elevation, or **(3)** species richness is the highest at mid elevations.

Our study focused on a detailed treatment of a single beetle genus (*Cetiocyon*) on Mt. Wilhelm, differing from the above studies which focused on large taxonomic groups. Twelve species were found, which is a surprising result by itself for two reasons: **(1)** we originally classified the specimens into two morphotypes only based on external morphology, and **(2)** the number of species on the slopes of a single mountain is higher than the number of species known previously for the whole of New Guinea (eight, Fikáček & Short 2010). The only study focused on single beetle genus in an elevational transect is that by Riedel et al. (2010) on the *Trigonopterus* weevils of Cyclops Mts. Similarly as in our study, it revealed a surprisingly high number of species inhabiting the single elevational transect (51 species) which were accurately recognized both by male genital morphology and *cox1* marker; the number of morphospecies recognized using only external morphology was lower and inaccurate.

The *Cetiocyon* species inhabiting Mt. Wilhelm are, so far as is currently known, restricted to a particular elevation and/or vegetation zone (Fig. 54, see also Supplementary Table S2). Only three species (*C. hanseni*, *C. loksai*, and *C. augai*) were found at two different (but adjacent) elevations. Our results are similar to those found for Hemiptera from the same elevational transect on Mt. Wilhelm, which showed that individual morphospecies were rarely collected from more than one elevation (Le Cesne et al. 2015). The largest number of *Cetiocyon* species were collected in research plots situated from intermediate elevations (1,700 m – 5 species, 1,200 m – 4 species), and the highest plot with *Cetiocyon* species was at 2,700 m (1 species) (Fig. 54). Similar mid-elevation peaks have been found in some groups of herbivorous insects (e.g. butterflies: Ashton et al. 2011; Heteroptera: Le Cesne et al. 2015), but not in others (Auchenorrhyncha: Le Cesne et al. 2015), and may be caused by elevational differences in plant diversity and species-composition (Le Cesne et al. 2015), differences in plant anti-herbivore defence strategies (Volf et al. 2017), phenological differences (Allison et al. 1993), or temperature (Lucky et al. 2011b). More detailed studies are necessary to reveal which of the above factors may influence *Cetiocyon* and hydrophilid beetles in general. However, *Cetiocyon* is not expected to be closely associated with particular host plants (they likely inhabit leaf litter or decaying plant material and are saprophagous as adults and predaceous as larvae). Wolda (1987) and McCoy (1990) demonstrated that sampling bias caused by short sampling periods can also lead to results showing mid-elevation peaks in species diversity. This cannot be completely excluded for some *Cetiocyon* species found on Mt. Wilhelm, which were found singly or in low numbers and may occur in a wider elevational range then is currently known. Alternatively, mid-elevation peak may result from higher probabilities of species range overlaps at intermediate elevations, and may be hence not related to ecology, environmental conditions or evolutionary history of *Cetiocyon* (so-called mid-domain effect; e.g., Colwell & Lees 2000, Colwell et al. 2004).

Toussaint et al. (2014, 2015) demonstrated that in additional to the ecological factors discussed above, the recent geological history of New Guinea strongly influenced the diversification pattern of insects on the island, and needs to be taken into account when the effect of elevation is evaluated. Three macroevolutionary scenarios were proposed to explain the high diversity of particular New Guinean clades: **(1)** the origin predating the formation of New Guinea, with diversification patterns corresponding to the arrangement of paleoislands before the collision which later formed New Guinea (e.g., Polhemus & Polhemus 1998); **(2)** the recent origin and speciation driven primarily by the colonization of new regions with suitable habitats (allopatric speciation; Toussaint et al. 2014); and **(3)** the recent origin and local speciation along elevational gradients (ecological speciation; Diamond 1972). The first scenario would not only predict a pre-Miocene *origin* but also a *diversification* of a particular clade, with lower elevations reconstructed as ancestral and subsequent colonization of higher elevations once these became available during the New Guinea orogeny. The second and third scenarios would both predict a possibly old origin but certainly more recent diversification (Miocene to Pleistocene) of the New Guinean clade with lower or higher elevations reconstructed as ancestral (as both would be available at the time of New Guinea colonization) and many (though probably not all) locally endemic species. They would however differ in expected distribution patterns: allopatric speciation would generate a pattern of sister species usually inhabiting the same or similar elevations but occurring in different parts of New Guinea. Ecological speciation would form locally endemic clades in which species from nearby elevations would be more closely related than those from distant ones.

Our analyses of the short *cox1* fragments of 10 *Cetiocyon* species show that mean interspecific distances are the same for species from nearby and distant elevations and do not indicate that *Cetiocyon* species recorded from Mt. Wilhelm form a clade of closely related species. This is incongruent with the ecological speciation scenario outlined above (but the extremely low genetic distance between *C. augai* and *C. cribripunctatus* and their strictly allopatric occurrence on Mt. Wilhelm may indicate that ecological speciation might have played a role in some cases). Based on our current data (notice that some species are only known from single or few collecting events), elevational ranges of *Cetiocyon* seem to be strongly stratified on Mt. Wilhelm which would conform with the allopatric speciation scenario. Unfortunately, the data about the distribution of *Cetiocyon* spe-

cies in New Guinea are limited and only the morphology-based species phylogeny is available for the whole genus (including species not living on Mt. Wilhelm). There is however at least one case of supposed sister species inhabiting similar elevations from different parts of New Guinea, as predicted by the allopatric model: *Cetiocyon gemellus* occurring at 1,700 m at Mt. Wilhelm and the extremely similar and likely sister *C. colossus* inhabiting a similar elevation (1,540 m) on Bird's Head Peninsula (e.g., Toussaint 2014; Georges et al. 2014). In contrast, many other *Cetiocyon* species are widespread rather than locally endemic. In particular, lowland species (*C. papuensis*, *C. hanseni*) seem widespread across the whole of New Guinea, but surprisingly, this pattern was also found for some high-elevation species. *C. riedeli* and *C. cribripunctatus* occur on Mt. Wilhelm, but were also found in the Indonesian part of the Central Orogen (Baliem Valley) ca. 700 km away (Fikáček & Short 2010). The most recent common ancestor of *Cetiocyon* was likely a lowland-inhabiting species, and intermediate elevations (1,700–2,200 m) were likely colonized by a single *Cetiocyon* clade. Correspondingly, analysis of genetic distances indicated higher genetic distances (i.e. higher genetic diversity and more ancient diversifications) among lowland species than among higher elevation ones. This would conform with the first (ancient diversification) scenario outlined above, but a dated phylogeny which is not available at the moment would be necessary to test it. A complex scenario combining all three models, similar to that proposed for New Guinean honeyeaters (Norman et al. 2007), or the 'competition upon secondary contact' model explaining the origin of elevation-stratified ranges by a sequence of evolutionary steps (Diamond 1973; Freeman 2015) cannot be excluded either at the moment.

5.2. Morphology and systematics of *Cetiocyon*

Our study, based on geographically limited material, surprisingly increases the number of New Guinean *Cetiocyon* from 8 species to 18, indicating that our knowledge of the New Guinean hydrophilid fauna is still very fragmentary. Twelve of these species were found on Mt. Wilhelm, indicating that local diversity is very high in New Guinea. The discovery of an additional ten new *Cetiocyon* species allowed us to revise some of the previous assumptions about the systematics of the genus made by Hansen (1990), Hebauer (2001) and Fikáček & Short (2010).

Hansen (1990) diagnosed *Cetiocyon* from other megasternine genera by the combination of a laterally slightly expanded clypeus, a non-carinate prosternum, an absence of antennal grooves, and a ribbon-line median part of male sternite 9. These characters, along with an elongate oval mesoventral plate and a metaventrite without arcuate anterolateral ridges led Fikáček & Short (2010) to assign the Neotropical aberrant *C. incantatus* Fikáček & Short, 2010 to the genus and assume a trans-Pacific disjunct distribution of *Cetiocyon*. Examination of the new material in this study revealed that the prosternum of some *Cetiocyon* species has a very distinct median keel (e.g. in *C. depilis* and *C. paweli*, Fig. 3) and hence the character cannot be considered as genus-diagnostic. On the other hand, two new tentative autapomorphies of *Cetiocyon* were discovered: **(1)** tufts of setae on male trochanters (Figs. 3, 48), and **(2)** the tuft of hairs on the abdominal apex (Fig. 49). Male trochanter tufts are absent in a few species (*C. hanseni*, *C. depilis*), which were reconstructed as early branching in morphological analyses (Fig. 50; also see Fikáček & Short 2010: figs. 59, 60), but revealed as deeply nested and/or closely related to species bearing the tufts in molecular analyses. This indicates that trochanter tufts may be ancestral for *Cetiocyon* and subsequently lost in some species. Abdominal tufts of setae were overlooked until now, but they are present in all *Cetiocyon* species (both sexes) and absent in all related genera examined. Interestingly, they are absent from the Neotropical *Cetiocyon incantatus*, which also lack trochanter tufts. Because of the poor DNA preservation of the New Guinean *Cetiocyon* studied here, we were not able to test the monophyly of *Cetiocyon* sensu Fikáček & Short (2010). The absence of the above potential synapomorphies of *Cetiocyon* in *C. incantatus* casts doubt on its generic placement, but the position of *C. incantatus* in the phylogeny must await further study.

Our detailed SEM examination revealed that the abdominal ventrites of *C. riedeli* (other species were not examined for this character) bear characteristic 'disc-like fields' (Fig. 47) which have previously been observed on the submentum of species from the genus *Oosternum* Sharp, 1882 (Fikáček 2009), and on the prosternum of *Motonerus andersoni* Fikáček & Short, 2006 (M. Fikáček unpubl. observation). All of these genera (including *Cetiocyon*) belong to the monophyletic *Oosternum* group of genera (Short & Fikáček 2013). The fields are mostly square in shape in *Cetiocyon*, while they are rounded both in *Oosternum* and *Motonerus*. Their function remains unknown.

The porose areas surrounding the dorsal punctation (Figs. 43, 44, 46) observed in some species by Fikáček & Short (2010) were found in all of the species of the 'high-elevation' clade, which is strongly supported by both morphological characters and *cox1* sequences. The apparent correlation between this character and elevation (only species occurring at ≥ 1,700 m have the porose areas) is therefore likely to be driven by phylogeny. The porose areas are usually larger than surrounding punctures, and thus more visible, on the head and pronotum (Fig. 44), while on the elytra they are smaller and usually present only on the sides of punctures (Fig. 46). Another character that showed a possible correlation with elevation is the morphology of the antenna: antennomere 7 is short in lowland species (Fig. 37) but tends to increase in length with increasing elevation (Figs. 38, 39). Our phylogenetic trees unfortunately differ in topology between morphology- and DNA based analyses, and do not allow

for testing whether this character is correlated with elevation or phylogeny.

Cetiocyon is very unusual within Megasternini as the genitalia may range from very simple, which is typical in other megasternine genera (Figs. 4, 5), to rather complex (Figs. 6–19). Species from the 'high elevation clade' especially, have a very complex median lobe of the aedeagus, with species-specific lateral projections (Figs. 10–13). Genitalia hence provide the best character for species identification, as they likely have undergone rapid morphological evolution within *Cetiocyon*. This is most evident when genitalia of *C. augai* (Fig. 11) and *C. cribripunctatus* (Fig. 13) are compared: they are very distinct from each other and clearly indicate the separation of these species. This is in contrast to the molecular data, where both species were so close genetically that the Bayesian analysis of *cox1* sequences failed to separate them (Fig. 51), and their interspecific distance (1.9%) was very close to the maximum intraspecific distance revealed in some other species (*C. hanseni*: 1.7%).

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Electronic Supplement Files

at http://www.senckenberg.de/arthropod-systematics

File 1: szczepański&al-cetiocyonnewguinea-asp2018-electronic supplement-1.nex. — Morphological data matrix in Nexus format.

File 2: szczepański&al-cetiocyonnewguinea- asp2018-electronic supplement-2.fasta. — Aligned *cox1* sequences of sequenced *Cetiocyon* specimens.

File 3: szczepański&al-cetiocyonnewguinea- asp2018-electronic-supplement-3.doc. — **Table S1.** Data matrix used for the morphology-based phylogenetic analysis. Cases of character inapplicability coded as (-), cases of missing character scoring as (?). — **Table S2.** Altitudinal distribution of *Cetiocyon* species based on their occurrence data. First 11 columns give number of collecting events / specimens per altitude examined for each species. Events and specimens from the Mt. Wilhelm survey are highlighted in bold. Altitudinal ranges of the species known from the single collecting event are indicated by an asterisk. — **Table S3.** List of sequenced *Cetiocyon* specimens from Mt. Wilhelm transect, with indication of successfully amplified gene fragments and GenBank accession numbers of Jerry-Tom *cox1* sequences used for the analyses. — **Table S4.** Genetic divergence between sequences (in %) estimated using the maximum composite likelihood model as implemented in MEGA7. — **Fig. S1.** Result of the maximum parsimony analysis of morphological data (top: strict consensus tree, middle: majority rule consensus, bottom: bootstrap tree) and altitudinal distribution mapped on the majority consensus tree. — **Fig. S2.** Result of the Bayesian phylogenetic analysis of *cox1* data and altitudinal distribution mapped on the tree. — **Fig. S3.** Result of the maximum likelihood phylogenetic analysis of *cox1* data and altitudinal distribution mapped on the tree. — **Fig. S4.** Result of the Bayesian phylogenetic analysis of combined *cox1* and morphological data, data and altitudinal distribution mapped on the tree.

Digitally Archived Data

at doi 10.5281/zenodo.1212736

The dataset submitted to Zenodo contains **(1)** the data matrices used for all phylogenetic analyses performed, **(2)** all data included in the electronic supplement file 3 above, and **(3)** original unedited versions of the photographs and SEM micrographs taken for this study, including those taken for comparative purposes only and not presented directly in the manuscript.

Zoobank Registrations

at http://zoobank.org

Present article: http://zoobank.org/urn:lsid:zoobank.org:pub:849925D5-B41B-4B83-AD8B-89EF27448F61

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