

Taxonomic revision and phylogeny of the genus *Cetiocyon* and its discovery in the Neotropical region (Insecta: Coleoptera: Hydrophilidae)

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> Abstract

The hydrophilid genus *Cetiocyon* Hansen (Sphaeridiinae: Megasternini) is diagnosed and revised, resulting in the first record of the genus in the Neotropical Region and recognition of eight species in New Guinea. One new species, *Cetiocyon incantatus* **new species**, is described from Suriname, and four new species from the central mountain range of New Guinea: *Cetiocyon cribripunctatus* **new species**, *Cetiocyon hebaueri* **new species**, *Cetiocyon riedeli* **new species**, and *Cetiocyon traipela* **new species**. Four previously described species are redescribed: *Cetiocyon goliathus* (Huijbregts, 1984), *Cetiocyon hanseni* Hebauer, 2001, *Cetiocyon loksai* Hebauer, 2001, and *Cetiocyon papuensis* (d'Orchymont, 1924). An identification key is included for all recognized species, along with photographs and illustrations of relevant morphological characters. A phylogenetic analysis based on 34 morphological characters supports the monophyly of the genus and its Australian–New Guinean origin, and suggests its close relationships to the New Guinean genus *Platycyon* Hansen and New Guinean species of *Pelosoma* Mulsant. Three distinctive lineages have been recognized within *Cetiocyon*, two represented by New Guinean species, the third by the Neotropical one. Possible reasons for the disjunct distribution of the genus are discussed, along with remarks about the composition of the Megasternini fauna in New Guinea.

> Key words

Hydrophilidae, Megasternini, *Cetiocyon*, new species, Australian Region, Neotropical Region, Gondwana, disjunct distribution, phylogeny, taxonomy.

1. Introduction

The tribe Megasternini (Hydrophilidae: Sphaeridiinae) is the most diverse group of the terrestrial hydrophilid beetles, containing slightly more than 500 described species accommodated in 51 genera (HANSEN 1999a; SHORT & HEBAUER 2006). The group is world-wide in distribution, but the highest diversity is found in the tropical regions, where the megasternines mainly inhabit forest leaf litter and other kinds of decaying plant

matter. The number of taxa in the tropics is, moreover, much higher than previously expected, judging from the number of undescribed (or misplaced) species in museums throughout the world (M. Fikáček & A. Short, unpubl. data).

The understanding of the phylogeny and evolutionary history of the Megasternini remains rather poor and started to be intensively studied only re-

cently (e.g., HANSEN 1990, 1999b; FIKÁČEK & SHORT 2004; FIKÁČEK et al. 2009; FIKÁČEK & HEBAUER 2009; FIKÁČEK 2010; HOSHINA & FIKÁČEK 2010; FIKÁČEK & SHORT 2010). Nevertheless, already the first detailed studies by HANSEN (1990) revealed the uniqueness of the Australian fauna: nine genera were recognized as endemic to the continent, most of them sharing an unusual morphology of male genitalia and associated abdominal sclerites. Representatives of three of these genera (*Cetiocyon* Hansen, 1990, *Pilocnema* Hansen, 1990 and *Pseudoosternum* Hansen, 1990) were discovered also in New Guinea (HEBAUER 2001; HANSEN 2003), along with another endemic genus, *Platyocyon* Hansen, 1999, occurring on the latter island but not in Australia (HANSEN 1999b; HEBAUER 2000, 2001). The genital morphology furthermore suggested close relationships of most of these Australian and New Guinean genera with the genus *Kanala* Balfour-Browne, 1939 endemic to New Caledonia (FIKÁČEK 2010) and with some Neotropical genera (*Motonerus* Hansen, 1989, *Sacosternum* Hansen, 1989, and *Oosternum* Sharp, 1882; FIKÁČEK & SHORT 2004; FIKÁČEK 2007, 2010). The genus *Australocyon* Hansen, 1990 was moreover found to occur both in Australia and South America (HANSEN 2003), even more suggesting that the uniqueness of the Australian fauna in fact concerns also the New Guinean and partly the South American fauna. The group was temporarily referred to as ‘Gondwanan genera’ in recent papers (e.g., FIKÁČEK 2007, 2010) and its monophyly is currently tested (ongoing work by M. Fikáček).

In 2005, we discovered an aberrant specimen of Megasternini collected in Suriname. Although the species was clearly different from all known Neotropical megasternine taxa and moreover very apparent for its unusual body shape and coloration, we were not able to find its generic placement at that time. Four additional specimens found recently allowed us to examine the species in more detail and led to the surprising discovery that the species belongs into the genus *Cetiocyon*, which was so far known from four species from New Guinea (HUIJBREGTS 1984; HANSEN 1990; HEBAUER 2001) and one record of *C. papuensis* (d’Orchymont, 1924) from northernmost Queensland, Australia (HANSEN 1990). The New Guinean species of the genus are among the largest known megasternine species, with *C. goliathus* (Huibregts, 1984) representing the largest known species of the tribe. In spite of their large body size making them hard to overlook, the material of most species is very rare in collections.

In order to understand the systematic position of the aberrant Suriname species, we have performed a taxonomic revision and a phylogenetic analysis of the New Guinean material. The results are presented in this paper, further supporting the close relationships between the New Guinean and the Neotropical megasternine

faunas and highlighting the uniqueness of the ‘Gondwanan group of genera’ within the tribe Megasternini.

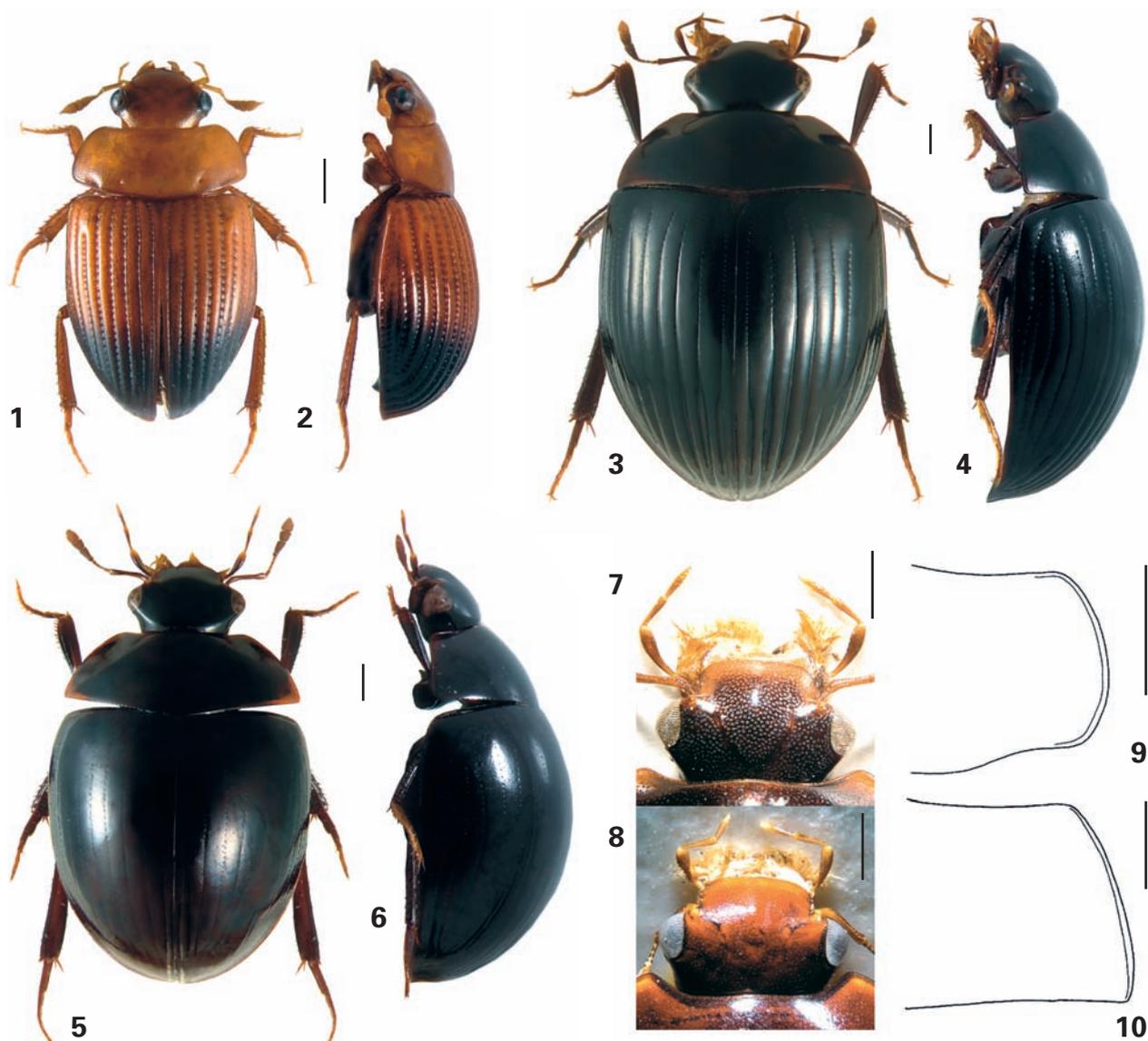
2. Methods

We examined 176 specimens of the genus *Cetiocyon* for this study, including the holotypes of all previously described species. A portion of each type series was dissected, genitalia were placed on a transparent plastic label below the beetle in water-soluble dimethyl hydantoin formaldehyde resin (DMHF) or glued on the label in dry condition using alcohol-soluble glue.

Label data are cited verbatim for type specimens and in adapted form for the additional material examined. Sex is indicated for dissected specimens only, remaining material is listed as unsexed specimens (sp.). Male genitalia drawings are based on the aedeagophores of the holotypes temporarily mounted in glycerine-gelatine and were traced from the photographs prepared using a Nikon Eclipse TS100 compound microscope. Habitus photographs were taken using an Olympus Camedia C-5060 camera attached to an Olympus SZX9 binocular microscope and subsequently edited in Adobe Photoshop 7.0 partly using the procedures described at Darci Kampschroeder’s website at <http://www.nhm.ku.edu/illustration/>. Drawings of non-genital structures were traced from photographs prepared using the same Olympus equipment. SEM micrographs of uncoated specimens were prepared at the Department of Paleontology of the National Museum in Prague using a Hitachi S-3700N scanning electron microscope. Morphological terminology follows KOMAREK (2004), FIKÁČEK (2010) and FIKÁČEK & SHORT (2010). Interocular distance (measured as the shortest distance between inner eye margins) is compared to maximum width of an eye in dorsal view in the descriptions.

Because of the great external similarity of all species from New Guinea, the complete description is provided only for *C. hanseni*, which is characterized by the plesiomorphic states of most characters (with the only exception of the morphology of the aedeagus); only the characters not conforming to *C. hanseni*, a detailed description of the male genitalia and associated abdominal sclerites, and the measurements are included for the remaining New Guinean species.

The phylogenetic analysis is based solely on the adult external morphological characters. Larvae are unknown for *Cetiocyon* and alcohol-fixed material suitable for DNA extraction is currently available for a single species of the genus (*C. hanseni* Hebauer, 2001 in coll. KSEM). The outgroup taxa represent all genera hypothesized as closely related to *Cetiocyon* in a



Figs. 1–10. *Cetiocyron* species, habitus in dorsal view (1, 3, 5), habitus in lateral view (2, 4, 6), head in dorsal view (7, 8), lateral portion of pronotum in dorsolateral view (9, 10). **1, 2, 9:** *Cetiocyron incantatus*. **3, 4:** *Cetiocyron traipela*. **5, 6:** *Cetiocyron riedeli*. **7:** *Cetiocyron cribripunctatus*. **8, 10:** *Cetiocyron loksai*. Scale = 0.5 mm.

preliminary analysis by FIKÁČEK (2010) (*Platycyon*, *Ercycodes* Hansen, 1990, *Cercycodes* Broun, 1886) and selected representatives of the remaining ‘Gondwanan’ genera (*Australocyron*, *Oosternum*, *Pseudoosternum*). In addition to the ‘Gondwanan’ genera, the New Guinean *Pelosoma eremita* Knisch, 1925 was included in the analysis as it was recently found to be very similar to *Cetiocyron* in all important characters (unlike the remaining Neotropical and Afrotropical species assigned to the genus). The tree was rooted using *Cercyon lateralis* (Marshall, 1802) as the only ‘non-Gondwanan’ taxon included into the analysis.

The combined matrix consisting of two continuous characters (chars. 1–2) and 32 discrete characters (chars. 3–34) was analysed using the TNT software (GOLOBOFF et al. 2008). Continuous characters were implemented as value ranges (for body size) or real

numbers (for body convexity) and analysed as additive (GOLOBOFF et al. 2006); discrete characters were analysed without any *a priori* considerations. All analyses were done using an exhaustive search (‘implicit enumeration’ option of TNT). An analysis including all taxa and all characters was performed first; nearest suboptimal trees (less than 0.5 steps longer than the most parsimonious tree) were also examined in this analysis. Subsequently, an analysis using only the discrete characters was performed. *Cetiocyron goliathus*, whose male and thus also states in the eleven male-specific characters are unknown, was subsequently excluded from the analysis in order to test its influence on tree topologies. Characters were mapped on the most parsimonious tree resulting from the analysis of all taxa and all characters, and on the strict consensus of the trees resulting from the analysis based on dis-

crete characters only, in both cases using the WinClada program (NIXON 2002); continuous characters were mapped as several discrete states (see section 5.1.). Jackknife analysis and Bremer support were used to evaluate the support of the clades by the characters; 1000 resampling replicates were used for jackknife analysis; Bremer support was calculated by setting the suboptimal tree length successively lower (with 1–4 additional steps) and repeating an exhaustive search for each setting. The data matrix in Nexus format (containing only discrete characters) and in TNT format (containing all characters) is available at the web site of the first author (<http://www.cercyon.eu/Publications.htm>) (see also Electronic Supplement of online version of this article).

3. Abbreviations of collections

ANIC	Australian National Insect Collection, Canberra, Australia (T. Weir)
ASCH	coll. Andre Skale, Hof, Germany
BMH	Bishop Museum, Honolulu, Hawaii, U.S.A. (S. Myers)
BMNH	The Natural History Museum, London, U.K. (M. Barclay, C. Gent)
CMN	Canadian Museum of Nature, Ottawa, Canada (R. Anderson)
FHCP	coll. Franz Hebauer, Plattling, Germany (to be deposited in SMNS)
KSEM	Natural History Museum, University of Kansas, Lawrence, U.S.A. (A. Short)
NHMW	Naturhistorisches Museum, Wien, Austria (M.A. Jäch)
NMPC	National Museum, Prague, Czech Republic (M. Fikáček)
NZCS	National Zoological Collection of Suriname, Paramaribo, Suriname
RMNH	National Museum of Natural History 'Naturalis', Leiden, the Netherlands (E. Gassó Miracle)
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany (W. Schawaller)
ZMUC	Zoological Museum, University of Copenhagen, Denmark (A. Solodovnikov)

4. Taxonomy

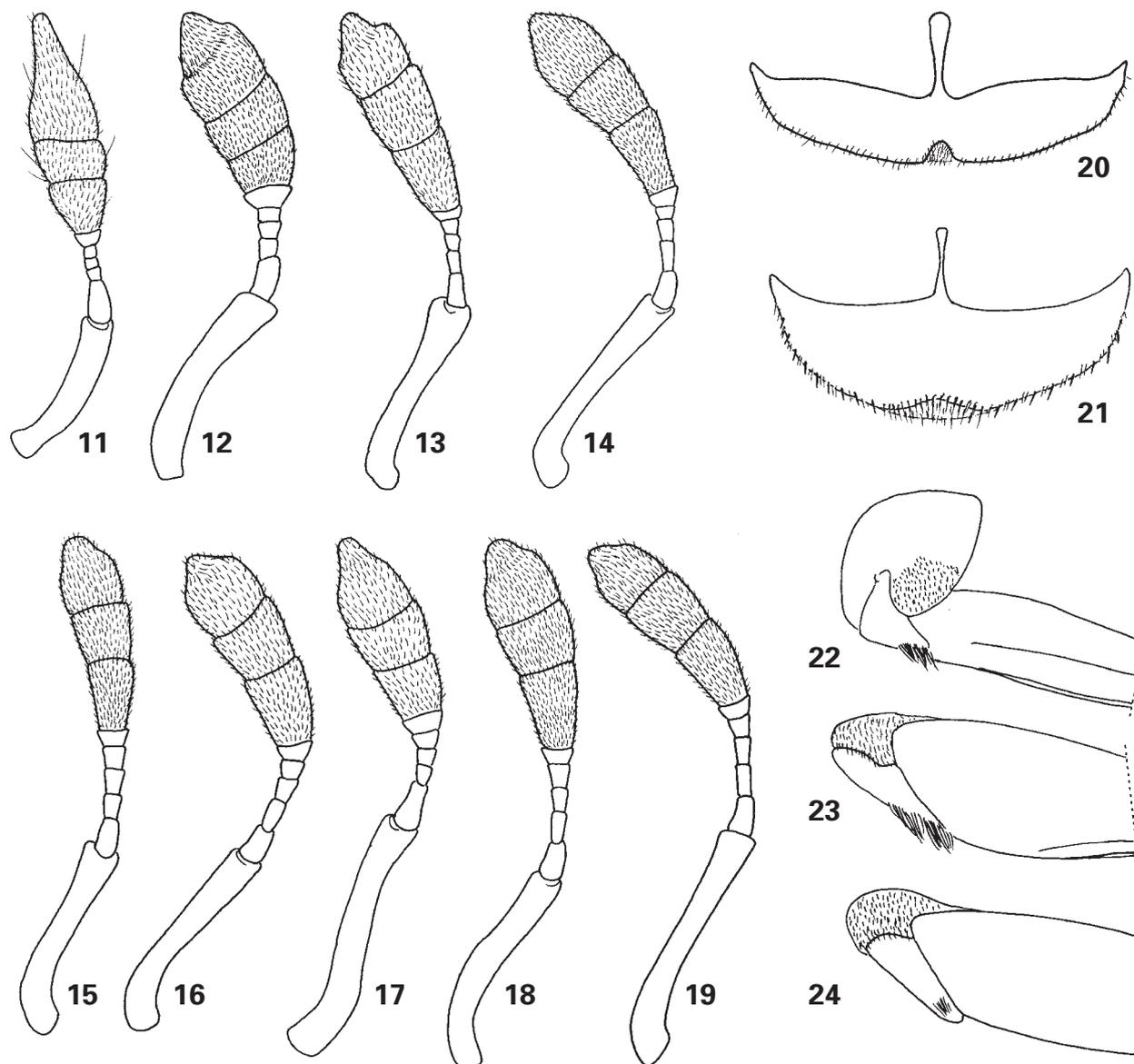
4.1. Genus *Cetiocyon* Hansen, 1990

Cetiocyon Hansen, 1990: 344.

Type species. *Cercyon papuensis* d'Orchymont, 1924 (by original designation).

Description. Eyes moderately large to small, separated by 4.9–7.0× width of one eye. Antenna with 9 antennomeres, antennal club compact, without sensorial fields, slightly to strongly projecting at apex (Figs. 11–19). Labrum membranous, largely retracted under clypeus. Mentum narrowing anteriorly, with large membranous anterolateral lobes, anterior margin deeply emarginate apically (Figs. 49, 50). Maxillary palpomere 2 slightly widened apically, palpomere 4 spindle-like. Gula moderately wide to very narrow, constricted posteriorly of tentorial pits, widely divergent posteriorly, tentorial pits small. Pronotal punctation uniform in size, each puncture bearing a short and fine indistinct seta; median portion of prosternum not differentiated from lateral portions, not carinate medially (Figs. 52, 53); anteromedian excision of prosternum absent; antennal grooves absent (Figs. 52, 53). Scutellar shield moderately large, in form of equilateral triangle. Elytron with 10 punctural series, lateral margin of elytron without denticles, epipleura narrower than pseudopipleura. Grooves for reception of procoxae small to moderately large, not reaching mesocoxal cavities posteriorly; preepisternal elevation of mesothorax with narrowly elongate oval plate lacking a median longitudinal carina, slightly overlapping anterior margin of metaventrite (Figs. 54, 55). Metaventrite with slightly elevated median portion, without depressions in both sexes; lateral portions densely pubescent and bearing fine microsculpture; anterolateral ridges continuous medially, not diverging from posterior margin of mesocoxal cavity, reaching anterolateral corner of metaventrite (Figs. 54, 55); femoral lines absent. Prothorax not emarginate on outer margin. Abdomen with 5 ventrites, ventrite 1 with median longitudinal carina, without additional longitudinal ridges; posterior margin of abdominal ventrites entire, not denticulate; ventrite 5 entire on posterior margin in both sexes. Aedeagus with base of median lobe attached to the base of parameres; male sternite 8 with anteromedian narrow projection (Figs. 20, 21); median portion of male sternite 9 without median tongue-like projection (Figs. 26, 29, 32, 35, 38, 41, 44, 47); body length 3.8–8.0 mm.

Diagnosis. Although the Neotropical *Cetiocyon incantatus* distinctly differs from the otherwise rather uniform-looking New Guinean species in its general appearance, the ventral morphology crucial for generic identification is very conservative in all *Cetiocyon* species and the genus may be therefore easily distinguished by the combination of the following characters: (1) prosternum without median carina; (2) antennal grooves absent; (3) preepisternal plate of mesothorax narrowly elongate oval; (4) anterolateral ridges of metaventrite not arcuately bent posteriorly sublaterally, parallel to posterior margin of mesocoxal cavities; (5) median portion of male sternite 9 crescent-like.



Figs. 11–24. Antenna (11–19), male sternite 8 (20, 21) and trochanter (22–24; ventral view) of *Cetiocyon* species. **11, 21:** *Cetiocyon incantatus*. **12:** *Cetiocyon hanseni*. **13:** *Cetiocyon cribripunctatus*. **14:** *Cetiocyon goliathus*. **15:** *Cetiocyon hebaueri*. **16:** *Cetiocyon loksai*. **17:** *Cetiocyon papuensis*. **18:** *Cetiocyon riedeli*. **19, 20, 22–24:** *Cetiocyon traipela* (22 pro-, 23 meso-, 24 metatrochanter).

Cetiocyon species resemble the following New Guinean and Australian megasternine genera by some characters: (1) *Platycyon*: differs from *Cetiocyon* by carinate prosternum, well-developed antennal grooves and anterolateral ridge of metaventricle bent posteriad sublaterally; (2) New Guinean '*Pelosoma*': differs from *Cetiocyon* by carinate prosternum, well-developed antennal grooves and preepisternal plate of mesothorax widely contacting anteromedian margin of metaventricle; and (3) *Pilocnema*: differs from *Cetiocyon* by carinate prosternum, well-developed antennal grooves, enlarged antennomere 6, ventral face of meso- and metatibiae bearing densely arranged long yellowish setae and median portion of male sternine 9 tongue-like. Besides these characters, all New Guinean *Cetiocyon* species may be distinguished from these genera

by much larger body size, and some of them also by the elongate antennomere 7, presence of tufts of long yellowish setae on male trochanters and head punctures surrounded by opaque porose areas. *Cetiocyon incantatus* cannot be confused with any other Neotropical megasternine species because of its unusual coloration and characteristic antennal morphology. All *Cetiocyon* species may resemble large species of *Cercyon* occurring in the Neotropical, Afrotropical and Oriental Regions (most of them undescribed, some of them currently placed in the subgenus *Clinocercyon* d'Orchymont, 1942), which however differ from *Cetiocyon* by the tongue-shaped median portion of male sternite 9 and the base of the median lobe not being attached to the base of the parameres (and thus freely movable within the tegmen).

4.2. Key to *Cetiocyon* species

- 1 General coloration pale reddish, posterior half of elytra black (Figs. 1, 2). Pronotum widely rounded posterolaterally, without defined corners (Fig. 9). Antennomere 9 long, pointed apically (Fig. 11). Neotropical species. *C. incantatus*
- General coloration dark, elytra unicoloured (e.g., Figs. 3–6). Pronotum with distinctly defined posterolateral corners (Fig. 10). Antennomere 9 slightly projecting apically, but blunt at apex (Figs. 12–19). New Guinean and Australian species. 2
- 2 Antennomere 7 (= basal segment of the club) much longer than wide; pedicel ca. as long as antennomere 3 (Figs. 13–16, 18, 19). Male mesotrochanter with conspicuous tuft of yellowish long hairs (as in Fig. 23). 3
- Antennomere 7 (= basal segment of the club) at most as long as wide; pedicel much longer than antennomere 3 (Figs. 12, 17). Male mesotrochanter with or without conspicuous tuft of yellowish long hairs. 8
- 3 Elytral series sharply impressed on whole elytral surface (Figs. 3, 4). Punctures on the head, pronotum and elytral intervals with or without surrounding porose areas. Male protrochanter with conspicuous tuft of long yellowish hairs (Fig. 22). Lateral portions of median lobe without lateral finger-like projections directed anteriad (Figs. 34, 37). 4
- Elytral series at most indistinctly impressed laterally and apically (Figs. 5, 6). Each puncture on the head surrounded by opaque area (Figs. 7, 51). Male protrochanter without tuft of yellowish hairs. Lateral portions of median lobe projecting into anteriad-directed lobes (Figs. 31, 40, 46). 6
- 4 Large species, body length 7.0–8.0 mm. Head, pronotum and elytra with or without porose areas around punctures. 5
- Moderately large species, body length 4.5–5.5 mm. Punctures on head, pronotum and elytra not surrounded by porose areas. Aedeagus as in Figs. 37, 39. *C. loksai*
- 5 Punctures on the head, pronotum and elytra surrounded by porose areas. [Male unknown.] *C. goliathus*
- Punctures on the head, pronotum and elytra not surrounded by porose areas. Aedeagus as in Figs. 34, 36. *C. traipela*
- 6 Male metatrochanter without tuft of long yellowish setae. Punctures on lateral portions of pronotum surrounded by \pm distinct porose areas. Aedeagus as in Figs. 31, 40. 7
- Male metatrochanter with tuft of long yellowish setae. Punctures on lateral portions of pronotum

without any trace of porose surrounding areas. Aedeagus as in Fig. 46. *C. riedeli*

- 7 Median portion of median lobe narrow, anteriad-directed projections of lateral lobes large, finger-like (Fig. 31). *C. cribripunctatus*
- Median portion of median lobe wide, anteriad-directed projections of lateral lobes small and wide (Fig. 40). *C. hebaueri*
- 8 Mesotrochanter of male with conspicuous tuft of long yellowish hairs (as in Fig. 23). Aedeagus massive; median lobe very wide, narrowing into rounded apex, phallobase with an asymmetrical manubrium basally (Fig. 43). *C. papuensis*
- Mesotrochanter of male without tuft of long yellowish hairs. Aedeagus subtile, median lobe narrow, nearly parallel-sided, phallobase symmetrical basally, without manubrium (Fig. 28). *C. hanseni*

4.3. *Cetiocyon incantatus* spec. nov.

Figs. 1, 2, 9, 11, 21, 25–27, 50, 53, 55

Type locality. Suriname, Brokopondo district, Brownsberg Nature Reserve, Witi Creek Trail, 4°56'55"N 55°10'53"W.

Type material. Holotype σ , 'SURINAME: Brokopondo | Brownsberg Nature Reserve, | Witi Creek Trail, 420 | 4°56'55"N, 55°10'53"W | 22–23 JUN 1999; Z. H. Falin, H. Hiwat | SURIF99 097 ex: flight intercept trap', '[barcode]/ SM0175636/ KUNHM-ENT', 'Holotype | *Cetiocyon incantatus* sp. nov. | Fikáček & Short det. 2009' (KSEM). – Paratypes: 1 sp., same data as holotype (NMPC); 1 sp., same data as holotype, but '23–25 JUN 1999' and 'SURIF99 114' (KSEM); 1 sp., 'SURINAM: Brokopondo | Brownsberg Nat. Reserve | 4°56'55"N, 55°10'53"W | 23.VI.1999, 450 m | Z Falin, FIT #097' (CMN); 1 σ , 'SURINAME: Sipaliwini Dept. | Kutari River, 2°10.521'N | 56°47.244'W, 228 m elev., 19–20.viii.2010 | leg. A.E.Z. Short, human dung, 2010 | CI-RAP Survey, SR10-0819-04A' (NZCS). All paratypes with attached label 'Paratype | *Cetiocyon incantatus* sp. nov. | Fikáček & Short det. 2009/2010'.

Diagnosis. *Cetiocyon incantatus* is easily distinguished from all remaining species of the genus by its general appearance (Figs. 1, 2) and bicolored body, and by the combination of the characters as evident from the key and listed in the following: Body weakly convex in lateral view; elytra bicolored. Punctures on clypeus, frons, pronotum and elytra not surrounded by porose areas. Pedicel much longer than antennomere 3; antennomere 7 as long as wide; antennomere 9 extremely elongate. Posterolateral corners of pronotum rounded. Elytral series of punctures impressed on whole elytral surface. Male trochanters without tufts of long yellowish setae. Phallobase symmetrical, without ba-

sal manubrium; median lobe narrow, lateral margins nearly parallel-sided; lateral projections of median lobe absent; median portion of male sternite 9 U-shaped, lateral struts arcuate.

Description. *Measurements.* Body length 3.8–4.3 mm (holotype: 4.2 mm); body width 2.1–2.4 mm (holotype: 2.4 mm). Eyes separated by $4.9\times$ width of one eye. Length of aedeagus 1.4 mm (holotype: 1.4 mm).

Body shape. Body elongate oval, widest ca. at midlength, weakly convex in lateral view, strongly narrowing posteriad; body outline interrupted between pronotum and elytra.

Coloration. Dorsal side reddish, elytra bicolored with posterior 0.4 of elytra black; serial punctures of elytra darkened. Ventral side of head and thorax reddish, abdominal ventrites black. Antennae, palpi, and fore and middle legs reddish, hind legs brown.

Head. Clypeus with moderately dense punctation consisting of small rounded punctures, each puncture bearing a protruding pale seta; interstices without microsculpture; anterior margin of clypeus indistinctly concave medially, with distinct rim; lateral portion of clypeus not deflexed. Interocular area with two shallow depressions defining a median triangular area. Frons with moderately dense punctation consisting of small rounded punctures; interstices without microsculpture. Head punctures not surrounded by porose areas. Eyes small. Mentum transverse, $1.8\times$ as wide as long; surface with sparse punctation consisting of small setiferous punctures and intermixed minute punctures lacking setae; interstices without distinct microsculpture. Gula moderately wide, indistinctly constricted posteriorly of tentorial pits, gular sutures divergent posteriad. Maxillary palpus with palpomere 2 $1.3\times$ as long as palpomeres 3 and 4 each. Antennal scapus longer than antennomeres 2–6 combined; pedicel much longer than antennomere 3; antennal club compact, $2.9\times$ as long as wide; antennomere 7 ca. as long as wide; antennomere 9 ca. $2\times$ as long as wide, indistinctly constricted subapically, with markedly prolonged pointed apex.

Prothorax. Pronotum not forming continuous curve with elytra in lateral view, evenly convex, with shallow sublateral pit on each side close to posterior margin; arcuately narrowed anteriorly, slightly emarginate on anterior margin, weakly triangular on posterior margin; lateral portions not deflexed, posterolateral corners rounded; lateral margin arcuate with wide and distinct lateral rim. Pronotal punctation sparse, ca. as dense as on frons, consisting of small rounded punctures similar on whole surface of pronotum; each puncture bearing a long fine decumbent seta, porose areas around punctures absent; interstices without microsculpture; transverse row of punctures on posterior margin of pronotum absent. Prosternum without ante-

rior bulge. Prosternal process truncated. Lateral glabrous part of hypomerion rather wide throughout.

Mesothorax. Scutellar shield bearing few minute punctures, interstices without microsculpture. Elytron not deflexed and only very narrowly explanate laterally; elytral series 1–5 and 7 starting basally, series 6 subbasally, series 8 in basal 0.4 of elytron; series 7 and 8 as widely separated from each other as from other series; series 9 abbreviated anteriorly, starting at midlength of elytra, not joining series 8 basally; series 10 developed throughout elytral length. Serial punctures moderately large, rounded, sparsely arranged, much larger than interval punctures, not connected to each other with fine and sharp longitudinal furrow. Elytra not costate; elytral intervals weakly convex at suture, becoming more convex laterad and posteriad; elytral series deeply impressed mesally, becoming slightly more impressed laterad and apicad; interval 2 of the same width and height as interval 3, reaching elytral apex; odd intervals as convex as even ones; interval punctation irregular on all intervals, moderately dense and consisting of fine punctures, each bearing a fine decumbent seta; interval interstices shiny, without microsculpture. Epipleura narrowing posteriad, reaching midlength of metaventrite. Pseudepipleura narrowing posteriad, reaching elytral apex. Preepisternal plate narrow, suboval, $2.7\times$ as long as wide; median part of the elevation slightly convex, bearing densely arranged small rounded setiferous punctures, interstices without microsculpture. Grooves for reception of procoxae small, not reaching anterior margin of mesocoxal cavities.

Metathorax. Metaventrite ca. as long as preepisternal elevation of mesothorax. Punctation of median portion of metaventrite sparse and fine, consisting of small setiferous punctures; interstices without microsculpture. Anterior margin of metaventrite not crenulate. Anepisternum $6.1\times$ as long as wide. Macropterous.

Legs. Rather long, tips of metafemora exceeding body outline. Procoxae without ventral ridge. Tibial grooves absent. All trochanters of male without tufts of long yellowish setae; proximal portions of trochanters without microsculpture, pubescent. Hind tibiae straight. Tarsi slightly shorter than tibiae, bearing long yellowish pubescence ventrally.

Abdomen. Ventrite 1 not crenulate anteriorly; ventrites 2–5 without longitudinal ridges; all ventrites pubescent.

Male genitalia and genital sclerites. Parameres $0.75\times$ as long as phallobase, gradually narrowing from base to apex, bearing a pair of short setae apically. Phallobase narrow, $1.9\times$ as long as wide, straight in lateral view. Median lobe slightly longer than parameres in lateral view, seemingly not overlapping tips of parameres in dorsal view, slightly widening from base towards apex, obtusely pointed with slightly pro-

jecting tip apically, markedly bent dorsad in lateral view; membranous lateral projections absent, lateral crenulate rim of apical portion absent; lateral margin straight, lacking setae; gonopore indistinct, apex of median lobe lacking setae. Sternite 8 with narrow anteromedian projection. Median portion of sternite 9 without anteromedian projection, its median portion deeply U-shaped, lateral struts arcuate.

Variation. None observed.

Collecting circumstances. Four specimens were collected on a summit of a small mountain ridge rising ca. 300 m above the Guyana shield lowlands covered with lowland rainforest. There is only a thin layer of litter over the shallow soil on the summit and the area is covered by wet tropical forest having an appearance similar to montane cloud forests. In spite of the small altitude difference between the locality and the lowland surrounding the ridge, its fauna seems to differ in many aspects from that found in the adjacent lowland forests (Z. Falin, pers. comm.). The specimen collected by A. Short was collected from human dung in lowland Guyana shield forest.

Etymology. *Incantatus* (Latin), enchanting, referring to the extraordinary grooved and colorful external appearance of this species.

Distribution. Known from two localities in Suriname.

4.4. *Cetiocyon hanseni* Hebauer, 2001

Figs. 12, 28–30, 49, 52, 54, 56

Cetiocyon hanseni Hebauer, 2001: 40.

Type locality. Papua New Guinea, Tekadu [near Kokoro], 300 m a.s.l. [ca. 7°49'S 146°33'E].

Type material examined. Holotype ♂, 'PAPUA N. G.: Morobe Prov. | Tekadu, 300 m, light | 28.2.–6.3.1996 | leg. A Riedel', [male symbol], 'HOLOTYPUS | *Cetiocyon* | *hanseni* sp.n. | des. F. Hebauer' (NHMW). – Paratype ♀, same label data as holotype, 'PARATYPUS | *Cetiocyon* | *hanseni* sp.n. | des. F. Hebauer' (FHCP).

Additional material examined. **INDONESIA:** *Papua:* 1 ♂, Hollandia [= Jayapura], 12.ii.[19]45, lgt. H. Hoogstraal (FMNH); 1 sp., Hollandia [= Jayapura], rain forest, v.[19]45, lgt. H. Hoogstraal (FMNH). **PAPUA NEW GUINEA:** *Madang:* 3 ♂♂, 67 spc., Finisterre Mts., Budemu, 4000 ft [1220 m], station no. 67, 15–24.x.1964, lgt. M.E. Bacchus (BMNH, ZMUC, NMPC, KSEM); 1 ♂, 2 spc., same locality and collection, station no. 72, 24.x.1964 (BMNH); 1 ♂, 3 spc., Finisterre Mts., Damanti, 3550 ft [1100 m], station no. 64, 2–11.x.1964,

lgt. M.E. Bacchus (BMNH). **Morobe:** 2 ♂♂, 26 spc., Herzog Mts., Vagau, ca. 4000 ft [1220 m], station no. 142, 4–14.i.1965, lgt. M.E. Bacchus (BMNH); 1 ♂, Gurakor [= Gurukor] env., i.1980, lgt. W.G. Ullrich (ZMUC); 1 ♂, 1 spc., same locality and collector, i.1981 (ZMUC). **Oro:** 1 ♂, Kokoda, 1300 ft [400 m], ix.1933, lgt. L.E. Cheesman (BMNH); 2 ♀♀, same locality and collector, 1200 ft [370 m], vii.1933 (BMNH). **South-eastern Highlands:** 1 ♂, 1 ♀, 6 spc., Papua New Guinea, Chimbu Province, Haia Village, Crater Mountain Research Area, 5–7.vii.2001, 06°42.35'S 145°0.16'E, Whiting et al. lgt. (KSEM, NMPC).

Diagnosis. *Cetiocyon hanseni* is easily distinguished from all remaining species except for *C. papuensis* by antennal morphology (pedicel much longer than antennomere 3, antennomere 7 ca. as long as wide, antennomere 9 not extremely prolonged). From *C. papuensis* it can be reliably distinguished only in males, which have very characteristic male genitalia and lack tufts of setae on mesotrochanters. The two species slightly differ in body shape (elytra rather strongly narrowing posteriad from humeral area in *C. hanseni*, slightly wider and rather arcuately narrowing posteriad in *C. papuensis*) in some cases, but the difference is obscured by the variability of body shape in *C. hanseni* and is therefore not very reliable for identification. Diagnostic characters that in combination allow for identification of *C. hanseni* are as follows: Body highly convex; elytra unicoloured; punctures on head not surrounded by porose areas; pedicel much longer than antennomere 3; antennomere 7 (first club antennomere) ca. as long as wide; antennomere 9 moderately projecting apically, 1.3× as long as wide; all elytral series weakly but sharply impressed; trochanters without tufts of yellowish setae; tibial grooves of femora present; phallobase symmetrical, without basal manubrium; median lobe narrow, lateral margins nearly parallel-sided; lateral projections of median lobe absent; median portion of male sternite 9 V-shaped, lateral struts arcuate.

Redescription. *Measurements.* Body length 4.3–5.2 mm (holotype: 4.4 mm); body width 2.8–3.7 mm (holotype: 2.8 mm). Eyes separated by 4.6× of width of one eye. Length of aedeagus 1.8–2.0 mm (holotype: 2.0 mm).

Body shape. Body widely oval, widest ca. at mid-length, highly convex in lateral view, gradually narrowing posteriad; body outline not interrupted between pronotum and elytra.

Coloration. Dorsal side dark brown, clypeus and lateral margins of pronotum and elytra reddish brown, elytra unicolored. Ventral side, coxae, femora, tibiae and antennal clubs brown, antennomeres 1–6 and maxillary palpi pale reddish.

Head. Clypeus with sparse punctation consisting of small rounded punctures slightly varying in size

and lacking setae, interstices without microsculpture; anterior margin slightly convex, with distinct rim, lateral portions slightly deflexed. Interocular area without depressions. Frons with sparse punctation consisting of small rounded punctures, interstices without microsculpture. All punctures on dorsal surface not surrounded by porose areas. Surface of mentum flat, with moderately dense setiferous punctation; interstices with weak mesh-like microsculpture anteriorly and laterally. Gula very narrow, constricted posteriorly of tentorial pits, gular sutures widely divergent posteriorly. Maxillary palpus with palpomere 2 $1.7\times$ as long as palpomeres 3 and 4 each. Antennal scapus longer than antennomeres 2–6 combined; pedicel longer than antennomere 3; antennomere 7 ca. as long as wide; antennomere 9 $1.3\times$ as long as wide, constricted subapically, blunt on apex.

Prothorax. Pronotum evenly convex, forming continuous curve with elytra in lateral view, widest posteriorly, arcuately narrowed anteriorly, slightly emarginate on anterior margin, continuously arcuate on posterior margin; lateral margins not deflexed, posterolateral corners forming obtuse angles; lateral margin arcuate, bearing narrow marginal rim. Pronotal punctation ca. as dense as on frons, consisting of very small rounded punctures similar on whole surface; punctures not surrounded by porose areas, lacking setae, interstices without microsculpture; transverse row of punctures on posterior margin of pronotum hardly defined. Prosternum bearing low anteromedian bulge. Prosternal projection cut off. Lateral glabrous part of hypomeron very narrow anteriorly, strongly widened posteriorly.

Mesothorax. Scutellar shield bearing sparse and fine punctation; interstices without microsculpture. Elytron not deflexed or explanate laterally; series 1–7 starting basally, series 8 subbasally; series 7 and 8 as widely separated from each other as from other series; series 9 abbreviated anteriorly, starting in basal 0.2 of elytral length, not joining series 8 anteriorly; series 10 developed throughout elytral length. Serial punctures small, rounded, sparsely arranged, slightly larger than interval punctures; lateral serial punctures connected to each other by a fine and sharp longitudinal furrow. Elytral intervals weakly convex at suture; becoming more convex laterad and posteriorly; elytral series not impressed mesally, becoming slightly more impressed laterad and apicad; elytral interval 2 of the same width and height as intervals 1 and 3, reaching elytral apex; intervals 5, 7 and 9 as convex as adjacent intervals; punctation on all intervals irregular, consisting of sparsely arranged minute punctures lacking setae. Elytral interstices shiny, without microsculpture. Epipleura narrowing toward level of mesoventrite, reaching elytral apex; pseudepipleura wide and strongly oblique basally, narrowing posteriorly, reaching elytral apex. Preepisternal plate narrow, suboval, $5.3\times$ as long as wide; median

part flat; bearing sparsely arranged, small rounded setiferous punctures; interstices without microsculpture. Grooves for reception of procoxae moderately large, not reaching anterior margin of mesocoxal cavities.

Metathorax. Metaventricle ca. as long as preepisternal elevation of mesothorax. Punctation of median portion of metaventricle moderately dense, consisting of small setiferous punctures; interstices without microsculpture. Anterior margin of metaventricle not crenulate. Anepisternum $9\times$ as long as wide. Macropterous.

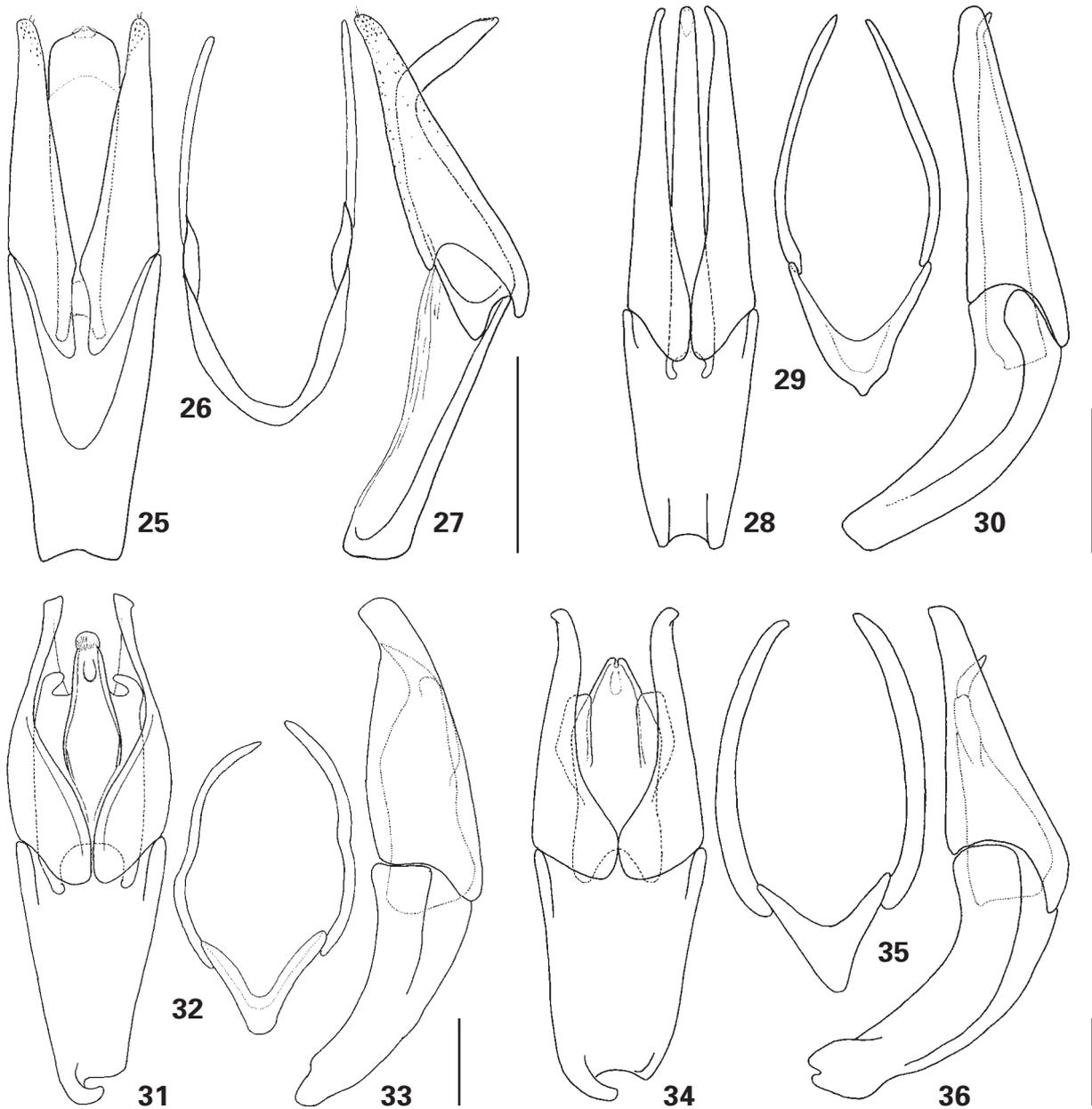
Legs. Short, tips of metafemora not exceeding body outline. Procoxae without ventral ridge. All trochanters of males without tufts of long yellowish setae; proximal portions of trochanters sparsely pubescent, not microsculptured. Tibial grooves on femora present. Hind tibiae slightly curved outwards (Fig. 56). Tarsi slightly shorter than tibiae, sparsely pubescent ventrally.

Abdomen. Ventricle 1 finely crenulate anteriorly; ventrites 2–5 without longitudinal ridges; all ventrites densely pubescent.

Male genitalia and genital sclerites. Phallobase symmetrical, without basal manubrium, arcuately bent in lateral view. Parameres gradually narrowing from base to apex, slightly bent inwards apically. Median lobe narrow, indistinctly narrowing from base to apex, lacking lateral projections; apex not divided apically; gonopore subapical. Sternite 8 with narrow median projection. Median portion of sternite 9 V-shaped, without median tongue-like projection; lateral struts arcuate.

Variation. The species is rather variable especially in body size (see “Measurements”) and shape. In most specimens examined (including the holotype), the elytra are rather strongly narrowing posteriorly of the humeral area, but in some specimens the elytra are rather weakly and arcuately narrowing posteriorly (resembling all remaining species of the genus). Specimens with different body size as well as with different elytral shape have totally identical aedeagus and do not differ in any other relevant character; for that reason, the variability of body shape is considered as intraspecific.

Distribution. Known from several localities in the eastern part of the central mountain range and in the Finisterre mountain range in Papua New Guinea. A single specimen is known from Jayapura (Indonesia) at the northern coast of the island.



Figs. 25–36. Male genitalia of *Cetiocyon* species, aedeagus in dorsal view (25, 28, 31, 34) and lateral view (27, 30, 33, 36), and sternite 9 (26, 29, 32, 35). **25–27:** *Cetiocyon incantatus*. **28–30:** *Cetiocyon hanseni*. **31–33:** *Cetiocyon cribripunctatus*. **34–36:** *Cetiocyon traipela*. Scale bars: 0.5 mm.

4.5. *Cetiocyon cribripunctatus* spec. nov.

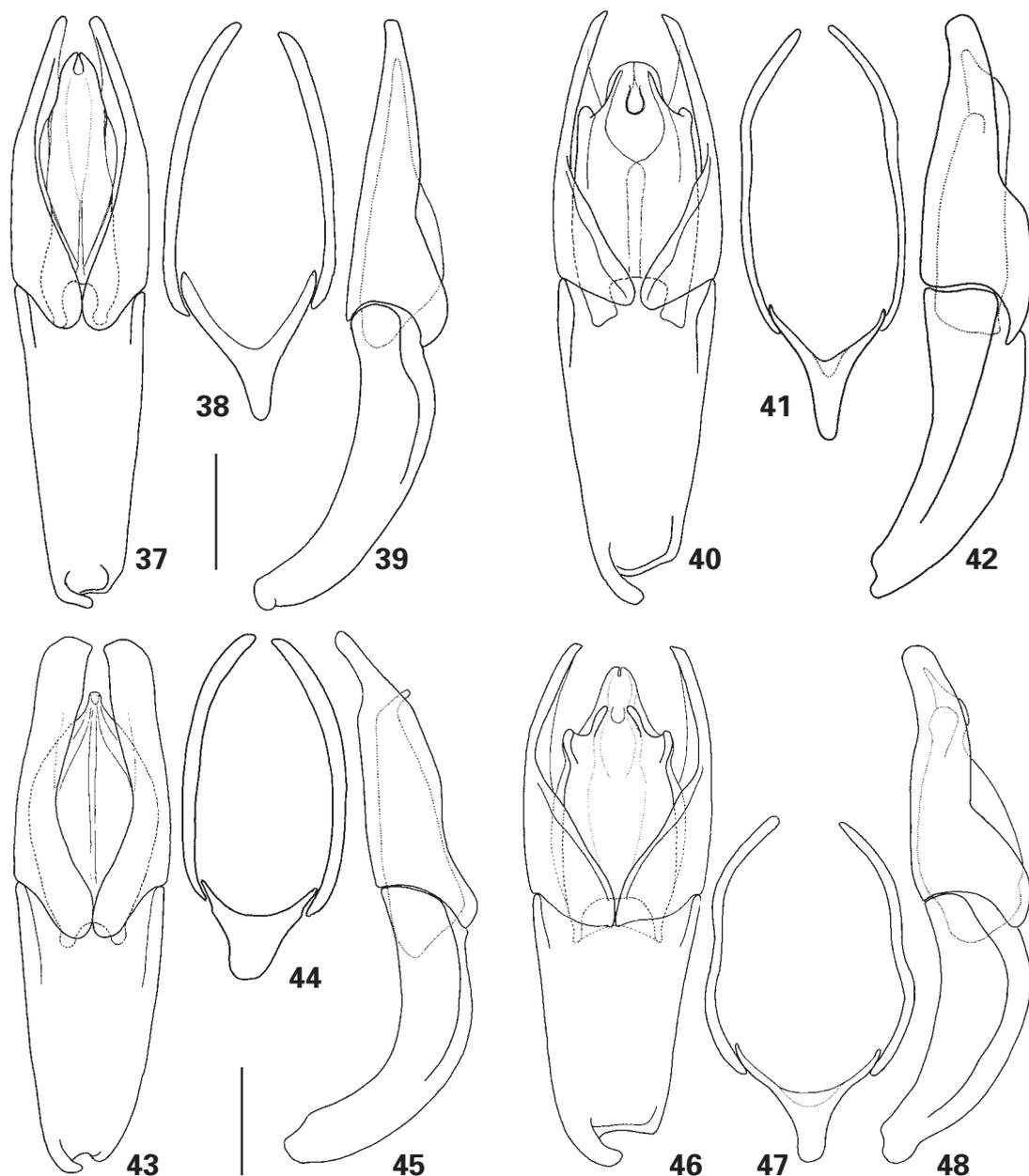
Figs. 7, 13, 31–33, 51

Type locality. Indonesia, Papua province, Baliem valley, Jiwika-Wandaku, 1700–2300 m a.s.l. [3°57.043'S 138°57.410'E].

Type material. Holotype ♂, 'Irian Jaya: Baliem- l Tal, Jiwika-Wandaku l 5.–6.9.1990 1700– l leg. A. RIEDEL 2300m', 'Cetiocyon l loksai m. l det. F. Hebauer', 'Holotype l Cetiocyon l cribripunctatus sp. nov. l M. Fikáček det. 2010' (SMNS). – Paratypes 2 ♂♂, 2 ♀♀: same label data as holotype, 'Paratype l Cetiocyon l cribripunctatus sp. nov. l M. Fikáček det. 2010' (NMPC, KSEM, FHCP).

Diagnosis. By the antennal morphology (elongate antennomere 7) and not impressed mesal elytral series, *C. cribripunctatus* is extremely similar to *C. hebaueri* and *C. riedeli*; from *C. riedeli* it differs by presence of porose areas around pronotal punctures and the absence of tufts of hairs on male metatrochanters. From both species it can be distinguished by the morphology of male genitalia.

Description. Measurements. Body length 5.0–5.5 mm (holotype: 5.0 mm); body width 3.4–3.6 mm (holotype: 3.4 mm). Eyes separated by 5.8× width of one eye. Length of aedeagus 2.8–3.0 mm (holotype: 2.8 mm).



Figs. 37–48. Male genitalia of *Cetiocyron* species, aedeagus in dorsal view (37, 40, 43, 46) and lateral view (39, 42, 45, 48), and sternite 9 (38, 41, 44, 47). 37–39: *Cetiocyron loksai*. 40–42: *Cetiocyron hebaueri*. 43–45: *Cetiocyron papuensis*. 46–48: *Cetiocyron riedeli*. Scale bars: 0.5 mm.

Morphology. Fully conforming with the description for *C. hanseni*, but with the following differences: Body highly convex in lateral view; elytra unicoloured. Punctures on clypeus, frons and lateral portions of pronotum surrounded by porose areas. Pedicel slightly longer than antennomere 3; antennomere 7 elongate, 1.3× as long as wide. Elytral series indistinctly impressed laterally and apically. Male mesotrochanters each with tuft of long yellowish setae; pro- and metatrochanters without such tufts.

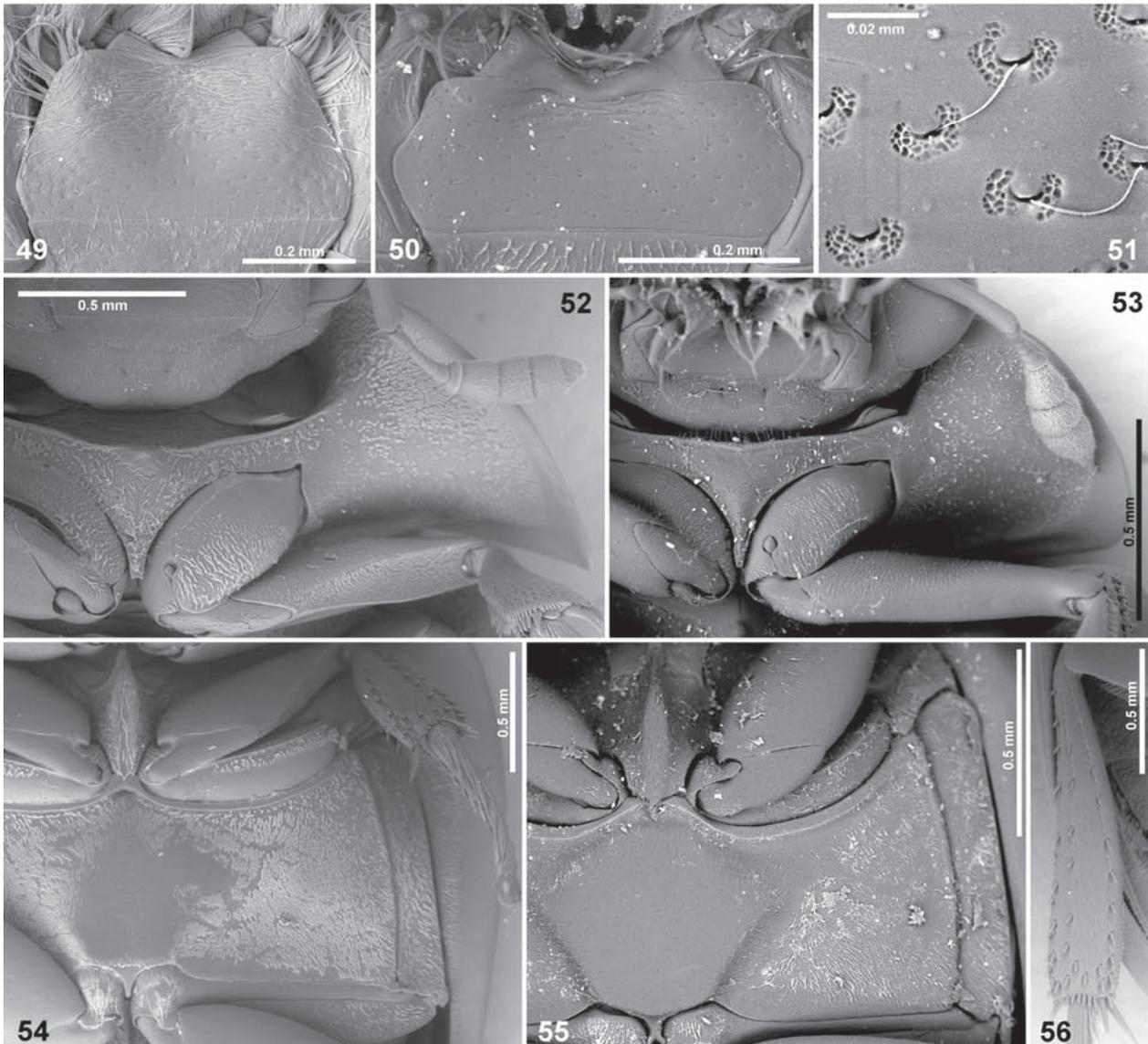
Male genitalia and genital sclerites. Phallobase with large asymmetrical manubrium. Parameres narrowly spatulate apically. Median lobe very wide basally, with anteriad directed finger-like lateral projections;

apex of median lobe unilobate, gonopore subapical, very distinct. Sternite 8 with narrow anteromedian projection. Median portion of sternite 9 V-shaped, lateral struts sinuate.

Variation. None observed.

Etymology. Species name is derived from Latin *cribrum* (sieve) and *punctatum* (punctate), referring to the pronotal and head punctures which are surrounded by a porose area in this species.

Distribution. Known only from the type locality.



Figs. 49–56. Morphological details of *Cetiocyon hanseni* (49, 52, 54, 56), *Cetiocyon incantatus* (50, 53, 55) and *Cetiocyon cribripunctatus* (51). **49, 50:** Mentum. **51:** Several punctures on frons. **52, 53:** Prothorax and antenna, ventral view. **54, 55:** Meso- and metathorax, ventral view. **56:** Metatibia, ventral view.

4.6. *Cetiocyon goliathus* (Huijbregts, 1984)

Fig. 14

Cercyon goliathus Huijbregts, 1984: 179.

Cetiocyon goliathus: HANSEN (1990: 346; 1999a: 272),
HEBAUER (2001: 39).

Type locality. Indonesia, Papua province, ‘Moss Forest Camp’ [= near the upper reaches of Baliem riv., ca. 4°15’S 139°00’E, cf. TOXOPEUS (1940) and HANSEN (1999a)].

Type material. Holotype, 1 ♀, [‘female symbol’]!, ‘Neth. Ind. Amer. New Guinea Exped. 2500–1 2800 m. Moss Forest Camp. 9.x.–5.xi.1938 | L. J. Toxopeus leg.’, ‘Cercyon | goliathus | Huijbregts’, ‘Museum Leiden | HOLOTYPE | Cercyon | goliathus | Huijbregts’, ‘Cetiocyon’, ‘Holotype’ (RMNH).

Diagnosis. By large body size, weakly convex elytra and distinctly impressed elytral series, *C. goliathus* is similar to *C. traipela*; it differs from it by the presence of porose areas around the punctures of clypeus, frons, whole pronotal surface and all elytral intervals.

Description. Measurements. Body length 7.2 mm; body width 4.7 mm. Eyes separated by 5.6× width of one eye.

Morphology. Fully conforming with the description for *C. hanseni*, but with the following differences: Body highly convex in lateral view; elytra unicoloured. Punctures on clypeus, frons, whole surface of pronotum and elytral intervals surrounded by porose areas. Pedicel as long as antennomere 3; antennomere 7 elongate, 1.5× as long as wide. Elytral series distinctly impressed on whole elytral surface.

Male genitalia and genital sclerites. Male unknown.

Variation. Unknown.

Collecting circumstances. TOXOPEUS (1940) characterises the collecting site as follows: ‘High mountain moss forest, of mainly *Sycopsis* (?) trees, few conifers, thick undergrowth of orchids and ferns. At hundred meters lower down local change into richer vegetation without thick moss, due to sheltered position’. The holotype was collected during the rainy season.

Distribution. Known only from the type locality.

4.7. *Cetiocyon hebaueri* spec. nov.

Figs. 15, 40–42

Type locality. Indonesia, Papua Province, Jayawijaya, Nalca env., Galbok, 1700–1800 m a.s.l.

Type material. Holotype ♂, ‘Irian Jaya: Jayawi- | Galbok b. Nalca | 3.10.1993 1700– | leg. A. RIEDEL 1800m’, ‘*Cetiocyon* | *loksai* m. | det. F. Hebauer’, ‘Holotype | *Cetiocyon* | *hebaueri* sp. nov. | M. Fikáček det. 2010’ (SMNS). – Paratype: 1 ♀, same label data as holotype, ‘Paratype | *Cetiocyon* | *hebaueri* sp. nov. | M. Fikáček det. 2010’ (FHCP).

Diagnosis. By the antennal morphology (elongate antennomere 7) and not impressed mesal elytral series, *C. hebaueri* is extremely similar to *C. cribripunctatus* and *C. riedeli*; from *C. riedeli* it differs by presence of porose areas around pronotal punctures and the absence of tufts of hairs on male metatrochanters. It can be distinguished from both species by the morphology of male genitalia.

Description. Measurements. Body length 5.8–6.9 mm (holotype: 5.8 mm); body width 3.8–4.2 mm (holotype: 3.8 mm). Eyes separated by 7.0× width of one eye. Length of aedeagus of holotype 2.6 mm.

Morphology. Fully conforming with the description for *C. hanseni*, but with the following differences: Body highly convex in lateral view; elytra unicoloured. Punctures on clypeus and frons surrounded by porose areas, punctures on lateral portion of pronotum surrounded by small porose areas. Pedicel slightly longer than antennomere 3; antennomere 7 elongate, 1.3× as long as wide. Elytral series indistinctly impressed laterally and apically. Male mesotrochanters each with tuft of long yellowish setae; pro- and metatrochanters without such tufts.

Male genitalia and genital sclerites. Phallobase with large asymmetrical manubrium. Parameres nar-

rowly spatulate apically. Median lobe very wide basally, bearing antieriad directed finger-like lateral projections, without constriction just below these projections; apex of median lobe bilobate, gonopore subapical, very distinct. Sternite 8 with narrow median projection. Median portion of sternite 9 V-shaped, lateral struts sinuate.

Variation. No variation was observed in the specimens examined.

Etymology. The species is dedicated to F. Hebauer (Germany), a specialist in hydrophilid beetles, as a thankyou for his support of our studies.

Distribution. Known only from the type locality.

4.8. *Cetiocyon loksai* Hebauer, 2001

Figs. 8, 10, 16, 37–39

Cetiocyon loksai Hebauer, 2001: 40.

Type locality. Papua New Guinea, Morobe Province, Mindik [W of Pindiu], 1400–1550 m a.s.l. [ca. 6°27.380’S 147°25.099’E].

Type material examined. Holotype ♂, ‘PAPUA N. G.: Morobe Prov. | Mindik, 1400–1550 m | 27.4.1998 | leg. A. Riedel’, [male symbol], ‘HOLOTYPE | *Cetiocyon* | *loksai* sp.n. | des. F. Hebauer’ (NHMW). – Paratype ♀, same label data as holotype, ‘PARATYPE | *Cetiocyon* | *loksai* sp.n. | des. F. Hebauer’ (FHCP).

Additional material examined. PAPUA NEW GUINEA: *Morobe*: 1 ♂, 5 spc., Finisterre Mts., Moro, ca. 5550 ft. [1700 m], station no. 85, 30.x.–15.xi.1964, lgt. M.E. Bacchus (BMNH, NMPC); 1 ♂, 3 spc., same locality, date and collector, station no. 111 (BMNH).

Diagnosis. *Cetiocyon loksai* is most similar to *C. traipela* based on the external characters (antennal morphology, impressed elytral series, punctuation of dorsal surface); see the identification key for diagnostic characters. Habitually, *Cetiocyon loksai* is similar to *C. hanseni* and *C. papuensis*, from which it differs by the elongate antennomere 7 and pedicel as long as antennomere 3.

Description. Measurements. Body length 5.0–5.8 mm (holotype: 5.8 mm); body width 3.2–4.0 mm (holotype: 3.7 mm). Eyes separated by 5.0× width of one eye. Length of aedeagus 2.5–2.6 mm.

Morphology. Fully conforming with the description for *C. hanseni*, but with the following differences: Body highly convex in lateral view; elytra unicoloured. Punctures on clypeus, frons, pronotum and elytra not

surrounded by porose areas. Pedicel as long as antennomere 3; antennomere 7 elongate, 1.2× as long as wide. Elytral series distinctly impressed on whole elytral surface. Male pro- and mesotrochanters each with tuft of long yellowish setae, metatrochanters bare.

Male genitalia and genital sclerites. Phallobase with large asymmetrical manubrium. Parameres blunt at apex, nearly straight in apical third. Median lobe moderately wide basally, with small lateral lobes; apex of median lobe bilobate, gonopore subapical, indistinct. Sternite 8 with narrow median projection. Median portion of sternite 9 V-shaped, lateral struts arcuate.

Variation. None observed in the examined specimens.

Distribution. Known from few localities of the Finis-terre mountain range and the adjacent part of the central mountain range of New Guinea.

4.9. *Cetiocyon papuensis* (d'Orchymont, 1924) Figs. 17, 43–45

Cercyon papuensis d'Orchymont, 1924: 29.

Cetiocyon papuensis: HANSEN (1990: 346), HANSEN (1999a: 272), HEBAUER (2001: 41).

Type locality. New Guinea, Dory [= Indonesia, West Papua, Manokwari].

Type material examined. Holotype ♀, 'Type', '59-58 Dory, | New Guinea', 'Cercyon | papuensis | Orch.', 'Cetiocyon papuensis | Orch. | det. M. Hansen 1989'.

Additional material examined. INDONESIA: *Papua*: 1 spc., 'Cotype', 'Dorey | N. Guinea | Wallace', 'Dor.', '63-106', 'Cercyon | papuensis | Orch.', 'Cetiocyon papuensis | Orch. | det. M. Hansen 1988', 'Cetiocyon | papuensis | (d'Orchymont, 1924) | M. Fikáček det. 2010', 'this is not the type | specimen! | M. Fikáček labelled 2010' (BMNH); 1 ♂, 'Dorey | Wallace', 'Sharp Coll. | 1905-313', 'Cercyon | papuensis Orchym. | Det. J. Huijbregts 1985' (BMNH). **Without precise locality:** 1 ♂, 'Papua', 'New Guinea', 'Sharp Coll. | 1905-313', "'no-vaguineesis'" (BMNH); 1 ♀, 'Papua', 'Sharp Coll. | 1905-313'.

Diagnosis. *Cetiocyon papuensis* is very similar to *C. hanseni*, from which it can be reliably distinguished only by the male genitalia and pubescence of male trochanters. For details, see *C. hanseni* above.

Description. Measurements. Body length 4.5–5.2 mm (holotype: 5.2 mm); body width 2.7–3.2 mm (holotype: 3.2 mm). Eyes separated by 5.0× width of one eye. Length of aedeagus 2.2–2.3 mm.

Morphology. Fully conforming with the description for *C. hanseni*, but with the following differences: Body highly convex in lateral view; elytra unicoloured. Punctures on clypeus, frons, pronotum and elytra not surrounded by porose areas. Pedicel much longer than antennomere 3; antennomere 7 ca. as long as wide. Elytral series distinctly impressed on whole elytral surface. Male mesotrochanters each with tuft of long yellowish setae, pro- and metatrochanters bare.

Male genitalia and genital sclerites. Phallobase with moderately large asymmetrical manubrium. Parameres wide throughout, blunt at apex. Median lobe moderately wide basally, strongly widened to mid-length, gradually narrowing into blunt narrow tip in apical half; apex of median lobe unilobate, gonopore apical, distinct. Sternite 8 with narrow median projection. Median portion of sternite 9 V-shaped, lateral struts arcuate.

Variation. No variation was observed in the examined specimens.

Distribution. Known only from the historical specimens collected in Manokwari in western-most New Guinea.

4.10. *Cetiocyon riedeli* spec. nov. Figs. 5, 6, 18, 46–48

Type locality. Indonesia, Papua province, Baliem valley, Jiwika-Wandaku, 1900–2300 m a.s.l. [ca. 3° 57.043'S 138° 57.410'E].

Type material. Holotype ♂, 'Irian Jaya: Baliem- | Tal, Jiwika-Wandaku | 5.-6.9.1990 1900- | leg. A. Riedel 2300 m', 'Cetiocyon | loksai m. | det. F. Hebauer', 'Holotype | Cetiocyon | riedeli sp. nov. | M. Fikáček det. 2010' (SMNS). – Paratypes. 1 ♂, same label data as holotype, only with altitudes '1700–12300 m' (NMPC); 1 ♂, 'New Guinea | Wabuang | 24.7.1974', 'H. Ohlmus | collector', 'ANIC | specimen' (ANIC). Both paratypes with label 'Paratype | Cetiocyon | riedeli sp. nov. | M. Fikáček det. 2010'.

Diagnosis. *Cetiocyon riedeli* is extremely similar to *C. cribripunctatus* and *C. hebaueri* by its body shape, antennal morphology and not impressed mesal elytral series. It differs from both of them by the presence of tufts of hairs on male metatrochanters, absence of porose areas around pronotal punctures and by the morphology of the aedeagus.

Description. Measurements. Body length 5.4–6.0 mm (holotype: 6.0 mm); body width 3.7–4.1 mm (holo-

type: 4.1 mm). Eyes separated by $5.7\times$ width of one eye. Length of aedeagus 2.2–2.7 mm.

Morphology. Fully conforming with the description for *C. hanseni*, but with the following differences: Body highly convex in lateral view; elytra unicoloured. Punctures on clypeus and frons surrounded by porose areas, pronotal and elytral punctation without porose areas. Pedicel slightly longer than antennomere 3; antennomere 7 elongate, $1.3\times$ as long as wide. Elytral series indistinctly impressed laterally and apically. Male meso- and metatrochanters each with tuft of long yellowish setae, prothrochanters bare.

Male genitalia and genital sclerites. Phallobase with large asymmetrical manubrium. Parameres narrowly spatulate apically. Median lobe wide basally, bearing antieriad directed finger-like lateral projections and small dorsal submedian projections; median lobe constricted just below lateral projections; apex of median lobe bilobate, gonopore subapical, distinct. Sternite 8 with narrow median projection. Median portion of sternite 9 V-shaped, lateral struts sinuate.

Variation. None observed in the examined specimens.

Etymology. The species is dedicated to A. Riedel (Germany) who collected the type specimens of the majority of known New Guinean species of the genus *Cetiocyon*.

Distribution. Known from two distant localities (Indonesia: Papua Province; Papua New Guinea: Enga Province) in central mountain range of New Guinea.

4.11. *Cetiocyon traipela* spec. nov.

Figs. 3, 4, 19, 20, 22–24, 34–36

Type locality. Papua New Guinea, Eastern Highlands Province, Kainantu area, Onerunka (in valley of upper Ramu river).

Type material. Holotype ♂, 'PAPUA N. GUINEA | Onerunka | nr Kainantu XII 80 | W. G. Ullrich', 'Holotype | *Cetiocyon traipela* sp. nov. | M. Fikáček det. 2010' (ZMUC). – Paratypes. 1 ♀, same label data as holotype (ZMUC); 1 ♂, 'NEW GUINEA: NE | Wau, Nami Ck. | 1700–1850m | II. 1966', 'J. Sedlacek | Collector | BISHOP MUS.' (BMH); 1 ♀, 'NEW GUINEA: | E. Highland Dist., | Waisa Nr. Okapa | c. 5000 ft, 15.ii.1965', 'M.E. Bacchus | B.M. 1965-120', 'Stn. No. | 193' (BMNH); 1 ♀, [female symbol], 'TERR. PAPUA | & NEW GUINEA: | Moke | 1.x.1957 | J. Smart', 'Brit. Mus. | 1957-693', *Cercyon* nr | *goliathus* Huijbr. | Det. J. Huijbregts 1985' (BMNH). All paratypes with label 'Paratype | *Cetiocyon traipela* sp. nov. | M. Fikáček det. 2010'.

Diagnosis. *Cetiocyon traipela* is easily distinguished from most *Cetiocyon* species except *C. goliathus* by its large body size (see the latter species for diagnostic characters). Based on its antennal morphology and distinctly impressed elytral series, it may be also confused with *C. loksai*, which is much smaller, lacks the tufts of long yellowish setae on male metatrochanters and has a more elongate aedeagus with parameres not bent outwards apically.

Description. Measurements. Body length 7.4–8.0 mm (holotype: 8.0 mm); body width 4.4–4.7 mm (holotype: 4.5 mm). Eyes separated by $6.0\times$ width of one eye. Length of aedeagus 2.8–2.9 mm.

Morphology. Fully conforming with the description for *C. hanseni*, but with the following differences: Body weakly convex in lateral view; elytra unicoloured. Punctures on clypeus, frons, pronotum and elytra not surrounded by porose areas. Pedicel as long as antennomere 3; antennomere 7 elongate, $1.7\times$ as long as wide. Elytral series distinctly impressed on whole elytral surface. Male pro-, meso- and metatrochanters each with tuft of long yellowish setae.

Male genitalia and genital sclerites. Phallobase with large asymmetrical manubrium. Parameres blunt at apex, slightly bent outwards apically. Median lobe very wide basally, with large lateral lobes lacking antieriad directed projections; apex of median lobe bilobate, gonopore subapical, indistinct. Sternite 8 with narrow median projection. Median portion of sternite 9 V-shaped, lateral struts arcuate.

Variation. None observed in the specimens examined.

Etymology. *Traipela* (in pidgin English used in Papua New Guinea) means large, reflecting the body size of this species. Used as noun in apposition.

Distribution. Known from the Provinces of Madang and Eastern Highlands in central Papua New Guinea; all localities are situated at altitudes between 1500 and 1900 m a.s.l.

4.12. Unidentified specimens from Australian Region

Only females are available from the following collecting events and the exact identification of these specimens is therefore not currently possible with confidence. The specimen from Australia (Queensland) was identified as *Cetiocyon papuensis* by HANSEN (1990). Its assignment to this species is improbable based on the different condition of the

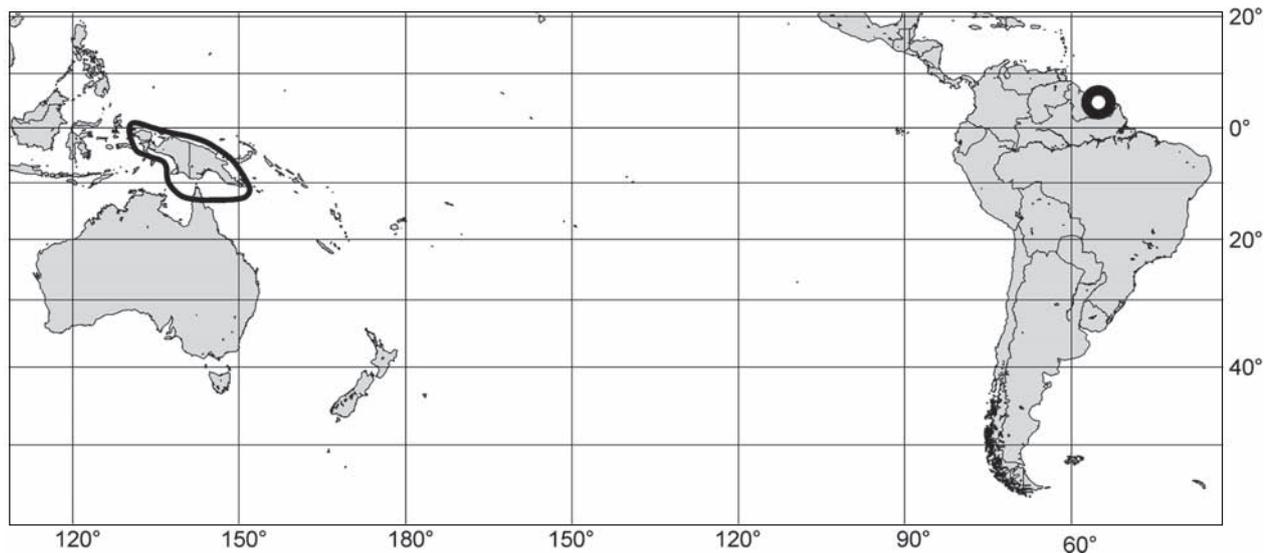


Fig. 57. General distribution of the genus *Cetiocyon*. Bold-line: known distribution in Australian Region. Empty circle: *Cetiocyon incantatus*.

punctuation of elytral series and on the fact that *C. papuensis* is only known from the extreme northwest of New Guinea. It may rather represent an undescribed species, but this has to be confirmed by the examination of males.

Material examined. INDONESIA: West Papua: 1 ♀, Mokwam (Siyoubrig), 1400–1800 m, 1°06.26'S 133°54.41'E, 24.–28.ii.2007, lgt. A. Skale (ASCH) [undescribed species close to *C. goliathus* and *C. traipela*]; 1 ♀, same locality data (ASCH) [close to *C. riedeli*]; 1 ♀, 5 km W of Fakfak [= Fak-fak], 8.vii.1996, lgt. Schüle & Stüben (FHCP) [close to *C. papuensis* and *C. hanseni*]. **Papua:** 2 ♀♀, Netherlands Indian-American Expedition, Araucaria Camp [= ca. 3°27'S 138°43'E; TOXOPEUS (1940)], iii.1939, lgt. L.J. Toxopeus (RMNH) [close to *C. loksai*]; 1 ♀, same locality data (RMNH) [close to *C. hanseni*]; 3 ♀♀, Netherlands Indian-American Expedition, Mist Camp [= ca. 3°22'S 138°17'E; TOXOPEUS (1940)], 1800 m, i.1939, lgt. L.J. Toxopeus (RMNH) [close to *C. cribripunctatus* and *C. hebaueri*]; 1 ♀, Cyclops Mts., Sabron Camp 2, 2000 ft [600 m], v.1936, lgt. L.E. Cheesman (BMNH) [close to *C. hanseni*]; 1 ♀, Jajawijaya, Wameana, Jiwika, 2300 m, 29.ix.1992, lgt. A. Riedel (FHCP) [close to *C. cribripunctatus* and *C. riedeli*]; 1 ♀, Nabire area, road Nabire-Ilaga, km 54, 3°29'517"S [sic!] 135°43'913"E [sic!], 750 m, iv.1998, lgt. M. Balke (FHCP) [close to *C. loksai*]; 1 ♀, same locality data (FHCP) [close to *C. hanseni* and *C. papuensis*]. **PAPUA NEW GUINEA: Madang:** 2 ♀♀, Finisterre Mts., Budemu [= Butemu], 4000 ft [1200 m], station no. 52, 15–24.x.1964, lgt. M.E. Bacchus (BMNH) [close to *C. hanseni* and *C. papuensis*]. **National Capital District:** 1 ♀, Bisiatabu, Port Moresby, W.N. Lock (ZMUC) [close to *C. hanseni* and *C. papuensis*]. **Without precise locality:** 1 ♀, Papua New Guinea (BMNH) [close to *C. hanseni* and *C. papuensis*]. **AUSTRALIA: Queensland:** 1 ♀, Iron Ra., S. slope of Mt. Lamond, rainforest, berlesate, ANIC. 314, lgt. R.W. Taylor & J. Feehan (ZMUC) [close to *C. hanseni* and *C. papuensis*].

5. Phylogenetic analysis

5.1. Characters used for the phylogenetic analysis

1. Body length in mm. Treated as a continuous character. Mapped on the trees (Figs. 59, 60) using the following intervals: (0) 1.2–1.8 mm; (1) 2.0–3.0 mm; (2) 3.1–4.2 mm; (3) 4.3–5.0 mm; (4) 5.1–6.9 mm; (5) 7.2–8.0 mm.
2. Relative convexity of the body; counted as length of pronotum and elytra combined divided by maximum height of elytra in lateral view. Treated as continuous character. Mapped on the trees (Figs. 59, 60) using the following intervals: (0) 2.1–2.2; (1) 2.3–2.5; (2) 2.6–2.8; (3) > 3.0.
3. Head punctures: (0) surrounded by porose areas (Figs. 7, 51); (1) not surrounded by porose areas (Fig. 8).
4. Anterolateral membranous lobes of mentum: (0) absent; (1) present (Figs. 49, 50).
5. First club antennomere: (0) ca. as long as wide (Figs. 11, 12, 17); (1) distinctly elongate (Figs. 13–16, 18, 19).
6. Pedicel: (0) as long as antennomere 3 (Figs. 13–16, 18, 19); (1) much longer than antennomere 3 (Figs. 11, 12, 17).
7. Ultimate antennomere: (0) with long apical projection (Fig. 11); (1) not extremely projecting apically (Figs. 12–19).
8. Median portion of prosternum: (0) with median keel; (1) at most weakly tectiform, but without median keel (Figs. 52, 53).

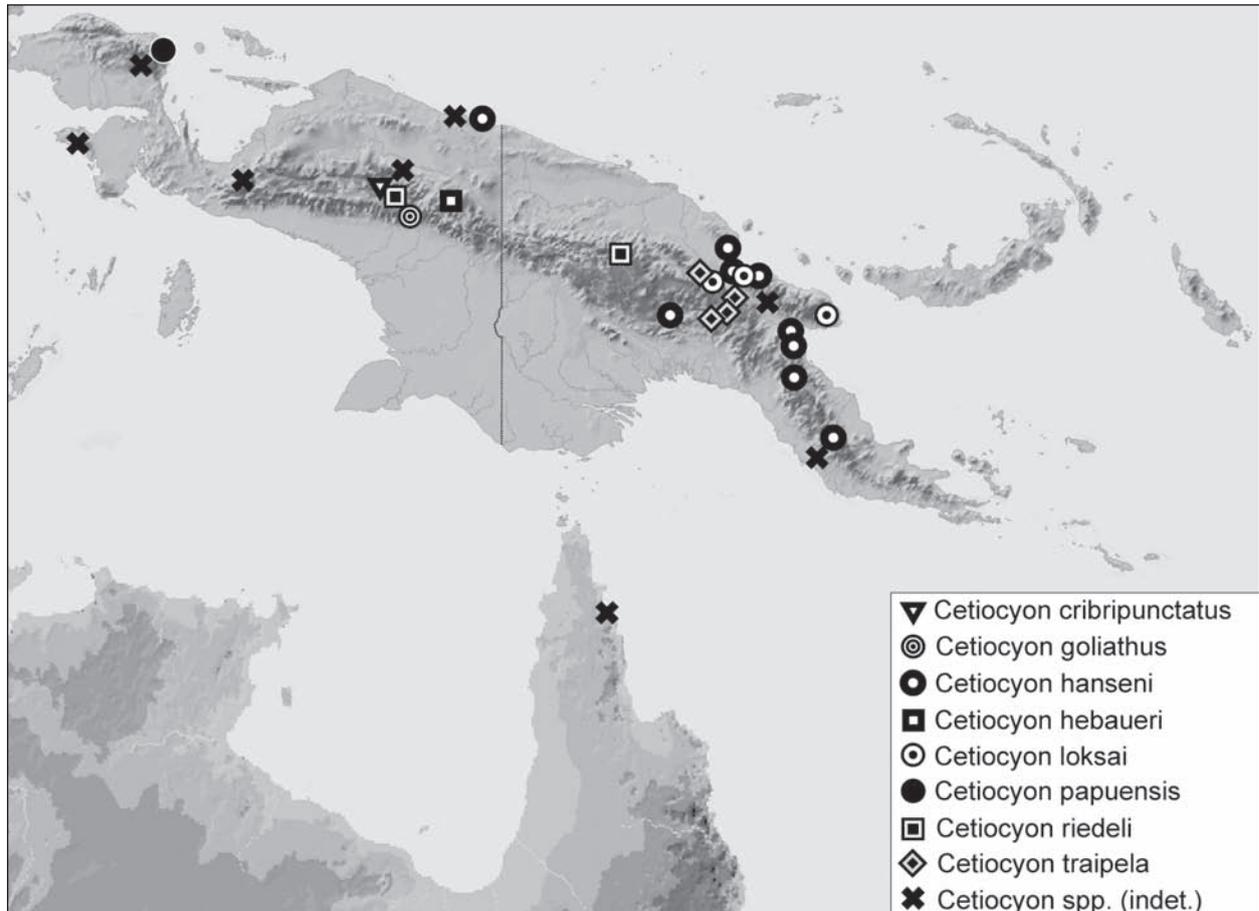


Fig. 58. Known distribution of the *Cetiocyon* species in the Australian Region.

9. Prosternal process: (0) deeply emarginate; (1) not deeply emarginate (Figs. 52, 53).
10. Antennal grooves: (0) absent (Figs. 52, 53); (1) present.
11. Size of antennal grooves: (0) extremely small (occupying much less than half of the width of the hypomeron); (1) moderately large (occupying at least half of the width of the hypomeron).
12. Lateral margin of antennal grooves: (0) rounded; (1) angular.
13. Pronotal punctures (at least those on lateral portions of pronotum): (0) surrounded by porose areas (as in Fig. 51); (1) not surrounded by porose areas.
14. Posterolateral corners of pronotum: (0) rounded (Fig. 9); (1) angulate (Fig. 10).
15. Elytral series 1–2: (0) not impressed into grooves (Fig. 5); (1) impressed into grooves (Figs. 1, 3).
16. Punctures of elytral intervals: (0) not surrounded by porose areas; (1) surrounded by porose areas (as in Fig. 51).
17. Preepisternal elevation of mesothorax: (0) narrow posteriorly (Figs. 54, 55); (1) wide posteriorly.
18. Preepisternal elevation of mesothorax: (0) overlapping over metaventricle margin; (1) not overlapping over metaventricle margin.
19. Anterolateral ridges of metaventricle: (0) connecting medially (Figs. 54, 55); (1) obliterate medially.
20. Anterolateral ridge of metaventricle: (0) parallel to posterior margin of mesocoxal cavities even laterally (Figs. 54, 55); (1) arcuately bent posteriad sublaterally.
21. Tuft of hairs on distal portion of male protrochanter: (0) absent; (1) present (Fig. 22).
22. Tuft of hairs on distal portion of male mesotrochanter: (0) absent; (1) present (Fig. 23).
23. Tuft of hairs on distal portion of male metatrochanter: (0) absent; (1) present (Fig. 24).
24. Proximal portion of trochanters: (0) smooth; (1) with microsculpture.
25. Proximal portion of trochanters: (0) pubescent; (1) bare.
26. Tibial grooves on femora: (0) absent (Fig. 53); (1) present (Fig. 52).
27. Median process of male sternite 8: (0) wide; (1) narrow (Figs. 20, 21).
28. Median portion of male sternite 9: (0) V-shaped (Figs. 29, 32, 35, 38, 41, 44, 47); (1) U-shaped (Fig. 26); (2) tongue-shaped (see e.g. SMETANA 1978: fig. 115).
29. Lateral struts of male sternite 9: (0) arcuate (Figs. 26, 29, 35, 38, 44); (1) sinuate (Figs. 32, 41, 47).

Tab. 1. Data matrix used for the phylogenetic analysis. Inapplicable characters denoted with a dash (-), missing characters with a question mark (?).

Taxon	0 1	0 2	0 3	0 4	0 5	0 6	0 7	0 8	0 9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	
<i>Cetiocyon incantatus</i>	3.8–4.3	2.8	1	1	0	1	0	1	1	0	-	-	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0
<i>Cetiocyon goliathus</i>	7.2	2.4	0	1	1	0	1	1	1	0	-	-	0	1	1	1	0	0	0	0	?	?	?	?	0	1	1	?	?	?	?	?	?	?	?
<i>Cetiocyon traipela</i>	7.4–8.0	2.7	1	1	1	0	1	1	1	0	-	-	1	1	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	1	1	0	1
<i>Cetiocyon hanseni</i>	4.3–5.2	2.2	1	1	0	1	1	1	1	0	-	-	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	-	0
<i>Cetiocyon papuensis</i>	4.5–5.2	2.3	1	1	0	1	1	1	1	0	-	-	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	0	0	-	1
<i>Cetiocyon loksai</i>	5.0–5.8	2.3	1	1	1	0	1	1	1	0	-	-	1	1	1	0	0	0	0	0	1	1	0	0	1	1	1	1	0	0	1	1	1	0	1
<i>Cetiocyon riedeli</i>	5.4–6.0	2.4	0	1	1	0	1	1	1	0	-	-	1	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	1	1	1	1
<i>Cetiocyon hebaueri</i>	5.8–6.9	2.4	0	1	1	0	1	1	1	0	-	-	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1
<i>Cetiocyon cribripunctatus</i>	5.0–5.5	2.4	0	1	1	0	1	1	1	0	-	-	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	1	0	1	1	1
<i>Platycyon wauensis</i>	3.0–4.3	3.0	1	1	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	1	0	0	-	1	
<i>Pelosoma eremita</i>	2.8–3.0	2.1	1	1	0	1	1	0	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0	-	1	
<i>Ercyodes fossus</i>	2.0–2.5	2.6	1	0	0	0	1	0	0	0	-	-	1	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	-	1	
<i>Cercyodes kingensis</i>	2.4–2.5	4.0	1	0	0	0	1	0	0	1	0	0	1	1	-	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	-	1	
<i>Pseudoosternum maculatum</i>	1.4–1.8	2.5	1	1	0	1	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	0	-	1	
<i>Australocyon variegatus</i>	1.8–2.2	2.2	1	0	0	1	1	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	-	0		
<i>Oosternum simplex</i>	1.2–1.6	2.3	1	0	1	1	1	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	-	0		
<i>Cercyon lateralis</i>	2.0–3.0	2.8	1	0	0	1	1	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	-	2	0	0	0	-	1		

- 30.** Median lobe of the aedeagus: (0) nearly parallel-sided (Figs. 25, 28); (1) wide at midlength, narrowing apicad (Figs. 31, 34, 37, 40, 43, 46).
- 31.** Apex of median lobe: (0) entire (Figs. 25, 28, 31, 43); (1) bilobate (Figs. 34, 37, 46).
- 32.** Lateral projections of median lobe: (0) absent (Figs. 25, 28, 43); (1) present (Figs. 31, 34, 37, 40, 46).
- 33.** Anteriad-directed lobes of lateral projections of median lobe: (0) absent (Figs. 34, 37); (1) present (Figs. 31, 40, 46).
- 34.** Asymmetrical manubrium of phallobase: (0) absent (Figs. 25, 28); (1) present (Figs. 31, 37, 40, 43, 46).

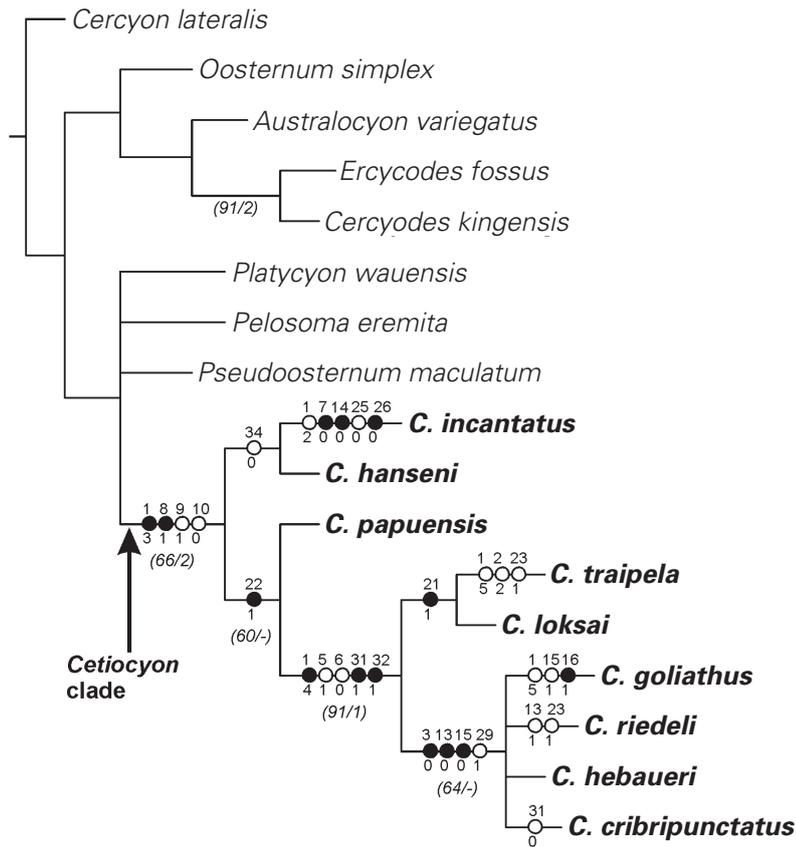
5.2. Results of analyses

The analysis of all taxa and all characters resulted in a single most parsimonious tree 66.1 steps long (CI = 62, RI = 77; Fig. 60). The analysis of all taxa and discrete characters yielded four most parsimonious trees 54 steps long (CI = 61, RI = 77; strict consensus shown in Fig. 59). The trees from the two analyses are congruent except for the position of *C. goliathus* (for which the male is unknown and 11 characters could therefore not be scored): it is sister to *C. traipela* in

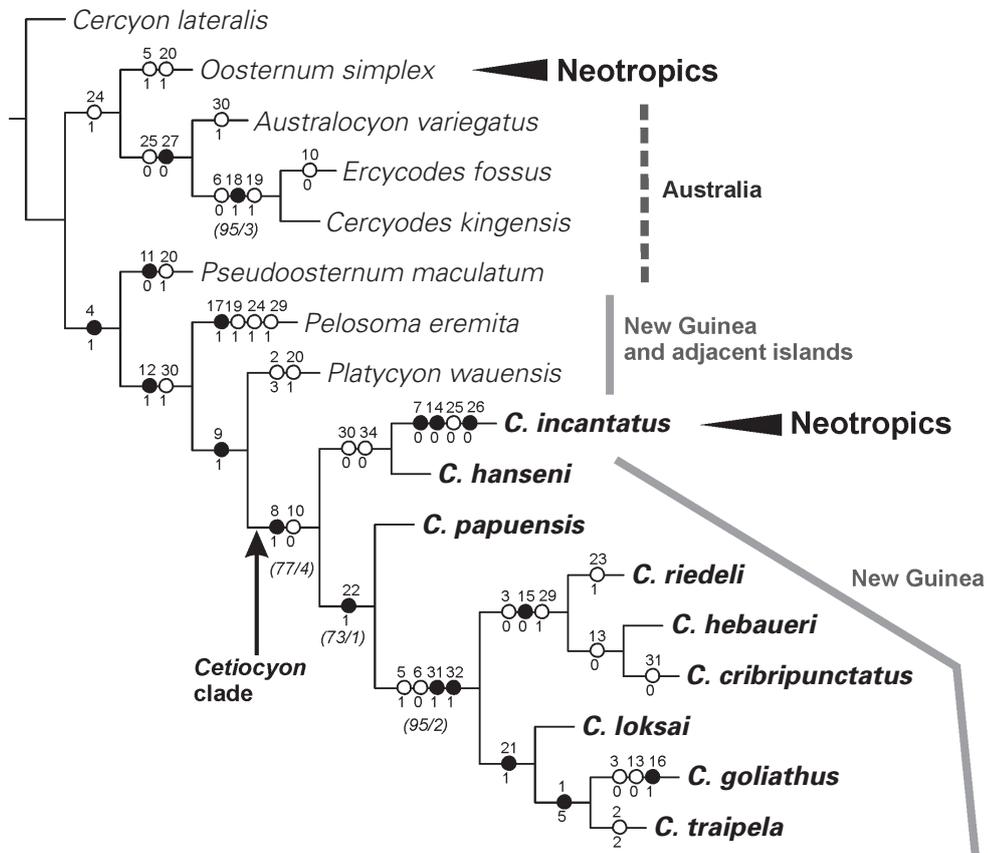
the all-characters tree, but placed in the *C. cribripunctatus* + *C. hebaueri* + *C. riedeli* clade in the discrete-characters tree. The latter position of *C. goliathus* was also obtained in the two nearest suboptimal trees (both 66.5 steps long) resulting from the all-character analysis. The topology of the remaining parts of the tree remained unchanged also after the exclusion of *C. goliathus* from the analysis.

All analyses supported the monophyly of the genus *Cetiocyon* including the Neotropical *C. incantatus*, based on the derived states of two characters (8-1: prosternum without median keel [unique synapomorphy]; 10-0: antennal grooves absent [independently developed also in *Ercyodes*]). Body size exceeding 4.3 mm (char. 1-3) is recognized as an additional unique synapomorphy under the ACCTRAN optimization (reversed in *C. incantatus* only). All analyses agree in the topology of the clade containing all New Guinean species of *Cetiocyon* except *C. hanseni*. *Cetiocyon hanseni* was recognized as sister species to *C. incantatus* based on the characters of the aedeagus (30-0: median lobe nearly parallel-sided; 34-0: asymmetrical manubrium of phallobase not developed), but is otherwise characterised by plesiomorphic character states only. Most analyses resulted in a well resolved (although weakly supported) topology of outgroup taxa, suggesting a close relationship of *Cetiocyon* with New Guinean *Platycyon* and *Pelosoma* species.

59



60



Figs. 59, 60. Results of the phylogenetic analyses. **59:** Strict consensus tree of 4 most parsimonious trees based on discrete characters (characters mapped only for *Cetiocyon* clade). **60:** Most parsimonious tree resulting from the analysis based on all characters. Black circle: unique apomorphy. Empty circle: homoplasy or reversal apomorphy. Support values given below branches as (*jackknife support* / *Bremer support*).

6. Discussion

The genus *Cetiocyon* seems to represent a monophyletic clade within the ‘Gondwanan group of genera’ of the tribe Megasternini. The analyses performed herein and in FIKÁČEK (2010) suggest an Australian–New Guinean origin of the genus, since all genera recognized as closely related to *Cetiocyon* are currently distributed in Australia and New Guinea only (Fig. 60). Three clades seem to be currently known within *Cetiocyon*: (1) the *C. papuensis* clade containing most of the New Guinean species, (2) the monotypic New Guinean *C. hanseni* clade, and (3) the monotypic Neotropical *C. incantatus* clade.

Two main scenarios may be speculated to explain the current disjunct distribution of the genus in New Guinea and northern South America (Fig. 57): (1) a vicariance-dispersal scenario presuming dispersal of *Cetiocyon* from the Australian Region to the Neotropics before the wide isolation of Australia, Antarctica and South America (i.e. dating to the Eocene latest; SANMARTÍN & RONQUIST 2004) and the subsequent reduction of its distribution to recent small areas; (2) a trans-Pacific dispersal scenario allowing for a more recent dating of the origin of the long distance Australian–Neotropical disjunction. Even though the dating of the divergence between the New Guinean and Neotropical *Cetiocyon* clades is currently impossible, the presence of highly derived recent hydrophilid genera in the Eocene (genera of the ‘greater hydrophilines’ clade of Hydrophilina; FIKÁČEK et al. 2010) implies that there is no reason to discard scenario (1) only because it presumes an Eocene (i.e. more ancient) divergence of the clades. During the Late Paleocene/Early Eocene thermal maximum, there, moreover, seem to have been suitable climatic conditions allowing the migration of tropical elements through Antarctica (MORLEY 1999), which also shows scenario (1) as a possible explanation of the current *Cetiocyon* distribution.

Based on the geological evidence, most of New Guinea is rather young as it emerged only during the Late Oligocene/Miocene after the collision of the Australian and Pacific plates (HEADS 2001; DE BOER & DUFFELS 1996). Thereafter, New Guinea was connected with Australia until rather recently (see HEADS 2001 for details) – also during the Miocene when Australia experienced a gradual drying of climate resulting in a withdrawal of the originally widespread tropical and paratropical forests to the north (MORLEY 1999). *Cetiocyon* may have been therefore originally more widely distributed through Australia and become more restricted in distribution after the demise of Australian wet forests; this may be supported by the fact that the genus is not exclusively New Guinean but occurs also in northern Australia. A presumed wide Australian dis-

tribution would be also congruent with the vicariance-dispersal scenario outlined above. On the other hand, high morphological similarity of the species of the *C. papuensis* clade and the restricted distribution of many of its species (e.g., *C. cribripunctatus*, *C. hebaueri* and *C. riedeli*, Fig. 58) may indicate that at least some of the clades of the *C. papuensis* group are descendants of a rather recent radiation held in the New Guinean mountain ranges.

The megasternine fauna of New Guinea seems to be a balanced mix of species of ‘Gondwanan genera’ (*Platycyon*, *Cetiocyon*, *Pseudoosternum*) and Oriental elements (*Cercyon*, *Cryptopleurum*, *Armostus*, *Pelosoma*, *Pilocnema*, *Paroosternum*, *Oosternum sorioides* group) based on the published data (HANSEN 1999a, 2003; HEBAUER 2000, 2001, 2004). The examination of the New Guinean *Pelosoma eremita*, however, led to the surprising discovery that this species is in fact closely related to *Platycyon* and *Cetiocyon*, both representing ‘Gondwanan genera’ based on the morphology of male genitalia. This stands in contrast to the remaining Neotropical and Afrotropical *Pelosoma*, which seem to be related to *Cercyon*. The same surprise resulted from the examination of some unidentified New Guinean material externally rather similar to the genus *Cercyon* (M. Fikáček, unpubl. data). The drawings of the genitalia of the New Guinean endemic *Cercyon* species described by HEBAUER (2001) also suggest their close relationships to ‘Gondwanan genera’. These preliminary results indicate that the megasternine fauna of New Guinea mostly consists of Australian elements (as it would be expected from its position east of the Wallace line), with very few non-Australian elements represented either by rare endemic species of the ‘continental genera’ (*Armostus*, *Paroosternum*, *Cryptopleurum*) or by widely distributed Oriental or pantropical species (*Oosternum sharpi* Hansen, 1999, *Paroosternum sorex* (Sharp, 1874)). *Pilocnema* remains the only genus endemic for the Australian region having the *Cercyon*-like type of male genitalia and thus not belonging to the ‘Gondwanan’ group of genera.

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Electronic Supplement Files

at <http://www.arthropod-systematics.de/> (“Contents”)

File 1: Fikacek&Short-HydrophilidaeCetiocyon-ASP2010-1. nex (Data matrix in Nexus format, containing only discrete characters).

File 2: Fikacek&Short-HydrophilidaeCetiocyon-ASP2010-2. tnt (Data matrix in TNT format, containing all characters).

