

Taxonomic revision of *Agraphydrus* RÉGIMBART, 1903

V. Philippine species and their first DNA barcodes

(Coleoptera: Hydrophilidae: Acidocerinae)

A. KOMAREK & H. FREITAG

Abstract

The genus *Agraphydrus* RÉGIMBART, 1903 (Coleoptera: Hydrophilidae) of the Republic of the Philippines is taxonomically reviewed aided by *COI* mtDNA barcodes. Nine new species are described, all currently regarded as endemic to the Philippines: *A. abrasus* sp.n., *A. ampullatus* sp.n., *A. batak* sp.n., *A. brevilobatus* sp.n., *A. occultus* sp.n., *A. palawanensis* sp.n., *A. pelingeni* sp.n., *A. tenuipalpis* sp.n., and *A. zetteli* sp.n. *Agraphydrus coomani* (ORCHYMONT, 1927), widespread in the Oriental and Australasian regions, is recorded from the Philippines for the first time. *COI* sequences and thorough morphological examination suggest that this and further species represent a group of closely related, partly cryptic species under current radiation. At least three of them are clearly distinguishable and summarized together with 16 other Oriental *Agraphydrus* species (*A. coomani* species group). Habitus, male genitalia and other morphological details are illustrated, distribution maps and a key to the species are presented. Their macro- and microhabitats are briefly discussed. All species are aquatic, although they were also caught at light and in emergence traps.

Key words: Coleoptera, Hydrophilidae, *Agraphydrus*, DNA barcode, integrative taxonomy, key to species, new species, Oriental Region, Philippines, revision.

Introduction

This is the fifth part of a comprehensive revision of the genus *Agraphydrus* RÉGIMBART, 1903 (KOMAREK & HEBAUER 2018, KOMAREK 2018, 2019, 2020), and it is the first integrative taxonomic study of the genus, where mtDNA barcodes were employed to aid in the development of taxonomic species concepts.

Partial *COI* sequences have originally been proposed as standard DNA barcode for animals by HEBERT et al. (2003). This standard barcode and other markers are a very useful tool in developing species delimitation hypotheses compared to traditional morphological methods, although this concept is not perfect either (e.g., MONAGHAN et al. 2006, SKALE et al. 2012). Simple approaches usually apply a 3 % genetic distance threshold (HEBERT et al. 2003), or “barcode gap”, to delimitate species. This threshold is also recommended for SE Asian Water Beetles (BALKE et al. 2013). However, this limit is rather theoretical and cannot be automatically applied to all kinds of samples and taxa (e.g., LIM et al. 2012, MEIER et al. 2006, 2008, MONAGHAN et al. 2006, HENDRICH et al. 2009, SROKA et al. 2012).

Barcode data do not aim to reveal phylogenetic relationships, and trees generated from short *COI* sequences can be misleading (HEBERT & GREGORY 2005). On the other hand, haplotype networks can group sequence data more suitably for DNA taxonomy. Their clusters usually agree well with proposed species and reflect taxonomic accuracy even better than the maximum likelihood approach of the GMYC (Generalized Mixed Yule Coalescent) algorithm (e.g., PONS et al. 2006, HART & SUNDAY 2007).

A very complex biogeographic history has shaped the Philippine archipelago’s water beetle distribution patterns (FREITAG et al. 2016). Based on interconnected island groups during Pleisto-

cene glacial maximums, ONG et al. (2002) defined 16 biogeographic regions in the Philippines (reflected as color overlay in Figs. 38–39).

Efforts to study the water beetle fauna of the Philippines have increased during the last two decades. More than 317 aquatic and riparian beetles have been recorded to date, among them are 39 Hydrophilidae, to which we have recently contributed 15 new species of *Anacaena* THOMSON, 1859 (KOMAREK & FREITAG 2014). The estimated total number of Philippine Hydrophilidae might exceed 140 (FREITAG et al. 2016). With this paper, we add ten species of *Agraphydrus* RÉGIMBART, 1903 and comment on additional, tentatively classified material.

Material and methods

More than 800 specimens of *Agraphydrus* collected in the Philippines, were examined and compared with *Agraphydrus* species known from the Oriental Region (KOMAREK 2018, 2019, KOMAREK & HEBAUER 2018). Most of the examined material is from the collection of the Biodiversity Laboratory, of the Ateneo de Manila University and was originally retrieved by manual microhabitat-specific collection methods (indicated by “M” in site codes) from aquatic habitats (see FREITAG 2015), by emergence traps (indicated by “E”) installed over streams as described by FREITAG (2004a) and by black light traps (indicated by “L”) operated in close proximity to streams and other water bodies. The limnological terms “pool” (calm portion of a stream with (almost) stagnant water), “run” (portion of a stream with distinct laminar water flow) and “riffle” (rapid, or portion of a stream with turbulent water flow) are used to describe the hydraulic conditions of microhabitats that were manually sampled. “Side pool” refers to a stream-associated, but isolated puddle that does not regularly receive freshwater inputs from the stream flow and commonly varies in physicochemical water parameters.

Within the precisely cited label data for holotype specimens, square brackets “[...]” are used for remarks by the authors, a backslash “\” indicates the change of line, a straight line “|” the change of label. DNA sample codes are provided in square brackets “[...]”, those which were successfully barcoded are indicated by an asterisk “*”.

Morphological terms used in this contribution are explained in KOMAREK & HEBAUER (2018).

Additional notes on geographical and ecological details are based on personal information by the collectors, if not indicated at the label. This study refers partly to material collected during comprehensive local faunistic studies at Puerto Princesa Subterranean River National Park (Palawan), Lake Manguao basin (Palawan), Lake Naujan and its tributaries (Mindoro) and Baroc River basin (Mindoro). More detailed locality descriptions and site maps of these areas are provided in the following papers: FREITAG (2004b), FREITAG & PANGANTIHON (2010), FREITAG & ZETTEL (2014), VIDAL et al. (2017). Therefore, multiple records of the same *Agraphydrus* species in these areas are condensed into a single record symbol, respectively (Figs. 38–39).

DNA was extracted from a total of 79 presorted, alcohol-preserved specimens by elution with Qiagen DNeasy kits (Qiagen, Hilden, Germany) following the standard protocol for animal tissues. DNA isolates underwent polymerase chain reactions (PCR) of the standard barcode partition of the cytochrome c oxidase subunit (*COI*) as described by GARCES et al. (2018), but with primer pair LCO1490 / HCO2198 (FOLMER et al. 1994). Successfully amplified PCR products were sequenced in both directions by MacroGen Europe Inc. (Amsterdam, Netherlands).

Sequences were polished and manually aligned in MEGA X (KUMAR et al. 2018). All sequences were submitted to the Barcode of Life Database (BOLD). GenBank (European Nucleotide Archive, ENA) and BOLD accession numbers are provided in Tab. 1. The same software was used to calculate genetic distances applying the K2P model (Tab. 2).

To illustrate different haplotypes in regard to their genetic distance and occurrence on different Philippine islands, a statistical parsimony network (TEMPLETON et al. 1992) was generated (Fig. 40) in PopART v1.7 (LEIGH & BRYANT 2015).

For methods concerning the morphological preparation of specimens and illustration, see KOMAREK (2018).

Abbreviations:

C.I.	clypeal index = ratio greatest width / median length of clypeus anterior to eyes
CPOM	Coarse Particulate Organic Matter
E.I.	elytral index = ratio greatest elytral length / greatest elytral width
P.I.	pronotal index = ratio greatest pronotal width / median pronotal length
SBMA	Subic Bay Metropolitan Authority
ADMU	Ateneo de Manila University (Biodiversity Laboratory & Collection), Philippines, (E. Delocado)
MNS	Museum für Naturkunde, Stuttgart, Germany (C. König, W. Schawaller)
NMW	Naturhistorisches Museum Wien, Austria (M.A. Jäch)
PCSD	Palawan Council for Sustainable Development, Puerto Princesa, Philippines (L. Lagrada)
PNM	Philippine National Museum of Natural History, Manila, Philippines (P.A. Buenavente)
SMTD	Senckenberg Naturhistorische Sammlungen Dresden, Germany (O. Jäger)
ZMB	Museum für Naturkunde, Berlin, Germany (J. Frisch)

Checklist of the *Agraphydrus* species of the Philippines

1. *A. abrasus* sp.n.
PHILIPPINES (Luzon, Mindoro, Palawan)
2. *A. ampullatus* sp.n.
PHILIPPINES (Leyte)
3. *A. batak* sp.n.
PHILIPPINES (Palawan)
4. *A. brevilobatus* sp.n.
PHILIPPINES (Negros, Panay)
5. *A. coomani* (ORCHYMONT, 1927)
SRI LANKA, SOUTHEAST ASIA including southern CHINA and southern JAPAN, AUSTRALIA,
PHILIPPINES (Luzon, Leyte)
6. *A. occultus* sp.n.
PHILIPPINES (Luzon, Mindoro, ? Palawan, ? Panay)
7. *A. palawanensis* sp.n.
PHILIPPINES (Busuanga, Palawan)
8. *A. pelingeni* sp.n.
PHILIPPINES (Palawan)
9. *A. tenuipalpis* sp.n.
PHILIPPINES (Leyte, Mindanao)
10. *A. zetteli* sp.n.
PHILIPPINES (Busuanga, Leyte, Luzon, Mindoro, Negros, Panay, Samar, Sibuyan)

Agraphydrus abrasus sp.n.

Agraphydrus "sp. D" (in part): FREITAG & ZETTEL 2014: 19, 30.

TYPE LOCALITY: Philippines, Luzon Island, Aurora Province, Maria Aurora Municipality, Barangay Wenceslao, Bingwangan River flowing through extensive coconut plantation, 60 m a.s.l., 15°45'48"N 121°25'21"E.

TYPE MATERIAL: **Holotype** ♂ (PNM): "PHIL.: Luzon, Maria Aurora, Wenceslao, Bingwangan \ River, extensive coconut plantation, littoral \ gravel, run, 60 m a.s.l., 15°45'48"N 121°25'21"E, \ 05.Feb1996, leg. J. Mendoza et al. (435a)M". **Paratypes: PHILIPPINES: Luzon:** 2 ♂♂ [FR433*], 1 ♀ (NMW, ADMU): same sampling data as holotype; 1 ♂ (SMTD): SBMA area, Batalan mountain river, ca. 14°45'N 120°21'E, 65 m a.s.l., secondary vegetation, grassland, fresh root bunches, run, 29.I.2018, leg. H. Freitag "(403h)M"; 1 ♀, 2 exs. (ADMU): same site, light trap "(403)L"; 2 ♂♂, 2 ♀♀ (NMW): Quezon, 30 km E Lucena City, Quezon National Park, 23.XI.1992, leg. M. Jäch "11"; 2 ♂♂, 2 ♀♀ (NMW): Laguna, Los Baños, small river, 28.XI.1995, leg. J. Kodada & B. Rigová; 3 exs. (NMW): Laguna, Mt. Makiling, stream above "Mad Springs", 700 m a.s.l., 22.XI.1995, leg. J. Kodada; 1 ♀ (NMW): same site, 400–500 m a.s.l., 19.XI.1995, leg. J. Kodada; 2 ♂♂ (NMW): Laguna, Mt. Makiling, Molawin Creek, "Flat Rocks", 200 m a.s.l., 22.XI.1995, leg. J. Kodada; 1 ♂, 2 ♀♀ (ZMB): Laguna, Majayjay, Bukal, Mimpis mountain river, 14°7'0"N 121°27'54"E, 425 m a.s.l., secondary forest, 26.VI.2018, leg. H. Freitag et al. "(431b)M"; 1 ♂ [FR484*], 1 ♀ (ADMU): Laguna, Sta.Maria, Cogeo-Infanta Road, mountain creek, 14°33'4"N 121°27'51"E, 430 m a.s.l., secondary forest, rocks, littoral sand, gravel, pool, 25.III.1996, leg. J. Mendoza "(410b)M"; 3 ♂♂ (ADMU): Albay, Guinobatan, Masarawag, ephemeral river, 13°15'15"N 123°38'16"E, 390 m a.s.l., littoral gravel, pool, 4.VII.1995, leg. J. Mendoza "(P538b)M".

ADDITIONAL MATERIAL EXAMINED:

PHILIPPINES: Mindoro: 2 ♀♀ (NMW): 28 km S Calapan, Balete, 100–700 m a.s.l., 27.–29.11. 1992, leg. M. Jäch "19"; 2 ♂♂ (NMW): same site and date, but leg. H. Schillhammer "13"; 3 ♂♂ (ADMU): Mt. Calavite, Paluan, Harrison, headwater creek SE summit, ca. 13°28'N 120°24'E, 750 m a.s.l., forest pocket in grassland, leaf litter, pool, 11.IX.1996, leg. J. Mendoza "(3151)M"; 1 ♂ (ADMU): Roxas, San Vicente, Taugad Daka River (Baroc River tributary), 12°37'33"N 121°22'18"E, 180 m a.s.l., secondary vegetation, littoral mud, sand, pool, 5.II.2012, leg. A. Vidal "(TDR1b)M"; 2 ♂♂ (ADMU): same river, 12°38'5"N 121°19'33"E, 530 m a.s.l., secondary forest, side pool, 23.I.2013, leg. C. Pangantihon "(TDR3e)M"; 2 ♀♀ (ADMU): same site, microhabitat and collector, but 9.III.2013 "(TDR3e)M"; 2 ♀♀ (ADMU): same site, light trap, 4.IV.2013, leg. H. Freitag "(TDR3L"; 1 ♀ (ADMU): same river, 12°38'0"N 121°19'15"E, 700 m a.s.l., secondary forest, bottom gravel, run, 4.IV.2017, leg. H. Freitag "(TDR4c)M"; 2 ♂♂, 12 exs. (ADMU): Roxas, San Vicente, Sapang Alupa, 12°37'48"N 121°20'52"E, 340 m a.s.l., secondary forest, littoral gravel, pool, 8.V.2015, leg. H. Freitag "(TACb)M"; 2 ♂♂ [FR441], 7 exs. (ADMU): Roxas, San Vicente, Batuwayang Creek (Taugad Daka River tributary), 12°38'9"N 121°19'45"E, 490 m a.s.l., 16.II.–9.III.2013, leg. C. Pangantihon "(TBC)E"; 1 ♀, 2 exs. (ADMU): Roxas, San Vicente, Taugad Diit River (Baroc River tributary), 12°37'32"N 121°21'17"E, 230 m a.s.l., secondary vegetation, submerged wood, run, 16.I.2013, leg. C. Pangantihon "(TIRf)M"; 1 ♂, 1 ♀ (ADMU): Roxas, San Vicente, community watersource creek, 12°37'1"N 121°23'18"E, 150 m a.s.l., secondary forest, hygropteris rock, 2.XI.2017, leg. C. Pangantihon "(TWCj)M"; 2 ♂♂, 6 exs. (ADMU): Roxas, San Vicente, Hinundangan River, downstream Hinagdanan Falls, 12°35'22"N 121°21'54"E, 200 m a.s.l., secondary vegetation, rocks, sand, pool, 28.XI.2018, leg. H. Freitag "(HR2b)M"; 2 ♂♂ (ADMU): Roxas, San Vicente, Quirao-na-Balete Creek, 12°35'38"N 121°23'34"E, 230 m a.s.l., secondary forest, littoral gravel, pool, 8.VII.2018, leg. C. Pangantihon "(HQCb)M"; 1 ♂, 2 exs. (ADMU): same site, microhabitat and collector, 30.VI.2018 "(HQCb)M"; 1 ♂ [FR515] (ADMU): same site, microhabitat and collector, but 21.IX.2018 "(HQCb)M"; 1 ♂ (ADMU): Roxas, San Vicente, Tagugay Creek (Quirao Buhay Creek tributary), 12°36'30"N 121°22'38"E, 200 m a.s.l., secondary forest, hygropteris rock, 12.XI.2018, leg. H. Freitag & C. Pangantihon "(HBTj)M"; 1 ♂ (ADMU): same site, but bottom gravel, run, 12.VIII.2018, leg. C. Pangantihon "(HBTc)M"; **Palawan:** 1 ♂ (PCSD): Taytay, Alipuran Stream (Lake Manguao affluent), ca. 10°46'N 119°31'E, 30 m a.s.l., 3.IV.2008, leg. H. Freitag "11"; 1 ♀ (PNM): Puerto Princesa, Concepcion, Tarabanan River 0.5 km N highway, 10°0'40"N 119°1'23"E, 10 m a.s.l., secondary forest, residual pool, 30.I.2015, leg. H. Freitag "(16Bt)M"; 1 ♂ (NMW): same river, ca. 13 km N San Rafael, 30 m a.s.l., 7.XII.1995, leg. J. Kodada & B. Rigová; 2 ♂♂ (NMW): Puerto Princesa, Cabayugan, upper Sabang Waterfall, 10°12'34"N 118°52'22"E, 70 m a.s.l., secondary forest, ultramaphic soil, rock pool, 26.III.2001, leg. H. Freitag "12"; 2 ♂♂, 1 ex. (ADMU): Puerto Princesa, Cabayugan, Mt. Bloomfield Waterfall, 10°12'3"N 118°53'4"E, 150 m a.s.l., primary forest, ultramaphic soil, residual pool, rocks, boulders, pool, 2.IV.2001, leg. H. Freitag "(18m)M"; 1 ♀ (ADMU): Puerto Princesa, 3 km SE Laptay (Napsan), upper Bubugtungan mountain stream, 9°40'52"N 118°27'46"E, 40 m a.s.l., disturbed primary forest, CPOM, side pool, 8.IX.2008, leg. H. Freitag "(23e)M".

COMPARATIVE MATERIAL EXAMINED: *Agraphydrus* cf. *abrasus*:

PHILIPPINE S: **Camiguine:** 1 ♂ [FR506*] (ADMU): 3 km S Mambajao, Balbagon, Maubog, ca. 1 km S Enigmata, small creek, ca. 9°13'N 124°44'E, ca. 50 m a.s.l., secondary vegetation, 16.IV.1995, leg. J. Mendoza "40". **Mindanao:** 1 ♂ [FR509*], 1 ♀ (ADMU): Agusan del Sur, San Francisco, Lapag Creek, 8°29'13"N 125°59'36"E, 200 m a.s.l., 5.XII.1995, leg. J. Mendoza "(896b)M".

DIFFERENTIAL DIAGNOSIS: Belongs to species with unicolored maxillary palpi. Differs in obsolete or almost obsolete ground punctation of head and elytra from all species of the Philippines. Specimens without clypeal microreticulation share this character with *Agraphydrus tenuipalpis* and *A. batak*. Differs in broad body, dark colored pronotum and elytra, eight antennomeres and stout maxillary palpi from *A. tenuipalpis*. Shares emarginate apex of median lobe with *A. batak*, differs in distinctly inflated apex of parameres. Shares similar aedeagus with distinct emargination of apex of median lobe and inflated apex of parameres with *A. excisus* KOMAREK, 2019, but differs in black pronotum, obsolete ground punctation of head and pronotum, and stout maxillary palpi. Specimens with microreticulate anterior clypeal margin share this character with *A. ampullatus*, *A. brevilobatus*, *A. palawanensis*, and *A. pelingeni*. Differs in black pronotum from *A. palawanensis*, in broad habitus from *A. pelingeni*; differs in excised apex of median lobe from all these species.

DESCRIPTION: Total length: 1.9 mm, elytral width: 1.0 mm, E.I.: 1.2–1.3, P.I.: 2.2, elytra 2.9–3.1 times as long as pronotum. Habitus (Fig. 28) broad, evenly oval, moderately to strongly convex.

Coloration: Labrum yellowish brown; clypeus black mesally with weakly defined dark yellow triangular preocular patches; frons black; maxillary palpi unicolored yellow; pronotum shining black with undefined yellow lateral and anterior margins; elytra black with light brown lateral margins and posterior area; legs dark brown, lighter than ventrites.

Head: Clypeus with weakly emarginate anterior margin, C.I.: 3.7; lateral length ratio clypeus/eyes = 1.7; ground punctation obsolete; microreticulation absent with very fine longitudinal wrinkles on lateral margins of clypeus in most individuals, anterior clypeal margin indistinctly microreticulate in specimens from Palawan; systematic punctures distinct. Eyes large, not protruding, slightly oblong. Antennae with eight antennomeres. Maxillary palpi (Fig. 19) stout, 0.9 times as long as pronotum in midline, 0.8 times as long as maximum width of clypeus, length ratio palpomeres 4:3 = 1.4–1.5, palpomere 4 almost symmetrical. Mentum with few very fine, widely spaced punctures laterally, microsculpture absent.

Thorax: Pronotal ground punctation obsolete or almost obsolete; systematic punctures distinct. Elytral ground punctation distinct, very fine, widely spaced; four rows of distinct systematic punctures present, mesal rows with strongly reduced number of punctures, not reaching anterior margin, additional row present along lateral margin on posterior 4/5 of elytra. Mesoventrite with distinct bulge.

Femora (Fig. 10): Pubescence present in proximal 2/3 of profemur with convexly rounded hairline, on proximal 3/4 of mesofemur with almost straight hairline, on proximal half of metafemur with slightly concave hairline.

Abdomen: Ventrite 5 with almost semicircular apical emargination.

Aedeagus (Fig. 1): Length: 0.28 mm. Phallobase as long as parameres, slightly longer than wide, abruptly narrowing to distinct, conical manubrium; border between pigmented and unpigmented portion of ventral face indistinct, almost reaching manubrium. Parameres with strongly curving margins, with strong subapical constriction; apex broadly rounded, distinctly inflated; basal portion deeply reaching into phallobase. Median lobe tongue-shaped, widest distal to mid-length; apex broadly rounded, not reaching apex of parameres; dorsal face with distinct semicircular

emargination; corona in apical third; styli absent; basal apophyses short, reaching mid-length of phallobase.

REMARKS: Specimens from Luzon vary slightly in the intensity of the coloration, especially pale areas of the clypeus are sometimes more extended, but never reach beyond the fronto-clypeal suture. Some minor variations are also evident in the subapical constriction of the parameres, which are either more pronounced at the inner (Fig. 1) or the outer margins. Mindoro and Palawan specimens are externally not distinguishable from the type material. However, we recognize some differences in the aedeagus, which is generally slightly smaller than in Luzon specimens, with relatively shorter phallobase and the inner subapical parameral constriction always less distinct, while the outer margin's constriction is less pronounced and the parameral apex only moderately inflated, particularly in Palawan specimens. We would consider those minor differences as conspecific variation if there wouldn't be another specimen each from Camiguin and Mindanao for which DNA barcodes are available (Tab. 1) and which also display slight differences in these characters, but vary in 6.3–7.2 % genetic distance from Luzon specimens (Tab. 2). This provides first hints that we might rather face an evolutionary young, geographically separated group of species. Since DNA barcodes are not available for any specimen from Palawan and Mindoro (amplification failed for several DNA extracts) we refrain from including these specimens in the type series. Further studies with more specimens from various Philippine localities and molecular-genetic evidence are needed to clarify the status.

ECOLOGY: The material was collected in creeks and small rivers, both in relative pristine forested areas, as well as in areas with disturbed or open vegetation. The species was predominantly found in calm stream sections in littoral bottom gravel, but also in isolated side pools, among mineral or organic deposits. A few specimens each were collected with emergence and black light traps. In Luzon, the species is found together with *A. coomani* and *A. zetteli*, in Mindoro with *A. zetteli* and *A. occultus*, in Palawan with *A. palawanensis* and *A. pelingeni*.

DISTRIBUTION (Fig. 38): Philippines: Luzon, Mindoro, Palawan.

ETYMOLOGY: The name *abrasus* (Latin adjective) (= bald-headed) refers to the reduced ground punctuation of the head.

Agraphydrus ampullatus sp.n.

TYPE LOCALITY: Philippines, Leyte Island and Province, Baybay Municipality, creek 2 km east of Visayas State University, ca. 10°44'46"N 124°48'50"E, ca. 140 m a.s.l.

TYPE MATERIAL: **Holotype** ♂ (MNS): "PHILIPPINES:LEYTE \ VISCA [Visayas State College of Agriculture] N Baybay, 1991 \ sec.forest, 100-200 m \ leg.SCHAWALLER & al. | 4.3.91". **Paratypes**: **P H I L I P P I N E S**: **Leyte**: 1 ♀ (MNS): same sampling data as holotype; 3 ♂ ♂ [FR516], 3 ♀ ♀ (ADMU, PNM, NMW): Baybay, Patag, E Visayas State University, small Lagu-Lagu River, ca. 10°45'N 124°48'E, 50 m a.s.l., degraded forest, volcanic rocks, gravel, pool, 27.V.1995, leg. H. Freitag "(229a)M".

DIFFERENTIAL DIAGNOSIS: Belongs to group of species with microreticulate anterior clypeal margin and unicolored maxillary palpi. Shares these features with *A. brevilobatus*, *A. palawanensis*, *A. pelingeni* and some specimens of *A. abrasus*. Differs in black clypeus and pronotum from *A. palawanensis*, in slightly broader habitus, absence of yellow preocular patches, and unicolored black elytra from *A. brevilobatus*, in distinctly broader habitus from *A. pelingeni*, in fine ground punctuation of head and pronotum from *A. abrasus*. Differs in features of aedeagus (e.g., bottle-shaped median lobe) from all species mentioned. Shares microreticulate anterior clypeal margin, unicolored maxillary palpi, and eight antennomeres with *A. schoedli* KOMAREK, 2019, differs in smaller size (body length of *A. schoedli* = 2.4–2.8 mm), black clypeus without distinct preocular patches, black pronotum and elytra (dark brown in *A. schoedli*), large eyes,

very fine ground punctation, and features of aedeagus (e.g., median lobe with narrowed apex and narrowly separated basal apophyses, basal lobe large).

DESCRIPTION: Total length: 2.1 mm; elytral width: 1.0–1.1 mm; E.I.: 1.3–1.4, P.I.: 2.3, elytra 3.3 times as long as pronotum. Habitus (Fig. 29) broad, evenly oval, moderately convex.

Coloration: Labrum, clypeus and frons black; clypeus with narrow yellowish rim along lateral margins; maxillary palpi unicolored yellow; pronotum black with narrow yellow lateral margins; elytra black; ventrites dark brown; legs lighter than ventrites.

Head: Clypeus with distinctly emarginate anterior margin, C.I.: 3.8, lateral length ratio clypeus/eyes = 1.7; narrowly microreticulated along lateral and anterior margins; ground punctation very fine, weakly impressed, interspaces 3–5 times as wide as punctures; systematic punctures moderately distinct. Eyes large, not protruding, slightly oblong. Antennae with eight antennomeres, antennomere 3 elongate. Maxillary palpi (Fig. 20) slender, as long as pronotum in midline, 0.8 times as long as maximum width of clypeus, length ratio palpomeres 4:3 = 1.5, palpomere 4 slightly asymmetrical. Mentum obsoletely punctate, microsculpture absent.

Thorax: Pronotal ground punctation as on head; systematic punctures distinct. Elytral ground punctation as on pronotum; four rows of distinct systematic punctures present, mesal rows with strongly reduced number of punctures, not reaching anterior margin. Mesoventrite with flat bulge.

Femora (Fig. 11): Pubescence present on more than proximal half of pro- and metafemur, on proximal 2/3 of mesofemur; hairline oblique on profemur, straight on mesofemur, concave on metafemur.

Abdomen: Ventrite 5 with shallow apical emargination.

Aedeagus (Fig. 2): Length: 0.32 mm. Phallobase longer than parameres, about as long as wide, manubrium destroyed in the holotype; border between pigmented and unpigmented portion of ventral face indistinct. Parameres short, stout, with weakly curving margins, almost equally wide from basis to apex, with very indistinct subapical constriction; apex bluntly rounded, slightly asymmetrical, slightly inclining mesad; ventral face distinctly wider than dorsal face; basal portion extending deeply into phallobase mesally. Median lobe bottle-shaped with strongly convex margins, strongly and abruptly narrowing to narrowly rounded apex, reaching apex of parameres; corona in subapical position; styli absent; basal apophyses long, reaching proximal third of phallobase, weakly separated mesally, strongly bending laterad.

REMARKS: Unfortunately, we cannot provide a barcode yet since the attempt to amplify *COI* sequences failed presumably due to the fact that material is too old for simple DNA amplification. However, all the examined material does not display any significant variations.

ECOLOGY: The species was collected only from presumably one and the same shallow creek running through secondary vegetation, surrounded by coconut plantations. During the more recent sampling event, specimens were retrieved from volcanic bottom gravel in a calm water section. *Agraphydrus ampullatus* and *A. tenuipalpis* were both collected north of Baybay, but it is unknown, whether they were collected in the same stream or not.

DISTRIBUTION (Fig. 38): Philippines: Leyte.

ETYMOLOGY: The name *ampullatus* (Latin adjective) is derived from *ampulla* (= bottle) and refers to the shape of the median lobe.

Agraphydrus batak sp.n.

Agraphydrus "sp. I": FREITAG & ZETTEL 2014: 20, 30.

TYPE LOCALITY: Philippines, Palawan Island and Province, Puerto Princesa City, Barangay Concepcion, Tarabanan River upstream of Batak village, secondary forest, ca. 100 m a.s.l., 10°2'7"N 119°1'10"E (Fig. 41).

TYPE MATERIAL: **Holotype** ♂ (PNM): "PHIL.: Palawan, Puerto Princesa; Concepcion, \ Tarabanan River; upstream Batak village, pool, \ littoral gravel; c. 100m asl., 10°2'7"N 119°1'10"E, \ 01.Feb.2015 leg. H.Freitag (16Cb)M". **Paratypes: P H I L I P P I N E S: Palawan:** 6 ♂♂, 3 ♀♀ (NMW): same sampling data as holotype; 1 ♂, 1 ♀, 3 exs. (ADMU): same site, date and collector, but leaf litter, side pool "16Ce"; 3 ♂♂ (PNM): same site, date and collector, leaf litter, pool "16Cl"; 1 ♂ (PNM): same river, date and collector, Camp Aga, ca. 8 km upstream highway, 10°5'8"N 119°0'33"E, 350 m a.s.l., littoral, gravel, pool "(16Eb1)"; 1 ♂ (ADMU): same site, date and collector, but leaf litter, hydropetric rocks "(16Ej)"; 2 ♂♂ (PNM): same river, date and collector, but ca. 9 km upstream highway, 10°6'0"N 118°59'38"E, 800 m a.s.l., leaf litter, side pool "(16Ye)"; 1 ♀ (NMW): Taytay, Poblacion, "Malaipit Campsite", Tubog Creek, 10°48'52"N 119°30'42"E, 80 m a.s.l., planted secondary forest, littoral gravel, run, 19.XI.2007, leg. H. Freitag "(64)M"; 1 ♀ (NMW): Taytay, Poblacion, creek near Taytay trail (Lake Manguao affluent), 10°47'12"N 119°31'40"E, 25 m a.s.l., residual pool, 3.IV.2008, leg. H. Freitag "(67)"; 1 ♂ [FR489] (ADMU): Taytay, Sinangalit Creek (Lake Manguao affluent), 10°46'46"N 119°31'5"E, 20 m a.s.l., gravel, rocks, CPOM, 27.IX.-16.X.2008, leg. H. Freitag "(73b)E"; 1 ♀ (NMW): Taytay, Poblacion, Malarad Creek (Lake Manguao affluent), 10°46'22"N 119°33'36"E, 20 m a.s.l., degraded primary forest, rocks, bolder, gravel, CPOM, pool, 4.XI.2007, leg. H. Freitag "(120)M"; 4 ♂♂, 4 exs. (ADMU): Taytay, Poblacion, small affluent of Lake Manguao, W coast, 10°45'57"N 119°31'29"E, 20 m a.s.l., secondary forest, 22.IV.2008, leg. H. Freitag "(68)M"; 1 ♂, 2 ♀♀ (ADMU): Roxas, Dumarao road km 158, Limapawan Creek, 10°28'47"N 119°21'18"E, secondary forest, littoral sand, shallow pool, 24.IX.1994, leg. J. Mendoza "(105b)M"; 2 ♂♂ [FR424], 2 ♀♀ (ADMU): Puerto Princesa, 0.5 km E Sabang, Sabang River estuary, 10°11'50"N 118°54'15"E, 2 m a.s.l., leaf litter, tree hole phytotelma, 29.III.2001, leg. H. Freitag "(26n)M"; 1 ♂ [FR473*] (ADMU): Puerto Princesa, Napsan, road km 42.5, Salakot Falls (small Iwahig River tributary), 9°42'5"N 118°31'18"E, 350 m a.s.l., degraded primary forest, leaf litter, rock pool, 1.IV.2008, leg. H. Freitag "(132e)M"; 4 ♂♂, 2 ♀♀, 4 exs. (ADMU, ZMB): Narra, 7 km N town center, mountain river downstream Estrella Falls, ca. 9°20'N 118°23'E, 50 m a.s.l., secondary forest, CPOM, pool, 16.12.2019, leg. H. Freitag "(180t)"; 1 ♂ (PCSD): Brooke's Point, Salogon, Manguguran mountain river, 8°44'7"N 117°42'15"E, 70 m a.s.l., secondary vegetation, rocks, CPOM, sand, riffle, 19.I.2020, leg. H. Freitag "(148)M"; 3 ♂♂ (SMTD): Brooke's Point, Salogon, mountain creek (Tagbinacao River tributary), 8°44'2"N 117°42'27"E, 120 m a.s.l., secondary vegetation, hydropetric rocks, 1.XI.2019, leg. H. Freitag "(147j)M"; 6 ♂♂, 4 ♀♀, 2 exs. (ADMU): same site, date and collector, but leaf litter, pool "(147l)M".

COMPARATIVE MATERIAL EXAMINED: *Agraphydrus* cf. *batak*:

P H I L I P P I N E S: Busuanga: 1 ♂ [FR422*] (ADMU): Salvacion Proper, lowland creek, 12°7'38"N 119°56'26"E, 50 m a.s.l., secondary forest, leaf litter, residual pools, 23.XII.2019, leg. H. Freitag "(174)M"; 1 ♂ (ADMU): "Y.K.R.", 1 km SE Airport, small lowland river, 12°6'48"N 120°6'6"E, 40 m a.s.l., secondary vegetation, 31.XII.2019, leg. H. Freitag "(179)M"; 1 ♂ [FR522] (ADMU): 1 km E Guadelupe, mountain creek, 12°3'22"N 120°11'10"E, 120 m a.s.l., secondary vegetation, CPOM, mud, residual pools, 25.XII.2019, leg. H. Freitag "(160a)M".

DIFFERENTIAL DIAGNOSIS: Shares absence of clypeal microreticulation and unicolored maxillary palpi with *A. tenuipalpis* and some specimens of *A. abrasus*. Differs in small eyes and explanate elytral margins posteriorly, shares broad habitus and emarginate apex of median lobe with *A. abrasus*; differs in distinct pronotal ground punctures and in apex of parameres not inflated from this species.

DESCRIPTION: Total length: 1.9–2.1 mm, elytral width: 1.0–1.2 mm, E.I.: 1.1, P.I.: 2.3, elytra 2.6 times as long as pronotum. Habitus (Fig. 30) broad, evenly oval, moderately convex, margins of elytra weakly explanate apically.

Coloration: Labrum yellowish brown; clypeus dark yellowish brown or black, dark yellow triangular preocular patches present, as large as diameter of eye; frons black; maxillary palpi unicolored yellow; pronotum dark brown to black with undefined narrow yellow lateral margins; elytra black; ventrites black; legs light brown.

Head: Clypeus with distinctly emarginate anterior margin, C.I.: 3.9, lateral length ratio clypeus/eyes = 2.5; ground punctation moderately fine; microreticulation indistinctly present along lateral margins, absent from anterior margin; systematic punctures indistinct. Eyes small, not protruding, oblong. Antennae with nine antennomeres, second intermediate segment (= antennomere 4) indistinctly separated, ca. 5 µm long. Maxillary palpi (Fig. 21) stout, 0.9 times as long as pronotum in midline, 0.7 times as long as maximum width of clypeus, length ratio palpomeres 4:3 = 1.4, palpomere 4 almost symmetrical. Mentum with very fine, widely spaced punctures, microsculpture absent.

Thorax: Pronotal ground punctation moderately fine; systematic punctures distinct. Elytral ground punctation moderately fine, punctures slightly larger than on pronotum; four rows of distinct systematic punctures present, mesal rows present in anterior half, but not reaching anterior margin. Mesoventrite with distinct bulge and very low horizontal ridge.

Femora (Fig. 12): Pubescence present on proximal 2/3 of profemur and metafemur, on proximal 3/4 of mesofemur, hairline oblique on pro- and mesofemur, rounded on metafemur.

Abdomen: Ventrite 5 without apical emargination in most specimens, present in one male specimen, ca. 5 µm deep.

Aedeagus (Fig. 3): Length: 0.32–0.43 mm. Phallobase slightly shorter than parameres, slightly longer than wide, evenly narrowing to distinct, very small manubrium; border between pigmented and unpigmented portion of ventral face indistinct. Parameres with very slightly curving margins; apex narrowly rounded, slightly inclining mesad; basal portion weakly reaching into phallobase. Median lobe moderately wide, margins almost parallel; apex not reaching apex of parameres, apex of ventral face broadly rounded, apex of dorsal face with distinct semicircular emargination; corona in apical third; styli absent; basal apophyses short, reaching distal fourth of phallobase.

REMARKS: The only sequenced specimen from Busuanga resembles *Agraphydrus batak* in major diagnostic characters, but varies in the overall distinctly paler, light brown color. However, especially the significant genetic distance of 8.4 % (Tab. 2) between this specimen and that from central Palawan does hardly justify treating it as conspecific. It might eventually be described when more material becomes available.

ECOLOGY: The species inhabits creeks and small rivers flowing through rather pristine, forested areas (Fig. 41), where it was collected predominantly from leaf litter and other CPOM deposits (Figs. 45–46), but also bottom gravel (Fig. 47) in calm zones. Several specimens were found in isolated side pools, hygropetric rocks (Fig. 48) and even a phytotelma, all with leaf litter deposits. One specimen was retrieved from an emergence trap sample. The species shares some collection sites with *Agraphydrus palawanensis* and *A. pelingeni*.

DISTRIBUTION (Fig. 38): Philippines: Palawan Island.

ETYMOLOGY: The name is dedicated to the ethnic group of the Batak, who inhabit a village near the type locality and welcomed and guided the collector very friendly. Noun in apposition.

Agraphydrus brevilobatus sp.n.

TYPE LOCALITY: Philippines, Negros Occidental, Silay, Patag, small mountain river, downstream Dumalabdab Falls, secondary forest, 800 m a.s.l., 10°41'10"N 123°10'43"E (Fig. 42).

TYPE MATERIAL: **Holotype** ♂ (PNM): "PHIL.: Negros Occ, Silay, Patag, small mount. Riv. \ downstr. Dumalabdab Falls, sec. forest; 800 m a.s.l., \ 10°41'10"N 123°10'43"E 3.V.2019 leg.Freitag(652)L". **Paratypes**: **PHILIPPINES**: **Negros**: 1 ♂ [FR531*] (ADMU): same sampling data as holotype; 1 ♂ [FR420*], 1 ♀

(NMW): Murcia, Pandanon River, 10°34'54"N 123°10'30"E, 440 m a.s.l., secondary vegetation, 1.V.2019, leg. H. Freitag et al. "(650)L".

ADDITIONAL MATERIAL EXAMINED:

PHILIPPINES: Panay: 1 ♂, 3 ♀ (NMW): Antique, 50 km NE San Jose, 20.III.1994, leg. S. Schödl "6"; 3 ♀ (ADMU, PNM): Aklan, Nabas, Lacerna, Malindug Valley, 11°50'33"N 122°1'31"E, 60 m a.s.l., secondary forest, leaf litter, rock pool, 23.II.2014, leg. H. Freitag & M. Manuel-Santos "(601e)M".

DIFFERENTIAL DIAGNOSIS: Belongs to group of species with microreticulate anterior clypeal margin and unicolored maxillary palpi. Shares these features with *A. ampullatus*, *A. palawanensis*, and *A. pelingeni*, and some specimens of *A. abrasus*. Differs in dark brown to black clypeus and pronotum from *A. palawanensis*, in slightly less broad habitus, presence of yellow preocular patches, and light brown areas on posterior parts of elytra from *A. ampullatus*, in slightly broader habitus from *A. pelingeni*, and in fine ground punctation of head and pronotum from *A. abrasus*. Differs in features of aedeagus (e.g., parameres very short, stout; ventral face of median lobe distinctly narrowed in mid-length, dorsal face of median lobe very wide) from all species mentioned. Shares microreticulate anterior clypeal margin, unicolored maxillary palpi, dark brown clypeus with yellow preocular patches, dark brown pronotum and elytra, and eight antennomeres with *A. schoedli* KOMAREK, 2019. Differs in smaller size (body length of *A. schoedli* = 2.4–2.8 mm), large eyes, very fine ground punctation, and features of aedeagus (e.g., parameres very short, basal lobe very large) from this species.

DESCRIPTION: Total length: 1.9–2.0 mm; elytral width: 0.9–1.0 mm; E.I.: 1.4, P.I.: 2.1, elytra 3.0 times as long as pronotum. Habitus (Fig. 31) moderately broad, elytra parallel-sided, moderately convex.

Coloration: Labrum, and clypeus dark brown to black; clypeus with yellow preocular patches about as wide as eye; frons black; maxillary palpi unicolored yellow; pronotum dark brown to black with narrow yellowish lateral margins; elytra dark brown to black with undefined light brown areas posteriorly; ventrites dark brown, legs lighter than ventrites.

Head: Clypeus with weakly emarginate anterior margin, C.I.: 3.9, lateral length ratio clypeus/eyes = 1.7, with narrow microreticulation at lateral and anterior margins; ground punctation very fine, widely spaced; systematic punctures distinct. Eyes large, not protruding, slightly oblong. Antennae with eight antennomeres. Maxillary palpi (Fig. 22) slender, as long as pronotum in midline, 0.8 times as long as maximum width of clypeus, length ratio palpomeres 4:3 = 1.4–1.5, palpomere 4 symmetrical. Mentum with few, very fine, widely spaced punctures, microsculpture absent.

Thorax: Pronotal ground punctation as on head; systematic punctures distinct. Elytral ground punctation as on head and pronotum; four rows of distinct systematic punctures present, mesal rows with strongly reduced number of punctures, not reaching anterior margin, additional coarse punctures present along lateral margins. Mesoventrite with mesal bulge.

Femora (Fig. 13): Pubescence present on more than proximal half of pro- and metafemur, on proximal 2/3 of mesofemur; hairlines slightly oblique.

Abdomen: Ventrite 5 with almost semicircular apical emargination, ca. 20 µm deep.

Aedeagus (Fig. 4): Length: 0.25 mm. Phallobase broad, distinctly longer and wider than parameres, as wide as long, abruptly narrowing to strong manubrium, border between pigmented and unpigmented portion of ventral face indistinct, almost reaching manubrium. Parameres short, with sigmoid margins; apex inflated, very slightly inclining mesad, ventral face slightly wider than dorsal face; basal portion reaching distal third of phallobase. Ventral face of median lobe screw-wrench-shaped, wide proximal and distal, narrowed in mid-length, dorsal face very wide, widest in mid-length; apex broadly rounded, reaching apex of parameres; corona in subapical

position; styli absent; basal apophyses short, distinctly separated, almost reaching mid-length of phallobase.

REMARKS: The attempt to generate a barcode for the Panay material failed. Since specimens agree well with those from the type locality and the two islands belong to the same intra-Philippine biogeographic region, we have no doubt that they are conspecific. The species varies by at least 4.8 % genetic distance (Tab. 2) from any other Philippine *Agraphydrus* species, and seems to be closely related to *A. abrasus* (Fig. 40).

ECOLOGY: All collection sites were in forested areas (Fig. 42). Except for ambiguously identifiable female specimens from an isolated side pool with leaf litter, no microhabitat information is available, since most of the type material was collected at black light. It shares one collection site with *A. zetteli* in Panay.

DISTRIBUTION (Fig. 38): Philippines: Negros, Panay.

ETYMOLOGY: The name *brevilobatus* is derived from *brevis* (Latin adjective) (= short) and *lobatus* (Latin adjective) (= lobed) and refers to the short parameral lobes.

Agraphydrus coomani (ORCHYMONT, 1927)

Helochaeres (*Agraphydrus*) *coomani* ORCHYMONT 1927: 248.

Agraphydrus coomani (ORCHYMONT); WATTS 1995: 115; KOMAREK & HEBAUER 2018: 34; KOMAREK 2018: 122; KOMAREK 2019: 174–179.

Agraphydrus (s.str.) *coomani* (ORCHYMONT); HANSEN 1999: 156.

Enochrus ryukyuensis MATSUI 1994: 217; KOMAREK & HEBAUER 2018: 34 (syn.).

Agraphydrus ryukyuensis (MATSUI); GENTILI et al. 1995: 208.

Agraphydrus (s.str.) *ryukyuensis* (MATSUI); HANSEN 1999: 157; PRZEWOŹNY 2019: 26.

TYPE LOCALITY: Vietnam, Hòa Bình Province, Lạc Tho.

TYPE MATERIAL: See KOMAREK & HEBAUER (2018).

ADDITIONAL MATERIAL EXAMINED:

P H I L I P P I N E S: **Leyte:** 1 ♀ [FR535*] (ADMU): Ormoc, Dolores, Lake Danao affluent creek, 11°4'37.8"N 124°41'46.0"E, 650 m a.s.l., secondary vegetation, 26.IX.2016, leg. J. Garces "(520)L"; **Luzon:** 4 ♂♂ [FR539*], 4 ♀♀ (ADMU, ZMB): Ilocos Sur, Suyo, big river downstream Sangbay ni Ragsak, 16°59'32"N 120°32'21"E, ca. 100 m a.s.l., littoral gravel, pool, 15.IV.2019, leg. H. Freitag, J. Garces & C. Pangantihon "(447b)M"; 1 ♂ (ZMB): Benguet, Tuba, Taloy Sur, upper Tapuacan River, 16°21'33"N 120°30'31"E, ca. 400 m a.s.l., secondary vegetation, littoral gravel, pool, 19.IX.1997, leg. W. Mey "(460b)"; 1 ♂ [FR501] (ADMU): Tarlac, Tibagan, river, 15°27'17"N 120°31'57"E, ca. 60 m a.s.l., grassland, secondary vegetation, sand, sun-exposed side pool, 4.IV.2015, leg. J. Mendoza "(402m)M"; 2 exs. (ADMU): Bulacan, 14 km E San Miguel, Biak-na-Bato National Park, 0.3 km upstream Batu Paniol Cave, ca. 15°6'N 121°6'E, littoral pool, 10.IV.1995 leg. J. Mendoza "(28a)M"; 5 exs. (ADMU): same sampling site, date and collector, but side pool "(28b)M"; 1 ♀ (ADMU): SBMA area, Jadjad River, 14°50'32"N 120°21'30"E, ca. 60 m a.s.l., secondary vegetation, littoral gravel, pool, 1.II.2016, leg. H. Freitag "(SJRb)M"; 1 ♂ (ADMU): SBMA area, Batalan mountain river, ca. 14°45'N 120°21'E, 65 m a.s.l., secondary vegetation, grass, fresh root bunches, run, 29.I.2016, leg. H. Freitag "(403h)M"; 5 ♂♂, 3 ♀♀ (ADMU): Rizal, Puray, Makapikapi, Rodriquez River tributary, ca. 14°45'N 121°12'E, ca. 130 m a.s.l., secondary forest, leaf litter, side pool, 25.II.1994, leg. J. Mendoza "(400e)M"; 14 exs. (NMW): Laguna, Los Baños, stream in botanical garden, 200 m a.s.l., 28.XI.1995, leg. J. Kodada; 3 exs. (NMW): same sampling site, date and collector, but small river; 1 ♂ [FR437*], 1 ♀ (NMW): 30 km E Lucena City, Quezon National Park, 23.XI.1992, leg. M. Jäch "11"; 5 ♂♂ [FR479], 2 ♀♀ (SMTD): Camarines Sur, Caramoan River, 23.X.1992, leg. J. Vichoza "P449"; 2 ♂♂ (SMTD): Camarines Sur, Bahi, Bicol National Park, 26.X.1992, leg. J. Vichoza "P452".

COMPARATIVE MATERIAL EXAMINED *Agraphydrus* cf. *coomani* (*A.* "sp. A"): FREITAG & PANGANTIHON 2010: 135, 145):

P H I L I P P I N E S: **Balabac:** 1 ♀ [FR477*] (ADMU): Indalawan, Suray River, 7°57'0"N 117°4'30"E, ca. 20 m a.s.l., secondary vegetation, littoral gravel, side pool, 25.VII.2019, leg. C. Pangantihon & A. Pelingan "(89t)M";

Busuanga: 1 ♂, 2 exs. [FR405*] (ADMU): 5 km NW Coron town, Mabintangan River tributary, creek upstream artificial pool, 12°1'44"N 120°12'19"E, 50 m a.s.l., secondary forest, gravel, root bunches, leaves, run, 2.II.2020, leg. H. Freitag "(167b)M"; 2 exs. [FR480*] (ADMU): New Busuanga, 3 km S Quezon, small lowland river, 12°14'20"N 119°55'42"E, 20 m a.s.l., farmland, leaf packs, riffle, 23.XII.1995, leg. J. Mendoza "(175b)M"; **Leyte:** 1 ex. [FR533*] (ADMU): Ormoc, Dolores, creek (Lake Danao affluent), secondary vegetation, 11°43'7.8"N 124°41'46.0"E, 650 m a.s.l., leg. J. Garces, 26.IX.2016 "(520)L"; 6 exs. (MNS): N Baybay, Visayas State University, 100–200 m a.s.l., secondary forest, 27.II.1991, leg. W. Schwallier et al.; 1 ♂ (ADMU): Baybay, Patag, E Visayas State University, small Lagu-Lagu River, ca. 10°45'N 124°48'E, degraded forest, volcanic rocks, gravel, pool, 27.V.1995, leg. H. Freitag "(229a)M"; **Mindoro:** 3 ♂♂ [FR476*], 2 ♀♀ (ADMU): Abra de Ilog, Balao, 13°23'31"N 120°39'55"E, 65 m a.s.l., littoral gravel, pool, 3.I.1995, leg. J. Mendoza "(372b)M"; 1 ♂ (NMW): 10 km W Puerto Galera, 17.XI.1992, leg. M. Jäch "5"; 1 ♀ (NMW): same site, 24.–25.XI.1992, leg. H. Schillhammer "12"; 1 ♀ (NMW): W Puerto Galera, Talipanan river 30.XI.1993, leg. M. Jäch "20"; 5 ♂♂, 3 ♀♀ (NMW): SE Puerto Galera, 14.XI.1992, 100 m a.s.l., leg. M. Jäch "3"; 2 ♂♂, 1 ♀ (ADMU): Puerto Galera, 2 km S Muelle, Tagbinai Munti River, hill creek, 13°29'0"N 120°57'12"E, 10 m a.s.l., coconut plantation, littoral gravel, pool, 22.IV.2019, leg. H. Freitag "(301b2)M"; 1 ♂, 1 ♀ (ADMU): Puerto Galera, road km 37.2, Tamaraw River, 13°27'3"N 120°59'27"E, 5 m a.s.l., secondary vegetation, littoral gravel, pool, 7.VIII.2014, leg. H. Freitag & M. Manuel-Santos "(302b1)M"; 1 ♂ (ADMU): Puerto Galera, Bisaa River tributary, 13°26'20"N 121°0'25"E, 30 m a.s.l., rural/secondary vegetation, 7.VI.2019, leg. H. Freitag "(340)L"; 10 ♂♂, 5 ♀♀ (ADMU): Baco, Pinagsabangan River, 13°19'56"N 121°7'39"E, 10 m a.s.l., rural meadow, littoral gravel, pool, 25.VIII.2018, leg. H. Freitag & C. Pangantihon & A. Baylon "(355b)M"; 1 ♀ (ADMU): Socorro, Lapug, S coast Naujan Lake, 13°6'46"N 121°19'0"E, 3 m a.s.l., shallow littoral, submersed plants, 22.II.2010, leg. H. Freitag & C. Pangantihon "(307b)M"; 3 ♂♂ [FR446], 2 exs. (ADMU): Sablayan, small karst river, 12°47'49"N 120°54'33"E, ca. 100 m a.s.l., disturbed primary forest, 1.I.1995, leg. J. Mendoza "(365h)L"; 2 ♂♂ [FR502], 1 ♀ (ADMU): Roxas, Formon, Pastuhan, Tangisan Falls, ca. 12°43'N 121°23'E, 200 m a.s.l., secondary forest, deep mountain valley, littoral sand, pool, 27.X.2018, leg. H. Freitag "(318b)M"; 1 ♂ (ADMU): same sampling site, date and collector, but bottom gravel, run "(318c)M"; 2 ♂♂, 1 ♀ (ADMU): Roxas, San Vicente, Sitio Taugad Diit, Taugad Daka River (Baroc River tributary), 12°37'33"N 121°22'18"E, 180 m a.s.l., secondary vegetation, littoral sand, mud, pool, 5.II.2018, leg. H. Freitag "(TDR1b)M"; 1 ♂ (ADMU): Roxas, San Vicente, Hiyong Creek, 12°37'27"N 121°22'48"E, ca. 150 m a.s.l., secondary vegetation, CPOM, side pool, 1.VII.2012, leg. K. Go & A. Vidal "(THCe)M"; 1 ♂, 2 ♀♀ (ADMU): Bulalacao, Bagonsikat, Paluguan River, 12°21'22"N 121°17'3"E, ca. 100 m a.s.l., secondary forest, limestone, lime sand, CPOM, pool, 29.XII.1994, leg. J. Mendoza "(361t)M"; **Mindanao:** 1 ♂ (NMW): Mindanao, ca. 5 km ESE Surigao, Cagniog Escalope River, ca. 9°45'N 125°31'E, 30 m a.s.l., secondary forest, limestone, 22.IV.1996, leg. H. Freitag "54M"; 11 exs. (NMW): Cagayan de Oro, 5 km S Balingoan, Caipaan River, ca. 8°57'N 124°49'E, 20 m a.s.l., secondary vegetation, side pool, 16.IV.1996, leg. H. Freitag "39M"; **Negros:** 19 exs. (NMW): Lizares W Bacolod, Bago River, ca. 500 m a.s.l., 17.III.1994, leg. S. Schödl "4"; 1 ♂ (NMW): SE Bacolod, Mambucal, ca. 900 m, 15.III.1994 leg. S. Schödl "1"; **Panay:** 2 ♂♂, 6 ♀♀ (ADMU): Aklan, Nabas, Lacerna, Malindug, small mountain river, 11°50'23"N 122°1'7"E, 90 m a.s.l., secondary forest, littoral sand, gravel, pool, 23.II.2014, leg. C. Pangantihon "(601b)M"; 3 exs. (NMW): Antique, 50 km NE San Jose, 20.III.1994, leg. S. Schödl "6"; 4 exs. (NMW): Ilo-Ilo, 2 km N Igaras, 22.III.1994, leg. S. Schödl "10"; 1 ♀ (NMW): Ilo-Ilo, 2 km N Igaras, Nadsadan River, 150 m a.s.l., 22.III.1994, leg. H. Zettel "46"; 2 exs. (NMW): Ilo-Ilo, 10 km N Igaras, ca. 400 m a.s.l., 22.III.1994 leg. S. Schödl "8"; **Palawan:** 2 ♂♂ [FR527*] (ADMU): El Nido, Pasadeña, Nagkalit-Kalit Falls, small mountain river, ca. 11°15'N 119°26'E, degraded primary forest, rocks, gravel, wood litter, littoral, 20.XII.2019, leg. A. Pelingen "(112b)M"; 3 exs. (NMW): Taytay, Cataban, highway km 230, lowland river, 10°59'15"N 119°24'12"E, farmland, gravel, slightly polluted, 16.X.2007, leg. H. Freitag "(115)M"; 1 ex. (NMW): Taytay, Poblacion, "Malaipit Campsite", Tubog Creek, 10°48'52"N 119°30'42"E, 80 m a.s.l., planted secondary forest, littoral gravel, run, 19.XI.2007, leg. H. Freitag "(64)M"; 25 exs. (NMW): Puerto Princesa, ca. 13 km N San Rafael, Tarabanan River, ca. 30 m a.s.l., 7.XII.1995, leg. J. Kodada & B. Rigová; 8 exs. (NMW): Puerto Princesa, 18 km NE San Rafael, Olangan River, 6.XII.1995, leg. J. Kodada & B. Rigová; 1 ♂, 1 ♀ (ADMU): Puerto Princesa, Concepcion, Tarabanan River, ca. 6 km upstream highway, 10°2'30"N 119°0'45"E, ca. 150 m a.s.l., littoral gravel, pool, 1.II.2015, leg. H. Freitag "(16Db)M"; 2 ♂♂ (ADMU): same date, river and collector, but Camp Aga, ca. 8 km upstream highway, 10°5'8"N 119°0'33"E, ca. 350 m a.s.l., littoral gravel, pool "(16Ew)M"; 1 ♂ (ADMU): same site, date and collector, but littoral gravel, pool "(16Eb1)M"; 4 exs. (NMW): 7 km N Narra, Estrella Falls, 5.IV.1994, leg. H. Zettel "59"; 2 exs. (NMW): Puerto Princesa, Sabang, 50–100 m a.s.l., degraded forest on slope, 30.XI.1995, leg. J. Kodada & B. Rigová; 1 ♂, 4 exs. (NMW): Puerto Princesa, Sta. Cruz, Calatobong River, highway km 29, 9°56'41"N 118°44'56"E, 25 m a.s.l., secondary vegetation, ultramaphic soil, CPOM, side pools, 14.XI.2007, leg. H. Freitag "(124)M"; 1 ♀ (ADMU): Puerto Princesa, 2 km SE Laptay (Napsan), Bubugtungan mountain stream, 9°41'14"N 118°27'17"E, semi-primary forest, 22.XI.2007, leg. H. Freitag "(23)L"; 2 exs. (ADMU): same site and collector, but littoral gravel, pool, 29.III.2008 "(23)M"; 4 exs.

(NMW): Puerto Princesa, 2 km SE Laptay (Napsan), Kalalagbong Forest, Tagbanua rainforest station, 9°41'20"N, 118°27'15"E, small puddles, 7.X.2008, leg. H. Freitag "(24b)M"; 2 ♂♂ [FR428], 2 exs. (ADMU): Narra, 5 km W town proper, Taritien River, 9°19'11"N 118°22'35"E, ca. 100 m a.s.l., boulders, gravel, wood litter, riffle, 6. VIII.2019, leg. C. Pangantihon "(182a)"; **Samar**: 1 ♂ [FR430*] (ADMU): Taft, San Rafael, small river, 11°49'39"N 125°16'29"E, 160 m a.s.l., rural/secondary vegetation, 22.X.1995, leg. J. Mendoza "(509)L"; 1 ♂ [FR514*] (ADMU): Borongan, San Mateo, hill creek below fall, 11°37'11"N 125°23'37"E, 25 m a.s.l., rural/secondary vegetation, littoral sand, pool, 21.X.1995, leg. J. Mendoza "(507b)M"; 2 ♂♂ [FR530*], 4 exs. (ADMU): Borongan, San Mateo, small hill creek, 11°37'15"N 125°23'36"E, 30 m a.s.l., secondary vegetation, gravel, side pool, 21.X.1995, leg. J. Mendoza "(506t)M"; **Tablas**: 1 ♀ [FR528*] (ADMU): Odiongan, small river, 12°25'7"N 122°2'55"E, ca. 120 m a.s.l., 26.III.2019, leg. A. Pelingen "(727)M".

DIFFERENTIAL DIAGNOSIS: Belongs to group of species with apically infuscated maxillary palpomere 4 and absence of clypeal microreticulation (*A. coomani* group, see Discussion), together with *A. occultus* and *A. zetteli*. Differs in eight-segmented antennae and features of aedeagus (parameres without lateral extensions, median lobe not reaching apex of parameres, corona situated near mid-length, styli present) from *A. occultus*. Differs in minor size, clypeus with distinct yellow preocular patches, lesser extension of femoral pubescence, and features of aedeagus (apex of parameres not inflated, median lobe moderately wide, corona situated near mid-length of median lobe) from *A. zetteli*.

DESCRIPTION: See KOMAREK & HEBAUER (2018). Species from the Philippines have the pronotum almost totally black, rarely dark brown, with narrow yellow lateral margins; individuals with narrowly and with broadly rounded parameres occur together.

REMARKS: We assign here a presumably rather basal sub-clade (FR437/FR535/FR539; Fig. 40) comprising specimens from Luzon and Leyte to this widespread species as they almost perfectly agree with the type material in external and genital characters. There is only 0.5–0.7 % genetic distance (Tab. 2) between these three specimens from Luzon and Leyte. Material that varies genetically by more than 6% (Tab. 2, Fig. 32) is presumably not conspecific. However, especially one clade from Mindoro (many specimens, but only FR476* successfully sequenced; Fig. 40) may represent an undescribed cryptic species, which cannot be distinguished morphologically. Among the remaining material there are several intra-Philippine regional clades, which vary by 5.3–12.6 % genetic distance from each other (Tab. 2), along with minor morphological differences. These minor differences are more or less consistent and include relative body width, extension, pattern and intensity of the dark pronotal areas, extension of femoral pubescence, shape of the parameral tips and length of the median lobe in relation to the parameres. Males are usually slightly smaller than females. See also the discussion below for further remarks.

ECOLOGY: Material of this complex of *Agraphydrus coomani* and closely related taxa was very frequently collected in the Philippines, although never in high numbers. Specimens treated here as *A. coomani* were collected in a wide range of aquatic habitats, from small creeks to large rivers, in almost pristine forests, open unshaded area, but also moderately disturbed, rural areas. They were found in calm stream sections, a sun-exposed, riverine side pool (Fig. 50) as well as in running water. The inhabited substrates were usually littoral sand and gravel deposits (Figs. 43, 47), but also submerged roots (Fig. 46) and grass. Some specimens were attracted by black light traps. They occurred commonly together with one or several of the endemic species, namely with *A. abrasus*, *A. ampullatus*, *A. occultus* and *A. zetteli*, sometimes in the same microhabitats.

DISTRIBUTION (Fig. 38): Sri Lanka, widespread in South East Asia (not yet found in Laos) including southern Japan and southern China, Taiwan, Australian Region (Papua New Guinea, Australia). Recorded from the Philippines for the first time.

Agraphydrus occultus sp.n.

TYPE LOCALITY: Philippines, Luzon Island, Laguna Province, Majayjay Municipality, Barangay Burgos, Taytay River downstream of Imelda Falls, secondary forest, 510 m a.s.l., 14°6'42"N 121°30'19"E.

TYPE MATERIAL: **Holotype** ♂ (PNM): "PHIL.: Luzon, Laguna, Majayjay, Taytay \ (mountain) River, littoral gravel, sec. forest, \ 510m asl. 14°6'42"N 121°30'19"E, \ 27Jun2018, leg. H. Freitag et al. (434b)M". **Paratypes:** **Luzon:** 2 ♂♂ [FR482*], 3 exs. (ADMU): same sampling data as holotype; 1 ♂, 2 ♀♀ (NMW): Ifugao, Banaue, 4.V.1994, leg. C.F. Lee; 2 ♂♂, 2 ♀♀ (NMW): Mountain Province, NE Sagada, Banga'an, Bomod-ok Waterfall, 22.II.1999, leg. S. Schödl "19"; 1 ♂ (SMTD): Mountain Province, Sagada, "Underground River", downstream of cave, ca. 1450 m a.s.l., ca. 17°5'N 120°54'E, 14.III.1995, leg. J. Mendoza "5"; 1 ♀ (NMW): Mountain Province, Gonogon Chico River, ca. 900 m a.s.l., 21.II.1999, leg. S. Schödl "18"; 3 ♂♂, 4 ♀♀ (ADMU, ZMB): Mountain Province, Bauko, mountain creek, 17°3'53"N 120°5'10"E, 1820 m a.s.l., secondary forest, mineral rich water, 17.XI.1997, leg. W. Mey "(454)L"; 4 ♂♂, 3 ♀♀, 3 exs. (ADMU, ZMB): Mountain Province, Bauko, Bayudan River tributary, 16°59'6"N 120°52'13"E, 1170 m a.s.l., rural/agricultural area, boulders, sand, side pool, 16.XI.1997, leg. W. Mey "(450t)M"; 1 ♂, 1 ex. (ADMU): Ilocos Sur, Suyog, Tagudin-Cervantes-Sabangan Road, Besang Pass area, mountain creek, 16°57'17"N 120°38'87"E, ca. 1200 m a.s.l., secondary forest, 15.IV.2019, leg. H. Freitag, J. Garcés & C. Pangantihon "(448)L"; 1 ♂ (SMTD): Ifugao, Banaue, Batad, Tapiyah Waterfall, ca. 750 m, ca. 16°56'N 121°9'E, 11.III.1995, leg. J. Mendoza "3"; 1 ♀ (NMW): Benguet, W Baguio, Asin Road, ca. km 7, 17.II.1999, leg. S. Schödl "11"; 1 ♂ (NMW): Benguet, S Baguio, Kennon Road, Bridal Falls, 16.II.1999, leg. S. Schödl "9"; 2 exs. (ZMB): Benguet, Bukod River, 16°29'12"N 120°49'49"E, ca. 1000 m a.s.l., 18.XI.1997, leg. W. Mey "(459)L"; 2 ♂♂ (ZMB): Benguet, Tuba, Taloy Sur, mountain creek, 16°21'33"N 120°30'31"E, ca. 400 m a.s.l., littoral gravel, pool, 19.XI.1997, leg. W. Mey "(460b)M"; 2 ♂♂ [FR438*], 2 exs. (ADMU): SBMA area, Jadjad River, 14°50'32"N 120°21'30"E, ca. 60 m a.s.l., secondary vegetation, littoral gravel, pool, 1.II.2016, leg. H. Freitag "(SJRb)M"; 2 ♂♂ [FR414*], 1 ♀ (ADMU, PNM): Baatan, Samal, Orani River, 14°44'15" N 120°24'58" E, 460 m a.s.l., secondary forest, 18.VI.2017, leg. H. Freitag "(442)L"; 2 ♂♂ [FR443] (ADMU): Rizal, Rodriguez, Puray, Sitio Mabolob, Puray Falls, 14°46'35"N 121°12'52"E, ca. 150 m a.s.l., CPOM, side pool, 25.II.1994, leg. J. Mendoza "(401e)M"; 1 ♂ (ADMU): Quezon, Real, Cogeo-Infanta Road, mountain creek near resort, 14°34'49"N 121°30'38"E, ca. 660 m a.s.l., secondary forest, littoral, sand, gravel, pool, 25.III.1996, leg. J. Mendoza "(411b)M"; 1 ♂ [FR475], 1 ♀ (ADMU): Batangas, Balete, small polluted creek (Lake Taal affluent), 14°0'33"N 121°5'44"E, 4 m a.s.l., secondary vegetation, littoral sand, pool, 22.V.1996, leg. J. Mendoza "(423b)M".

ADDITIONAL MATERIAL EXAMINED:

P H I L I P P I N E S: **Mindoro:** 1 ♂, 1 ♀ (NMW): 28 km S Calapan, Balete, 100–700 m a.s.l. 27.–29.XI.1992, leg. M. Jäch "19"; 1 ♂ [FR512] (ADMU): Roxas, San Vicente, Sitio Taugad Diit, Taugad Diit River (Baroc River tributary), 12°37'32"N 121°22'17"E, 180 m a.s.l., secondary vegetation, littoral sand, gravel, pool, 5.IV.2018, leg. H. Freitag "(TIR1b)M"; 1 ♀ (ADMU): Roxas, San Vicente, Sitio Taugad Diit, Taugad Daka River (Baroc River tributary), 12°37'33"N 121°22'18"E, 180 m a.s.l., secondary vegetation, bottom gravel, run, 4.IV.2018, leg. H. Freitag "(TDR1c)M"; 1 ♂ (ADMU): same site, but CPOM, side pool, 23.I.2013, leg. C. Pangantihon "(TDR1e4)M".

COMPARATIVE MATERIAL EXAMINED: *Agraphydrus* cf. *occultus*:

P H I L I P P I N E S: **Palawan:** 2 ♂♂ (ADMU): Puerto Princesa, SSW Martapi, Cabayugan River, 10°9'46"N 118°49'29"E, 21.X.2000, leg. H. Freitag "CR1"; **Panay:** 2 ♂♂ [FR413], 5 ♀♀ (ADMU): Aklan, Nabas, Lacerna, Malindug, small mountain river, 11°50'23"N 122°1'7"E, 90 m a.s.l., secondary forest, sand, gravel, pool, 23.II.2014, leg. C. Pangantihon "(601b)M"; 2 ♀♀ (ADMU): NW Panay Peninsula Natural Park, middle Bulanan River, 11°46'54"N 121°58'25"E, ca. 100 m a.s.l., secondary vegetation, littoral gravel, pool, 26.II.2014, leg. C. Pangantihon & M. Manuel-Santos "(603b)M".

DIFFERENTIAL DIAGNOSIS: Belongs to group of species with apically infuscated maxillary palpomere 4 and absence of clypeal microreticulation (*coomani* group, see Discussion). Shares these characters with *A. coomani* and *A. zetteli*. Differs in larger size and larger extension of femoral pubescence from *A. coomani*, in eight antennomeres from *A. coomani* and *A. zetteli*, in features of aedeagus (parameres with lateral projection apically, median lobe almost reaching apex of parameres, styli absent) from both species. Shares very similar aedeagus with *A. jilanzhui* KOMAREK & HEBAUER, 2018, differs in light brown elytra (black in *A. jilanzhui*). Shares eight antennomeres with *A. manfredjaechi* KOMAREK, 2019, but differs in lateral extensions of apex of parameres.

DESCRIPTION: Total length: 2.1–2.5 mm; elytral width: 0.9–1.2 mm; E.I.: 1.4–1.5, P.I.: 2.0, elytra 3.2–3.4 times as long as pronotum. Habitus (Fig. 33) moderately slender, elytra slightly widening posterior to mid-length, weakly convex.

Coloration: Labrum, clypeus and frons black; clypeus with distinct, defined, preocular patches, slightly smaller than diameter of eye; maxillary palpi yellow, palpomere 4 with apical infuscation; pronotum black with narrow yellow lateral margins; elytron light brown in mesal half, undefined dark brown in lateral half; ventrites and legs dark brown.

Head: Clypeus with distinctly emarginate anterior margin, C.I.: 3.1, lateral length ratio clypeus/eyes = 1.9; microsculpture absent; ground punctation moderately strong, interspaces 1–2 times as wide as punctures; systematic punctures distinct. Eyes large, not protruding, slightly oblong. Antennae with eight antennomeres, antennomere 3 incompletely subdivided in some individuals. Maxillary palpi (Fig. 23) slender, 1.2–1.4 times as long as pronotum in midline, 1.0–1.1 time as long as maximum width of clypeus, length ratio palpomere 4:3 = 1.2–1.3, palpomere 4 slightly asymmetrical. Mentum with moderately strong punctures, mesal portion slightly rugose.

Thorax: Pronotal ground punctation as on head; systematic punctures distinct. Elytral ground punctation as on head and pronotum; four rows of distinct systematic punctures present, mesal row with reduced number of punctures, not reaching anterior margin. Mesoventrite with mesal bulge.

Femora (Fig. 14): Pubescence present on proximal 2/3 of profemur, on proximal 3/4 of meso- and metafemur; hairlines slightly oblique on pro- and mesofemur, straight on metafemur.

Abdomen: Ventrite 5 with almost semicircular apical emargination, ca. 10 µm deep.

Aedeagus (Fig. 5): Length: 0.34–0.35 mm. Phallobase about as long as parameres, longer than wide, evenly narrowing proximad, distinct manubrium absent; border between pigmented and unpigmented portion of ventral face indistinct. Parameres slender, with slightly curving margins, with slight subapical constriction; apex widening, with broadly rounded lateral projection and weakly rounded mesal edge; basal portion of dorsal face reaching distal third of phallobase. Median lobe moderately wide, narrowing in mid-length; apex broadly rounded, almost reaching apex of parameres; corona situated apically; styli absent; basal apophyses moderately long, almost reaching distal third of phallobase.

REMARKS: The species is quite variable in size (2.1–2.5 mm total length) even among specimens from the same site, particularly some (but not all) male specimens are obviously smaller (2.1 mm) than the average (2.4 mm).

The material from Mindoro, Palawan and Panay is externally not distinguishable from the type material. Size and shape of the aedeagi in specimens from Panay and Palawan agree also quite well with the type material, except for a slightly more conical apical phallobase, more pronounced outer and additionally slight inner subapical parameral constrictions, emphasizing the impression of inflated parameral apices; both, inner and outer parameral margins, are slightly concave (vs. entirely straight inner margin in type specimens); styli tend to be more prominent and usually overreach the broadest area of the median lobe.

Since DNA barcodes are only available from Luzon specimens (Tab. 1), we only treat specimens from this island as type material, given the cryptic nature observed in other ‘morpho-species’.

ECOLOGY: The species is quite common. It was mainly collected in slightly disturbed areas from small creeks to medium sized rivers (Figs. 43–44). Specimens were most commonly retrieved from calm river sections and associated side pools with littoral gravel and sand deposits (Fig. 47), more rarely among leaf litter and other CPOM deposits (Figs. 45–46). The species was

also frequently encountered at black light traps. In Luzon and Mindoro it occurred sympatrically with *Agraphydrus abrasus* and *A. zetteli* (e.g., Fig. 44), but not in the exactly same microhabitats.

DISTRIBUTION (Fig. 39): Philippines: Luzon, Mindoro, ? Palawan, ? Panay.

ETYMOLOGY: The name *occultus* (Latin adjective) (= hidden) refers to the fact that the specimens were “hidden” among specimens of the very similar *A. zetteli*.

Agraphydrus palawanensis sp.n.

Agraphydrus “sp. F”: FREITAG & ZETTEL 2014: 19, 30.

TYPE LOCALITY: Philippines, Palawan Island and Province, Puerto Princesa City, Barangay Cabayugan, presumably Cabayugan River tributary, primary forest, ca. 100 m a.s.l., ca. 10°9'N 118°52'E.

TYPE MATERIAL: **Holotype** ♂ (NMW): “Philippines, PALAWAN centr. \small stream in primary forest \ ca. 100 m, Cabayugan env., \ 2. 12. 1995, Ján Kodada lgt.”. **Paratypes: P H I L I P P I N E S: Palawan:** 40 exs. (NMW): same sampling data as holotype; 1 ex. (NMW): Puerto Princesa, near Cabayugan, degraded rain forest, 150 m a.s.l., 2.XII.1995, leg. J. Kodada & B. Rigová; 2 exs. (NMW): Puerto Princesa, SSW Martapi, Cabayugan River, 10°9'46"N 118°49'29"E, 1.III.2001, leg. H. Freitag “CR1”; 1 ex. (PCSD): same site and collector, but 21.X.2000 “CR1”; 1 ex. (PCSD): same site and collector, but 16.III.2001 “CR1”; 1 ♀ [FR507] (ZMB): El Nido, New Ibahay, 11°13'6"N 119°29'32"E, ca. 150 m a.s.l., disturbed primary forest, mountain creek, littoral gravel, 29.XI.2019, leg. A. Peligen “(197b)M”; 1 ex. (SMTD): Taytay, Poblacion, “Malaipit Campsite”, Tubog Creek, 10°48'52"N 119°30'42"E, 80 m a.s.l., planted secondary forest, littoral gravel, run, 19.XI.2007, leg. H. Freitag “(64)M”; 2 exs. (SMTD): Taytay, Poblacion, creek near Taytay trail (Lake Manguao affluent), 10°47'12"N 119°31'40"E, 25 m a.s.l., residual pool, 3.IV.2008, leg. H. Freitag “(67)”; 1 ex. (PNM): Taytay, East Enolbong Creek (ephemeral Lake Manguao affluent), 10°47'7"N 119°33'2"E, 20 m a.s.l., degraded primary forest, gravel, sand, CPOM, pool, 29.VIII.2008, leg. H. Freitag “(121a)M”; 1 ex. (NMW): Taytay, Pahok Creek (Lake Manguao affluent), 10°46'42"N 119°31'55"E, 25 m a.s.l., secondary forest, gravel, sand, CPOM, pool, 14.IX.2008, leg. H. Freitag “(74b)M”; 1 ex. (PNM): same site, date and collector, but emergence trap “(74)E”; 1 ♂ (SMTD): Tatyay, Poblacion, Alipuran Stream (Lake Manguao affluent), 10°45'N 119°32'E, 40 m a.s.l., degraded primary forest, pool, 29.IV.2008, leg. H. Freitag “(13)M”; 10 exs. (NMW): Taytay, Poblacion, small ephemeral creek (Lake Manguao affluent), 10°46'0"N 119°30'47"E, ca. 30 m a.s.l., primary forest, pools, 16.IV.2007, leg. H. Freitag “(63a)M”; 3 exs. (SMTD): Taytay, upper Malbongbong Creek (Lake Manguao affluent), 10°44'27"N 119°31'15"E, 20 m a.s.l., secondary forest, sand, leaves, residual pool, 7.V.2007, leg. H. Freitag “(71a)M”; 1 ♂ (NMW, lacking head and pronotum, aedeagus damaged): Taytay, upper Malbongbong Creek (Lake Manguao affluent), 10°44'29"N 119°31'25"E, 20 m a.s.l., secondary forest, helocrene, 7.V.2007, leg. H. Freitag “(72a)M”; 12 exs. (ADMU): same site and collector, but emergence trap, 7.–16.V.2007, leg. H. Freitag “(72a)E”; 3 exs. (NMW): Roxas, Bagong Bayan, creek downstream of Ilian Falls, 10°26'35"N 119°32'39"E, ca. 50 m a.s.l., degraded primary forest, boulders, sand, CPOM, run, 17.XI.1995, leg. J. Mendoza “(129c)M”; 1 ♂ (NMW): Puerto Princesa, Cabaugan, Sabang, Mt. Bloomfield Waterfall, 10°12'3"N 118°53'4"E, ca. 150 m a.s.l., rocks, CPOM, pool, 8.X.2007, leg. H. Freitag “(18)M”; 1 ♂ [FR538] (ADMU): Puerto Princesa, Kapakwan, Purok Bagong Silay small Langogan River tributary, 10°4'55"N 119°6'34"E, 40 m a.s.l., secondary forest, 15.XII.2019, leg. H. Freitag “(163d)”; 1 ex. (NMW): Roxas, Poblacion near water plant, Umalad Falls, ca. 15 m a.s.l., secondary forest, 10°2'30"N 119°23'46"E, 24.IV.1995, leg. J. Mendoza “(69)M”; 3 exs. (NMW): Puerto Princesa, Langogan, highway km 79.8, small ephemeral creek, 10°1'26"N 119°6'48"E, ca. 20 m a.s.l., secondary vegetation, gravel, CPOM, run, 21.I.2019, leg. H. Freitag “(142a)”; 1 ♂ (NMW): Puerto Princesa, 18 km NE San Rafael, Olanguan River, 6.XII.1995, leg. J. Kodada & B. Rigová; 1 ♀ (NMW): Palawan central, Tarabanan River, ca. 13 km N San Rafael, ca. 30 m a.s.l., 7.XII.1995, leg. J. Kodada & B. Rigová; 2 ♂♂ (ZMB): Puerto Princesa, Iwahig, Balsahan River, upstream dam, 9°46'36"N 118°39'55"E, boulders, gravel, wood, moss, riffle, 5.VII.2019, leg. H. Freitag “(20)M”; 1 ♂ (NMW): 7 km N Narra, Estrella Falls, 2.IV.1994, leg. H. Zettel “57”.

ADDITIONAL MATERIAL EXAMINED:

P H I L I P P I N E S: Busuanga: 1 ♂, 1 ♀ [FR498*] (ADMU): 5 km NW Coron town, Mabintangan River tributary, creek upstream artificial pool, 12°1'44"N 120°12'19"E, 50 m a.s.l., secondary forest, gravel, root bunches, leaves, riffle, run, 2.II.2020, leg. H. Freitag “(167b)M”; 1 ♂ [FR423] (ADMU): Salvacion Proper, lowland creek, 12°7'38"N 119°56'26"E, 50 m a.s.l., secondary forest, leaf litter, residual pools, 23.XII.2019, leg. H. Freitag “(174)M”.

DIFFERENTIAL DIAGNOSIS: Belongs to group of species with microreticulate anterior clypeal margin and unicolored maxillary palpi. Shares these features with *A. ampullatus*, *A. brevilobatus*, and *A. pelingeni*, and some specimens related to *A. abrasus*. Differs in largely yellow pronotum and slender parameres from them, in slightly broader habitus from *A. pelingeni*. Shares microreticulate anterior clypeal margin, unicolored maxillary palpi, yellow clypeus, yellow pronotum, and eight antennomeres with *A. cantonensis* KOMAREK & HEBAUER, 2018, *A. mirabilis* KOMAREK, 2019, and *A. musculus* KOMAREK, 2019. Differs in larger size from *A. musculus* and *A. cantonensis*, in dark brown elytral coloration from *A. mirabilis* and *A. musculus*, in broader habitus and larger eyes from *A. musculus*, in lesser extension of femoral pubescence from *A. cantonensis*. Differs in long basal lobe from *A. cantonensis*, in smaller and narrower median lobe from *A. mirabilis*, and in narrower parameres from *A. musculus*.

DESCRIPTION: Total length: 2.0–2.2 mm; elytral width: 1.0–1.2 mm; E.I.: 1.3, P.I.: 2.4, elytra 3.3 times as long as pronotum. Habitus (Fig. 34) broad, evenly oval, moderately convex.

Coloration: Labrum, clypeus, and lateral portions of frons yellow, posterior portion of frons and mesal portion of clypeus dark brown, or clypeus and frons dark brown, clypeus with distinct yellow preocular patches; maxillary palpi unicolored yellow; pronotum yellow or dark brown with wide yellow lateral margins; elytra dark brown to black, unicolored or with lighter brown area at apex and/or on larger area on disc; ventrites dark brown; femora yellow.

Head: Clypeus with weakly emarginate anterior margin, C.I.: 4.2, lateral length ratio clypeus/eyes = 1.6; microreticulation present along lateral and anterior margins; ground punctation very fine, interspaces 4–6 times as large as punctures; systematic punctures indistinct. Eyes large, not protruding, slightly oblong. Antennae with eight antennomeres. Maxillary palpi (Fig. 24) slender, 1.1 times as long as pronotum in midline, 0.9 times as long as maximum width of clypeus, length ratio palpomeres 4:3 = 1.2–1.3, palpomere 4 almost symmetrical. Mentum weakly microsculptured laterally, with punctures in lateral thirds.

Thorax: Pronotal ground punctation as on head; systematic punctures distinct. Elytral ground punctation very slightly stronger than on pronotum, shallow, interspaces 3–4 times as large as punctures; four rows of distinct systematic punctures present, mesal rows with strongly reduced number of punctures, not reaching anterior margin, additional larger punctures present along lateral margins. Mesoventrite with mesal bulge.

Femora (Fig. 15): Pubescence present on more than proximal half of pro- and metafemur, on proximal 2/3 of mesofemur; hairlines oblique on pro- and mesofemur, straight on metafemur.

Abdomen: Ventrite 5 with almost semicircular apical emargination, ca. 20–30 µm deep.

Aedeagus (Fig. 6): Length: 0.27–0.29 mm. Phallobase as long as parameres, slightly longer than wide, very abruptly narrowing to defined manubrium; border between pigmented and unpigmented portion of ventral face reaching proximal fourth of phallobase; parameres moderately slender; margins weakly curving, with slight subapical constriction; apex broadly rounded, slightly inflated; basal portion slightly extending into phallobase. Median lobe narrow, slightly widening in mid-length; apex narrowly rounded, reaching or almost reaching apex of parameres; corona in subapical position; styli absent; basal apophyses long, reaching distal third of phallobase, distinctly inclining laterad.

REMARKS: A sequenced specimen from Busuanga Island (Greater Palawan) varies in 2.5 % genetic distance (Tab. 2) from the specimen from El Nido, Palawan. We consider them conspecific despite of very minor differences in the (mutilated) aedeagus.

ECOLOGY: *Agraphydrus palawanensis* is one of the most common species of the genus in Palawan, but seems to be restricted to natural forests (Fig. 41), where it is almost exclusively found

in small rivers and creeks, some of which are temporary and disappear during distinct dry seasons (Fig. 49). The microhabitats include foremost littoral sand and gravel (Fig. 47), but also leaf litter (Fig. 45) and other CPOM deposits in calm stream sections and associated puddles. A good number of specimens was also caught in emergence traps at Lake Manguao tributaries (see FREITAG & ZETTEL 2014), indicating that individuals commonly leave their aquatic habitat. The species was found together with *A. abrasus*, *A. batak*, and *A. pelingeni* (e.g., Fig. 41), partly even syntopically in the same microhabitats.

DISTRIBUTION (Fig. 39): Philippines: Palawan, Busuanga.

ETYMOLOGY: The name refers to Palawan (Philippines), where the type specimens were collected.

Agraphydrus pelingeni sp.n.

Agraphydrus (s.str.) cf. *orientalis* (ORCHYMONT, 1932): FREITAG & ZETTEL 2014: 19, 30.

TYPE LOCALITY: Philippines, Palawan Island and Province, Puerto Princesa City, Barangay Concepcion, Tarabanan River upstream of Batak village, secondary forest, ca. 30 m a.s.l., ca. 10°11'N 119°1'E (Fig. 41).

TYPE MATERIAL: **Holotype** ♂ (NMW): “Philippines, Palawan central \ Tarabanan river, ca. 13 km N \ San Rafael, ca. 30 m, 7.XII. \ 1995, Kodada & Rigová lgt.”. **Paratypes**: **PHILIPPINE S: Palawan**: 6 ♂♂, 1 ♀ (NMW, ZMB, SMTD): same sampling data as holotype; 1 ♂, 1 ♀ (PNM): Puerto Princesa, Concepcion, upstream Batak village, Tarabanan River, 10°27'N 119°1'10"E, ca. 100 m a.s.l., secondary forest, littoral gravel, 1.II.2015, leg. H. Freitag “(16Cb)M”; 1 ♂ [FR541*] (ADMU): El Nido, Barutuan, road km 291.5, small lowland river below irrigation dam, ca. 11°18'N 119°27'E, secondary vegetation, sand, gravel, pool, 20.XII.2019, leg. A. Pelingen “(111a)M”; 1 ♂, 1 ♀, 2 exs. (ADMU): Taytay, Bgy. Cataban, Cataban Brdg. I, Nat. highway km 230, medium lowland river, farmland, gravel, slightly polluted, 10°59'15"N 119°24'12"E 16.X.2007, leg. H. Freitag “(115)M”; 1 ♀ (PCSD): Taytay, East Enolbong Creek (ephemeral Lake Manguao affluent), 10°47'7"N 119°33'2"E, 20 m a.s.l., degraded primary forest, gravel, sand, CPOM, pool, 29.VIII.2008, leg. H. Freitag “(121a)M”; 1 ♀ (NMW): 7 km N Narra, Estrella Falls, 5.IV.1994, leg. H. Zettel “59”.

COMPARATIVE MATERIAL EXAMINED: *Agraphydrus* cf. *pelingeni*:

PHILIPPINE S: Mindoro: 1 ♀ (NMW): 10 km W Puerto Galera, 17.XI.1992, leg. Jäch “5”; 1 ♀ (NMW): 10 km W Puerto Galera, 24.–25.XI.1992, leg. H. Schillhammer “12”.

DIFFERENTIAL DIAGNOSIS: Belongs to group of species with microreticulate anterior clypeal margin and unicolored maxillary palpi. Shares these characters with *A. ampullatus*, *A. brevilobatus*, *A. palawanensis*, and some specimens related to *A. abrasus*. Differs in black clypeus and pronotum from *A. palawanensis*, in slenderer habitus from all species mentioned. Shares microreticulate anterior clypeal margin, unicolored maxillary palpi, and eight antennomeres with *A. schoedli*, but differs in smaller size (body length 2.0–2.2 mm vs. 2.4–2.8 mm in *A. schoedli*), black clypeus without distinct preocular patches, black pronotum (dark brown in *A. schoedli*), larger eyes, and very fine ground punctation from this species. Differs in features of aedeagus (e.g., parameres short, margins distinctly constricted subapically, apex with distinct mesal projection) from all species mentioned.

DESCRIPTION: Total length: 2.0–2.2 mm; elytral width: 0.9–1.1 mm; E.I.: 1.3, P.I.: 2.2, elytra 3.1 times as long as pronotum. Habitus (Fig. 35) moderately broad, evenly oval, moderately convex.

Coloration: Labrum, clypeus and frons black; clypeus with narrow yellowish rim along lateral margins; maxillary palpi unicolored yellow; pronotum black with narrow, yellow lateral margins; elytra black with dark brown, undefined, oval area in posterior half of disc; ventrites dark brown to black; legs lighter than ventrites.

Head: Clypeus with weakly emarginate anterior margin, C.I.: 3.8, lateral length ratio clypeus/eyes = 2.0; microreticulation present along lateral and anterior margins; ground punctation very fine, widely spaced; systematic punctures distinct. Eyes large, not protruding, very slightly oblong. Antennae with eight antennomeres, intermediate segment 1 elongate. Maxillary palpi (Fig. 25) slender, 1.1 times as long as pronotum in midline, as long as maximum width of clypeus, length ratio palpomeres 4:3 = 1.3–1.4, palpomere 4 symmetrical. Mentum with very fine, very widely spaced punctures, grouped laterally, microsculpture absent.

Thorax: Pronotal ground punctation as on head; systematic punctures distinct. Elytral ground punctation fine, slightly stronger than on pronotum; four rows of moderately distinct systematic punctures present, mesal rows with strongly reduced number of punctures, not reaching anterior margin. Mesoventrite with distinct mesal bulge.

Femora (Fig. 16): Pubescence present on more than proximal half of pro- and metafemur, on proximal 2/3 of mesofemur; hairline oblique in pro- and mesofemur, concave on mesofemur.

Abdomen: Ventrite 5 with shallow apical emargination.

Aedeagus (Fig. 7): Length: 0.38 mm. Phallobase more than twice as long as parameres, longer than wide, abruptly narrowing to distinctly defined, moderately sized manubrium; border between pigmented and unpigmented portion of ventral face indistinct, reaching manubrium. Parameres short, wide; margins distinctly constricted subapically; apex asymmetrical, with distinct mesal projection, weakly sclerotized and almost unpigmented; basal portion reaching half-length of phallobase mesally. Median lobe moderately slender, widest in midlength, distinctly curving in lateral view; dorsal face weakly sclerotized, weakly pigmented; apex reaching apex of parameres, tectiform, strongly bending dorsad; corona situated in distal third; styli absent; basal apophyses very short, narrowly separated, inclining laterad, reaching proximal third of phallobase.

REMARKS: Despite of their great similarity, we doubt that the females from Mindoro are really conspecific with the type material. The single barcode obtained (Tab. 1) suggests a close relationship with *A. palawanensis* (Tab. 2, Fig. 40).

ECOLOGY: The collection sites of the species are in both, rather pristine and slightly disturbed areas, where they were found in creeks to medium sized rivers. The shallow littoral with sand and gravel deposits (Fig. 47) in calm or slow-flowing river sections is its typical microhabitat. The species was not yet collected outside of water bodies. It was found partly together with *Agraphydrus batak* and *A. palawanensis*.

DISTRIBUTION (Fig. 39): Philippines: Palawan.

ETYMOLOGY: The species is dedicated to Mr. Arthien L. Pelingen (alumnus of the Ateneo de Manila University and associate researcher of the Ateneo Biodiversity Laboratory), who collected the barcoded specimen.

Agraphydrus tenuipalpis sp.n.

TYPE LOCALITY: Philippines, Leyte Island and Province, Baybay Municipality, secondary forest near Visayas State University, ca. 10°45'N 124°48'E, ca. 100–200 m a.s.l.

TYPE MATERIAL: **Holotype** ♂ (MNS): “PHILIPPINES:LEYTE \ VISCA [Visayas State College of Agriculture] N Baybay, 1991 \ sec.forest, 100-200 m \ leg.SCHAWALLER & al. | 27.2.91 | ♂”. **Paratypes**: **P H I L I P P I N E S**: **Leyte**: 2 ♂♂, 1 ♀ (MNS, NMW): same sampling data as holotype. **Mindanao**: 2 ♂♂ [FR434], 1 ♀ (ADMU, PNM): Surigao del Sur, 10 km N Tandag, Sibahay, Magkawas Falls, river, 30.V.2019, leg. C. Pangantihon (“P371”).

DIFFERENTIAL DIAGNOSIS: Shares absence of clypeal micropunctation and unicolorated maxillary palpi with *A. batak* and some specimens of *A. abrasus*. Differs in fine ground punctation

of head and pronotum, nine antennomeres, lesser extension of pubescence on pro- and mesofemora, and larger extension of pubescence on metafemur from *A. abrasus*; differs in slender body, light colored pronotum and elytra, slender maxillary palpi, distinct ground punctation of head and pronotum, and features of aedeagus (parameres with almost straight margins, median lobe with styli) from both species. *Agraphydrus coomani* and *A. zetteli* with similar aedeagus (absence of distinct manubrium, presence of styli) differ in apically infuscated palpomere 4.

DESCRIPTION: Total length: 1.9–2.0 mm; elytral width: 0.9–1.0 mm; E.I.: 1.3, P.I.: 1.9–2.0, elytra 2.9–3.0 times as long as pronotum. Habitus (Fig. 36) slender, evenly oval, moderately convex.

Coloration: Labrum, clypeus and frons black; clypeus with yellow preocular patches about as wide as diameter of eye; maxillary palpi unicolored yellow; pronotum yellow with darkened mesal portion; elytra unicolored yellow; ventrites and legs rufous.

Head: Clypeus with distinctly emarginate anterior margin, C.I.: 3.9, lateral length ratio clypeus/eyes = 1.4; microreticulation absent; ground punctation moderately strong, distinctly impressed, interspaces about twice as wide as punctures; systematic punctures moderately distinct. Eyes large, not protruding, slightly oblong. Antennae with nine antennomeres, antennomere 4 minute, weakly separated from antennomere 3. Maxillary palpi (Fig. 26) slender, 1.3–1.4 times as long as pronotum in midline, 1.2–1.3 times as long as maximum width of clypeus, length ratio palpomeres 4:3 = 1.1–1.3, palpomere 4 slightly asymmetrical. Mentum obsoletely punctate, microsculpture absent.

Thorax: Pronotal ground punctures as on head; systematic punctures distinct. Elytral ground punctation as on head and pronotum; systematic punctures moderately distinct, mesal rows with strongly reduced number of punctures, not reaching anterior margin. Mesoventrite with distinct bulge.

Femora (Fig. 17): Pubescence present on proximal half of profemur, on proximal 2/3 of meso- and metafemur; hairlines very slightly oblique on profemur, slightly convex on metafemur.

Abdomen: Ventrite 5 with very shallow apical emargination, ca. 10 µm deep.

Aedeagus (Fig. 8): Length: 0.32 mm. Phallobase as long as parameres, slightly longer than wide, evenly narrowing to very short, wide, indistinctly defined manubrium, border between pigmented and unpigmented portion of ventral face very indistinct. Parameres slender, with almost straight margins, very weakly narrowing apicad; apex with broadly rounded lateral edge and narrowly rounded mesal edge, slightly inclining mesad; basal portion slightly extending into phallobase mesally. Median lobe moderately slender, narrowing in mid-length, spatula-shaped, weakly pigmented; corona situated subapically; pair of styli present; basal apophyses moderately long, straight, reaching distal third of phallobase.

REMARKS: Specimens from Tandag, situated on the north-eastern portion of Mindanao Island agree well with specimens from the type locality on Leyte Island in all characters. Since both islands belong to the intra-Philippine biogeographic region of Greater Mindanao, we have no doubt about the conspecificity of the material, despite of the lack of DNA barcodes.

ECOLOGY: The two collection sites are in secondary forest; the specimens from Mindanao were collected in a river.

DISTRIBUTION (Fig. 39): Philippines: Leyte, Mindanao.

ETYMOLOGY: The name is derived from *tenuis* (Latin adjective) (= thin, weak, slender) and *palpis* (Latin adjective) (= regarding the palps) and refers to the slender maxillary palpi.

Agraphydrus zetteli sp.n.

Agraphydrus "sp. B": FREITAG & PANGANTIHON 2010: 135, 145.

TYPE LOCALITY: Philippines, Mindoro Island, Province Oriental Mindoro, Victoria Municipality, Barangay Malayas, Malayas Creek (Lake Naujan affluent) flowing through secondary vegetation, ca. 20 m a.s.l., ca. 13°9'26"N 121°18'29"E.

TYPE MATERIAL: **Holotype** ♂ (PNM): "PHIL.: Mindoro Oriental, Municipality Victoria, Bgy. \ Malayas, Malayas River; W Naujan tributary; \ second. veget., 20 m asl., 13°9'26"N 121°18'29"E; \ 22.Feb.2010 leg. Freitag & Pangantihon (308)L"; aedeagus and terminal parts of abdomen removed and glued on the same card. **Paratypes**: **P H I L I P P I N E S**: **Mindoro**: 27 ♂♂ [FR418*], 22 ♀♀, 60 exs. (ADMU, NMW, PNM, SMTD ZMB): same sampling data as holotype; 3 exs. (ADMU): same site, date and collectors, but littoral gravel, pool "(308c)M"; 1 ♂ (ADMU): same site, date and collectors, but root bunches, run "(308d)M"; 9 exs. (ADMU): eutrophic helocrene, shallow, gravel, slow run "(308e)M"; 2 ♂♂ [CC054, CC055] (ADMU): Abra de Ilog, creek 500 m S port, 13°27'50"N 120°46'15"E, ca. 10 m a.s.l., rural farming area, littoral gravel, sand, shallow pool, 8.VI.1992, leg. J. Mendoza "(333a)M"; 1 ♂, 2 ♀♀ (ADMU): Puerto Galera, "Hidden Paradise", river upstream Tukunan Falls, 13°25'57"N 120°58'29"E, 60 m a.s.l., secondary vegetation, CPOM, run, 23.IV.2019, leg. H. Freitag "(303b)M"; 1 ♂, 1 ♀ (ADMU): same site, and collector, but sand, algae, pool, 6.VII.2018 "(303m)M"; 1 ♂ [FR478] (ADMU): Baco, Dulangan, torrent Lantuyan mountain river, 13°16'8"N 121°4'56"E, 55 m a.s.l., secondary vegetation, wood debris, riffle, 2.IV.2019, leg. H. Freitag "(310a)M"; 1 ♂ [FR447] (ADMU): Sablayan, small karst river, 12°47'49"N 120°54'33"E, ca. 100 m a.s.l., disturbed primary forest, 1.I.1995, leg. J. Mendoza "(365h)L"; 2 ♂♂ [FR524], 1 ♀ (ADMU): Sablayan, large mountain river, 12°50'2"N 120°56'10"E, 110 m a.s.l., gravel, sand, warm exposed side pool, 2.I.1995, leg. J. Mendoza "(369m)M"; 1 ♀ (ADMU): Bongabong, Lisap, lower Siange River, 12°41'28"N 121°20'56"E, ca. 150 m a.s.l., mountain plain, grassland, gravel, boulders, riffle, 28.X.1991, leg. J. Mendoza "(319b)M"; 5 ♂♂, 1 ♀ (ADMU): Roxas, San Vicente, upper Baroc River, 12°37'7"N 121°24'6"E, 90 m a.s.l., flood plain, littoral gravel, pool, 10.VIII.2018, leg. H. Freitag "(BR1b)M"; 1 ♀ [FR490] (ADMU): same site, and collector, but root bunches, run "(BR1h)M"; 1 ♂ [FR486] (ADMU): Roxas, San Vicente, Sitio Taugad Diit, Taugad Diit River (Baroc River tributary), 12°37'32"N, 121°22'17"E, 180 m a.s.l., secondary vegetation, leaf packs, 5.IV.2018, leg. H. Freitag & C. Pangantihon "(TIR1d)M"; 4 ♀♀ (ADMU): Roxas, San Vicente, Sapang Dalid (Baroc River tributary), 12°37'27"N 121°22'48"E, ca. 150 m a.s.l., secondary vegetation, littoral sand, side pools, 5.II.2018, leg. H. Freitag "(TDCt)M"; 2 ♂♂, 1 ♀ (ADMU): Roxas, San Vicente, Taugad River (Baroc River tributary), 12°37'6"N 121°23'49"E, ca. 100 m a.s.l., secondary vegetation, CPOM, side pools, 29.II.2018, leg. H. Freitag "(TR1e)M"; 2 ♂♂ (ADMU): same river (more upstream) and collector, but 12°37'18"N 121°22'58"E, 140 m a.s.l., secondary vegetation, mixed littoral deposits of mud, sand, and gravel, pool, leg. H. Freitag, 16.VI.2018 "(TR2b)M"; 1 ♂, 1 ♀ (ADMU): same site, and collector, but submerged grass and root bunches, run, 28.XI.2017 "(TR2h)M"; 1 ♂, 1 ♀ (ADMU): same site, but gravel side pool, 1.II.2017, leg. I. Saen et al. "(TR2t)M"; 2 ♂♂, 1 ♀ (ADMU): same site, but light trap, 20.VIII.2018, leg. H. Freitag "(TR2L)"; 1 ex. (ADMU): Roxas, San Vicente, Hinundugan River, downstream Hinagdanan Falls, 12°35'22"N 121°21'54"E, 200 m a.s.l., secondary vegetation, side rivulet, run, 8.II.2018, leg. H. Freitag "(HR2a)M".

ADDITIONAL MATERIAL EXAMINED:

P H I L I P P I N E S: **Busuanga**: 2 ♂♂ [FR522*] (ADMU): 1 km E Guadelupe, roadside, mountain creek, secondary vegetation, rocks, leaf litter, mud, residual pools, 120 m a.s.l., 12°3'22"N 120°11'10"E 25.12.2019, leg. H. Freitag "(160a)M"; **Leyte**: 1 ♂ [FR534*], 1 ♀ (ADMU): Ormoc, Dolores, Lake Danao affluent creek, secondary vegetation, 11°4'38"N 124°41'46"E, 650 m a.s.l., 26.IX.2018, leg. J. Garces "(520)L"; 1 ex. (MNS): VISCA [Visayas State College of Agriculture], N Baybay, cultivated land, 28.II.1991, leg. W. Schawaller et al.; 3 exs. (2 MNS, 1 NMW): SW Abuyog, river bank, 28.II.1991, leg. W. Schawaller et al.; **Luzon**: 1 ♀ (ADMU): Ilocos Sur, Suyo, large river downstream Sangbay ni Ragsak, 16°59'32"N 120°32'21"E, ca. 100 m a.s.l., littoral gravel, pool, 15.IV.2019, leg. H. Freitag, J. Garces & C. Pangantihon "(447b)M"; 5 ♂♂, 3 ♀♀ (ADMU): La Union, Sudipen, Amburayan River, 16°54'38"N 120°28'40"E, 20 m a.s.l., agricultural land, 14.IV.2019, leg. H. Freitag, J. Garces & C. Pangantihon "(445)L"; 1 ♀ (ZMB): Benguet, Bukod River, 16°29'12"N 120°49'49"E, ca. 900 m a.s.l., 18.XI.1997, leg. W. Mey "(459)L"; 1 ex. (ADMU): Aurora, Baler, Zabali, Dicaluyongan River, bottom gravel, run, 4.II.1996, leg. J. Mendoza "(429c)"; 1 ex. (ADMU): Aurora, Baler, small river, 15°44'9"N 121°34'16"E, 25 m a.s.l., secondary forest, 4.II.1996, leg. J. Mendoza et al. "(430)L"; 1 ♂, 1 ♀ [FR417] (ADMU): Bulacan, 14 km E San Miguel, Biak-na-Bato National Park, river 300 m upstream Paniki Cave, ca. 15°6'N 121°6'E, ca. 100 m a.s.l., 10.IV.1995, leg. J. Mendoza "(28)L"; 1 ♂ [CC065] (ADMU): Bulacan, San Jose del Monte, San Isidro, Karahume River, 14°49'0"N 121°9'20"E, ca. 200 m a.s.l., rural/secondary vegetation, gravel, pool, 13.VIII.1990, leg. J. Mendoza "(296)M"; 1 ♂, 3 ♀♀ (ADMU): SBMA area, Batalan mountain river, ca. 14°45'N 120°21'E, 65 m a.s.l., secondary vegetation, 29.I.2018, leg. H. Freitag "(403)L"; 2 ♂♂, 2 exs.

(ADMU): Laguna, Majajay, Taytay River, downstream Majajay Fall, 14°6'30"N 121°30'30"E, 480 m a.s.l., secondary vegetation, sand, CPOM, littoral pool, 27.VI.2018, leg. H. Freitag & C. Pangantihon "(294b)M"; **Negros**: 7 ♂♂, 5 ♀♀ (NMW): Lizares W Bacolod, Bago River, ca. 500 m a.s.l., 17.III.1994, leg. S. Schödl "4"; **Panay**: 2 ♂♂, 1 ♀ (NMW): Antique, 50 km NE San Jose 20.III.1994 leg. S. Schödl "6"; 1 ♂ (NMW): Ilo-Ilo, 10 km N Igaras, ca. 400 m a.s.l., 22.III.1994, leg. S. Schödl "8"; **Samar**: 1 ♂ [FR429*] (ADMU): Taft, San Rafael, small river, 11°49'39"N 125°16'29" E, 160 m a.s.l., rural secondary vegetation, 22.X.1995, leg. J. Mendoza "(509)L"; 1 ♀ (ADMU): Borongan, San Mateo, hill creek below fall, 11°37'11"N 125°23'37"E, 25 m a.s.l., secondary vegetation, littoral gravel, pool, 21.X.1995, leg. J. Mendoza "(507b)M"; **Sibuyan**: 1 ♂ (NMW): Magdiwang, Jao-asan, Fato-o River, 18.XI.1994, leg. H. Zettel "67"; 1 ♂ [FR456] (ADMU): Magdiwang, large mountain river, 12°27'N 122°34'E, ca. 300 m a.s.l., secondary forest, sand, gravel, pool, 19.II.2019, leg. C. Pangantihon "(P501b)M".

DIFFERENTIAL DIAGNOSIS: Belongs to group of species with apically infuscated maxillary palpomere 4 and absence of clypeal microreticulation (*coomani* group, see Discussion), together with *A. coomani* and *A. occultus*. Differs in nine antennomeres and presence of styli on median lobe from *A. occultus*, in larger average size, slenderer habitus, absence of distinct preocular patches and stronger ground punctation from *A. coomani*, in inflated apex of parameres from both species. Shares black elytra with *A. jilanzhui* and *A. ater* KOMAREK, 2018. Differs from all species of the group in the inflated apex of the parameres.

DESCRIPTION: Total length: 2.1–2.7 mm; elytral width: 0.9–1.1 mm; E.I.: 1.3–1.5, P.I.: 1.9, elytra 2.8–2.9 times as long as pronotum. Habitus (Fig. 37) slender, almost cylindrical, elytra slightly widening posterior to mid-length, moderately convex.

Coloration: Labrum, clypeus and frons black; clypeus with indistinct, narrow, orange lateral margins in some individuals; maxillary palpi yellow, palpomere 4 with apical infuscation; pronotum black with very narrow yellow lateral margins; elytra black with very narrow yellow lateral margins, center of disc dark brown in some cases; ventrites dark brown to black; legs dark brown.

Head: Clypeus with distinctly emarginate anterior margin, C.I.: 2.9, lateral length ratio clypeus/eyes = 1.6; microsculpture absent; ground punctation fine, interspaces 2–3 times as wide as punctures; systematic punctures distinct. Eyes large, slightly protruding, slightly oblong. Antennae with nine antennomeres. Maxillary palpi (Fig. 27) slender, 1.3 times as long as pronotum in midline, 1.2 times as long as maximum width of clypeus, length ratio palpomeres 4:3 = 1.3, palpomere 4 almost symmetrical. Mentum with moderately strong punctures, microsculpture absent.

Thorax: Pronotal ground punctation as on head; systematic punctures distinct. Elytral ground punctation as on head and pronotum; four rows of distinct systematic punctures present, rows 1 and 3 strongly reduced in number, not reaching anterior margin. Mesoventrite with mesal bulge.

Femora (Fig. 18): Pubescence present on proximal 2/3 of profemur, on proximal 3/4 of meso- and metafemur; hairline slightly oblique on pro- and mesofemur, almost straight on metafemur.

Abdomen: Ventrite 5 with semicircular apical emargination.

Aedeagus (Fig. 9): Length: 0.41–0.46 mm. Phallobase slightly shorter than parameres, longer than wide, evenly narrowing proximad, defined manubrium absent; border between pigmented and unpigmented portion of ventral face almost reaching manubrium. Parameres slender, with weakly curving margins, with subapical constriction; apex slightly inflated, slightly inclining mesad; basal portion reaching distal third of phallobase. Median lobe narrow, evenly narrowing apicad, finger-shaped, apex not reaching apex of parameres; corona situated apically; pair of styli present; basal apophyses moderately long, reaching distal third of phallobase.

REMARKS: This species is quite variable in size (2.1–2.7 mm total length), observed for instance in the numerous specimens from the type locality. Male specimens tend to be smaller,

but can also reach the maximum length. The additional material is externally not distinguishable from the type material, but these specimens from other islands than Mindoro tend to have very slightly broader aedeagi and the apical infuscation of palpomere 4 is usually slightly more extended. However, these character variations are within the observed range of Mindoro specimens (type material). The only reason that prevents us from designating all material as types, is the rather unusually high genetic distance (5.5–6.1 %, Tab. 2).

ECOLOGY: Most specimens were collected with black light traps. For specimens directly collected from their aquatic habitat, littoral sand and gravel, but also CPOM deposits in calm littoral river sections (Figs. 45, 47), side pools (Fig. 50) and residual pools (Fig. 49) were the most common microhabitats. More rarely, specimens were retrieved from submerged root (Fig. 46) and grass bunches, or bottom gravel in running water.

Predominantly, the collection sites were in disturbed areas, such as farmland and rural areas with secondary vegetation in lowlands. *Agraphydrus zetteli* was occasionally found together with *A. abrasus* and *A. occultus* in Mindoro (e.g., Fig. 44) and Luzon, as well as with *A. brevilobatus* in Panay. Based on the label data, there is no evidence whether these records are syntopic or not.

DISTRIBUTION (Fig. 39): Philippines: Busuanga, Leyte, Luzon, Mindoro, Negros, Panay, Samar, Sibuyan.

ETYMOLOGY: The species is dedicated to Herbert Zettel (NMW), who collected this species on Sibuyan Island (Philippines).

Key to the *Agraphydrus* species of the Philippines

- 1 Maxillary palpomere 4 infuscated apically..... 2
- Maxillary palpomere 4 not infuscated apically..... 4
- 2 Eight antennomeres; aedeagus: apex of parameres without lateral extension, median lobe almost reaching apex of parameres, styli absent (Fig. 5)..... **occultus**
- Nine antennomeres; aedeagus: apex of parameres without lateral extension, median lobe not reaching apex of parameres, styli present..... 3
- 3 Clypeus without distinct yellow preocular patches; body length 2.1–2.6 mm; pubescence on proximal 2/3 of profemur, on proximal 3/4 of meso- and metafemur (Fig. 18); aedeagus: apex of parameres slightly inflated, median lobe very narrow, corona in apical position (Fig. 9)..... **zetteli**
- Clypeus with distinct yellow preocular patches; body length 1.8–2.2 mm; pubescence on proximal half of profemur, on proximal 2/3 of meso- and metafemur; aedeagus: apex of parameres not inflated, median lobe moderately wide, corona slightly distal of mid-length of median lobe (KOMAREK 2018: fig. 118)..... **coomani**
- 4 Clypeus without anterior microreticulation 5
- Clypeus with anterior microreticulation 7
- 5 Habitus (Fig. 36) slender; pronotum and elytra largely yellow; maxillary palpi slender; apex of median lobe without emargination; aedeagus: Fig. 8 **tenuipalpis**
- Habitus broad (Figs. 28, 30, 34); pronotum and elytra dark brown or black; maxillary palpi stout; apex of median lobe with emargination; aedeagus: Figs. 1, 3, 6 6
- 6 Pronotum obsoletely punctate; metafemoral pubescence present on proximal half; aedeagus (Fig. 1): apex of parameres inflated..... **abrasus** (partim)
- Pronotum with distinct ground punctation; metafemoral pubescence present on proximal 3/4; aedeagus (Fig. 3): apex of parameres not inflated **batak**

7	Clypeus yellow with or without mesal infuscation, pronotum yellow; aedeagus: Fig. 6.....	<i>palawanensis</i>
–	Clypeus and pronotum dark brown or black, with or without narrow yellow lateral margins; aedeagus: Figs. 1, 2, 4, 7.....	8
8	Aedeagus (Fig. 1): Apex of median lobe emarginate.....	<i>abrasus</i> (partim)
–	Aedeagus (Figs. 2, 4, 7): Apex of median lobe without emargination.....	9
9	Aedeagus (Fig. 2): Median lobe bottle-shaped.....	<i>ampullatus</i>
–	Aedeagus (Figs. 4, 7): Median lobe not bottle-shaped.....	10
10	Aedeagus (Fig. 7): Apex of parameres with distinct extension mesally.....	<i>pelingeni</i>
–	Aedeagus (Fig. 4): Apex of parameres without distinct mesal extension.....	<i>brevilobatus</i>

Discussion

Distribution: Ten species of *Agraphydrus* are now known from the Philippines (Figs. 38–39). We examined material from all major islands, although collection efforts are somewhat biased towards Luzon, Mindoro and Palawan. Nevertheless, it seems justified to conclude that almost all Philippine species are restricted to one or few intra-Philippine biogeographic regions. *Agraphydrus batak*, *A. palawanensis* and *A. pelingeni* are endemic to Greater Palawan, *A. brevilobatus* to Greater Negros/Panay, *A. ampullatus* (Leyte) and *A. tenuipalpis* to Greater Mindanao.

Interestingly, a rather unusual distribution pattern (Palawan, Mindoro, Luzon) is recognized in *A. abrasus*.

The only somewhat more widely distributed Philippine species is *A. zetteli*, which occurs across many islands of the archipelago from Busuanga in the west to Samar in the east.

Agraphydrus coomani, which is widespread in the Oriental and Australasian regions, is also found in the Philippines. However, as long as DNA barcodes from its type locality in Vietnam are not available, uncertainty of real conspecificity of the material remains, given the obvious radiation process observed, which currently hampers a proper conclusion on its real distribution (see below).

Ecology: As observed already in previous studies on Philippine aquatic beetles (FREITAG & BALKE 2011, KOMAREK & FREITAG 2014), mountain river systems in little disturbed areas such as Tarabanan River (Fig. 41), which drains Cleopatra's Needle in central Palawan, Batalan River of the Subic Bay Forest Reserve in Luzon, or the upper Baroc River tributaries at Mt. Hinundugan (Fig. 44) in southern Oriental Mindoro – all of them key biodiversity areas – harbor the highest number of *Agraphydrus* species recorded in this study. This emphasizes once more the need of an effective protection of the last remaining primary forest and unpolluted river systems.

Agraphydrus species predominantly inhabit shallow calm zones with coarse sand or gravel (Fig. 44), less frequently leaf litter (Fig. 45), root packs (Fig. 46), grass bunches, or other CPOM among which they can hide. Usually, these microhabitats are connected to streams and receive water inputs from there (Figs. 44–47). Less frequently, *Agraphydrus* individuals dwell in bottom substrates of running water (Fig. 47), on hygropetric rocks (Fig. 48) with crevices and dead plant material. They remain also in temporary riverine habitats until the water has entirely dried up, such as residual pools of ephemeral creeks (Fig. 49), and sun-exposed isolated side pools along larger rivers (Fig. 50), as well as in litho- and phytotelmata. Such microhabitats are partly exposed to high water temperature, high saprobity and dissolved oxygen deficit.

Although the actual microhabitats are predominantly lentic, they are mostly associated with lotic stream systems. In a comprehensive assessment by FREITAG & PANGANTIHON (2010) at Lake Naujan (seven sites) and its affluents (eight sites) in Mindoro, only one specimen (*A. cf. coomani*) was found at the lake shore, while 13 (*A. zetteli*) were collected along affluent streams. Following RIBERA & VOGLER (2000), riparian systems (including associated lentic ecological niches) are more stable in geological time-scale, facilitating regional speciation and the evolution of endemic taxa.

Specimens of *Agraphydrus* are usually very good flyers that immediately attempt to escape through flight once they are not submerged anymore. They are also frequently collected at light. Therefore, it can be concluded that *Agraphydrus* has higher migration abilities than many other hydrophilids. PAPADOPOULOU et al. (2008) illustrated strikingly that already low levels of dispersal lead to less discrete mtDNA clusters as recognized in this study too (Fig. 40). This is very evident when compared to aquatic beetles with lower dispersal ability (e.g., Elmidae: *Ancyronyx* ERICHSON, 1847) from the region (FREITAG 2013, FREITAG & KODADA 2017a) for which distinct species clusters are observed.

Systematics: Based on morphological similarities, three species of the Philippines can be grouped together with sixteen species of the Oriental Region. According to the most widespread species, they are here referred to as *A. coomani* group: *A. ater*, *A. bacchusi* KOMAREK, 2019, *A. borneensis* KOMAREK, 2019, *A. cinnamum* KOMAREK, 2018, *A. comes* KOMAREK & HEBAUER, 2018, *A. confusus* KOMAREK & HEBAUER, 2018, *A. constrictus* KOMAREK, 2018, *A. coomani*, *A. heinrichi* KOMAREK, 2018, *A. imitans* KOMAREK, 2019, *A. ishiharai* (MATSUI, 1994), *A. jilanzhui* KOMAREK & HEBAUER, 2018, *A. manfredjaechi*, *A. occultus*, *A. papuanus* KOMAREK, 2019, *A. robustus* KOMAREK & HEBAUER, 2018, *A. sarawakensis* KOMAREK, 2019, *A. zetteli*. Shared characters: body slender, elytra slightly widening posterior to mid-length; clypeus black with yellow preocular patches (absent in some individuals of *A. jilanzhui* and *A. manfredjaechi*); frons black; clypeus distinctly emarginate anteriorly; absence of clypeal microreticulation; eyes large; antennae with nine antennomeres (eight-segmented antennae in *A. manfredjaechi* and *A. occultus*); maxillary palpi slender, palpomere 4/3 = 1.2–1.4, palpomere 4 infuscated apically; mesoventrite not carinate, with mesal bulge; systematic elytral punctuation distinct; femoral pubescence extended on at least proximal half; parameres and median lobe slender, basal lobe as long as parameres or very slightly shorter, border between pigmented and unpigmented portion of basal lobe distinct, almost reaching proximal end of basal lobe, manubrium absent or very indistinct.

The Statistical Parsimony Network supports the close affiliation of the three Philippine species, along with several still uncertainly identified specimens (Fig. 40). Test runs of a maximum likelihood phylogenetic analysis based on our data confirm the clade, however we refrain from presenting such tree because a 569 bp mtDNA data set lacks support and seems generally not sufficient to conclude on phylogenetic relationships (HEBERT & GREGORY 2005).

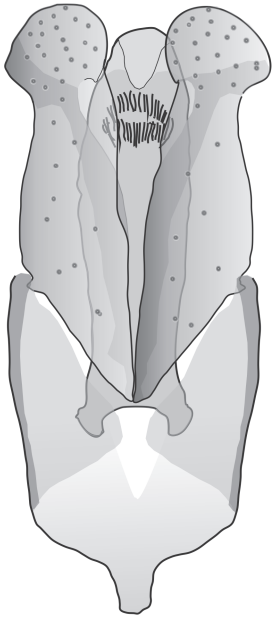
Both, morphological and genetic data suggest that the *Agraphydrus coomani* group is under radiation. The clearly distinguishable and further evolved representatives in the Philippines (*A. occultus* and *A. zetteli*) have distributed already to a wider range beyond intra-Philippine biogeographic borders and undergo further radiation as seen in rather high intraspecific genetic distances (up to 6.1 % in *A. zetteli*). The closest *A. coomani* relatives (here referred to as *A. cf. coomani*), on the other hand, seem to undergo current radiation. Their sub-clades are genetically and morphologically very weakly differentiated and may represent undescribed cryptic species. Therefore, we refrain from formal determination or description, at least until more sequencable material is available.

Tab. 1: GenBank and BOLD accession numbers of *COI* mtDNA sequences, geographical origins, collection sites and organismic sample references of specimens used for the molecular-genetic analysis.

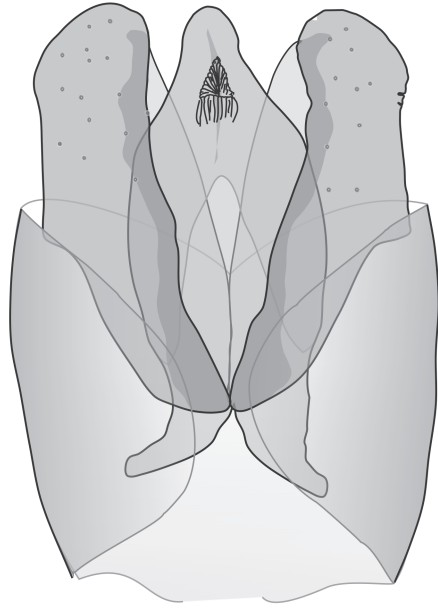
<u>Species</u>	<u>Locality</u>	<u>Site</u>	<u>Voucher</u>	<u>ENA</u>	<u>BOLD</u>
<i>A. abrasus</i>	Luzon	435a	ADMU FR433	MT899150	COLPH017-20
<i>A. abrasus</i>	Luzon	410b	ADMU FR484	MT899181	COLPH018-20
<i>A. cf. abrasus</i>	Mindanao	896b	ADMU FR509	MT899151	COLPH019-20
<i>A. cf. abrasus</i>	Camiguin	40	ADMU FR506	MT899152	COLPH020-20
<i>A. batak</i>	Palawan	132e	ADMU FR473	MT899153	COLPH021-20
<i>A. cf. batak</i>	Busuanga	174	ADMU FR422	MT899154	COLPH022-20
<i>A. brevilobatus</i>	Negros	652L	ADMU FR531	MT899155	COLPH023-20
<i>A. brevilobatus</i>	Negros	650L	ADMU FR420	MT899156	COLPH024-20
<i>A. coomani</i>	Luzon	SJRb	ADMU FR437	MT899157	COLPH025-20
<i>A. coomani</i>	Luzon	447b	ADMU FR539	MT899158	COLPH026-20
<i>A. coomani</i>	Leyte	520L	ADMU FR535	MT899159	COLPH027-20
<i>A. cf. coomani</i>	Balabac	89t	ADMU FR477	MT899160	COLPH028-20
<i>A. cf. coomani</i>	Busuanga	167b	ADMU FR405	MT899161	COLPH029-20
<i>A. cf. coomani</i>	Busuanga	175b	ADMU FR480	MT899162	COLPH030-20
<i>A. cf. coomani</i>	Leyte	520L	ADMU FR533	MT899163	COLPH031-20
<i>A. cf. coomani</i>	Mindoro	372b	ADMU FR476	MT899164	COLPH032-20
<i>A. cf. coomani</i>	Palawan	112b	ADMU FR527	MT899165	COLPH033-20
<i>A. cf. coomani</i>	Samar	506t	ADMU FR530	MT899166	COLPH034-20
<i>A. cf. coomani</i>	Samar	507b	ADMU FR514	MT899167	COLPH035-20
<i>A. cf. coomani</i>	Samar	509L	ADMU FR430	MT899168	COLPH036-20
<i>A. cf. coomani</i>	Tablas	727	ADMU FR528	MT899169	COLPH037-20
<i>A. occultus</i>	Luzon	434b	ADMU FR482	MT899170	COLPH038-20
<i>A. occultus</i>	Luzon	SJRb	ADMU FR438	MT899171	COLPH039-20
<i>A. occultus</i>	Luzon	442L	ADMU FR414	MT899172	COLPH040-20
<i>A. palawanensis</i>	Palawan	197b	ADMU FR507	MT899173	COLPH041-20
<i>A. palawanensis</i>	Busuanga	167b	ADMU FR498	MT899174	COLPH042-20
<i>A. pelingeni</i>	Palawan	111a	ADMU FR541	MT899175	COLPH043-20
<i>A. zetteli</i>	Mindoro	308L	ADMU FR418	MT899176	COLPH044-20
<i>A. zetteli</i>	Busuanga	160a	ADMU FR522	MT899177	COLPH045-20
<i>A. zetteli</i>	Leyte	520L	ADMU FR534	MT899178	COLPH046-20
<i>A. zetteli</i>	Luzon	28L	ADMU FR417	MT899179	COLPH047-20
<i>A. zetteli</i>	Samar	509L	ADMU FR429	MT899180	COLPH048-20

Tab. 2: Pairwise Kimura 2-parameter (K2P) genetic distance of aligned partial CO1 sequences (569 bp length) of Philippine *Agraphhydrus* specimens, DNA sample code and island of origin (abbreviated) in order as treated in the text.

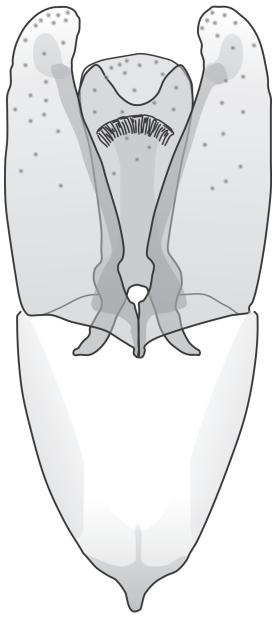
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1FR484 abrasus LUZ																															
2FR433 abrasus LUZ	.002																														
3FR509 cf. abrasus MNA	.063	.065																													
4FR506 cf. abrasus CAM	.071	.072	.059																												
5FR473 bataak PAL	.127	.129	.127	.140																											
6FR422 cf. bataak BUS	.134	.136	.123	.137	.084																										
7FR531 brevilobatus NEG	.061	.063	.048	.059	.131	.118																									
8FR420 brevilobatus NEG	.065	.067	.055	.066	.140	.127	.007																								
9FR437 coomani LUZ	.178	.178	.181	.185	.130	.163	.183	.188																							
10FR539 coomani LUZ	.174	.174	.174	.178	.130	.158	.176	.181	.005																						
11FR535 coomani LEY	.176	.176	.178	.183	.133	.165	.181	.185	.005	.007																					
12FR477 cf. coomani BAL	.165	.165	.163	.174	.120	.147	.158	.163	.074	.072	.072																				
13FR405 cf. coomani BUS	.165	.165	.163	.169	.150	.156	.158	.163	.116	.110	.114	.104																			
14FR480 cf. coomani BUS	.167	.167	.165	.176	.126	.149	.160	.165	.080	.074	.078	.005	.106																		
15FR533 cf. coomani LEY	.171	.173	.160	.180	.120	.156	.165	.169	.092	.086	.090	.062	.120	.064																	
16FR476 cf. coomani MDO	.171	.171	.167	.174	.141	.152	.178	.187	.084	.078	.078	.064	.126	.066	.08																
17FR527 cf. coomani PAL	.167	.167	.165	.176	.126	.149	.160	.165	.080	.074	.078	.005	.106	.000	.064	.066															
18FR530 cf. coomani SAM	.171	.174	.160	.185	.135	.160	.162	.167	.093	.087	.087	.070	.123	.072	.036	.084	.072														
19FR514 cf. coomani SAM	.167	.169	.151	.171	.116	.149	.151	.156	.095	.088	.092	.068	.118	.070	.016	.090	.070	.031													
20FR430 cf. coomani SAM	.165	.167	.149	.169	.114	.149	.154	.158	.088	.082	.086	.062	.112	.064	.011	.084	.064	.025	.005												
21FR528 cf. coomani TAB	.169	.169	.165	.173	.135	.143	.169	.174	.070	.064	.068	.053	.114	.055	.076	.042	.055	.078	.082	.076											
22FR482 occultus LUZ	.165	.165	.156	.178	.147	.149	.135	.139	.128	.137	.102	.122	.104	.108	.132	.104	.102	.099	.097	.108											
23FR438 occultus LUZ	.165	.165	.156	.176	.154	.151	.132	.137	.137	.130	.139	.112	.126	.114	.106	.135	.114	.100	.097	.095	.110	.012									
24FR414 occultus LUZ	.158	.158	.150	.169	.149	.147	.130	.135	.133	.126	.130	.097	.114	.099	.102	.122	.099	.100	.093	.091	.102	.023	.025								
25FR507 palawanensis PAL	.080	.082	.072	.092	.137	.129	.068	.072	.169	.162	.167	.154	.151	.156	.162	.167	.156	.160	.149	.151	.162	.149	.154	.141							
26FR498 palawanensis BUS	.080	.080	.068	.098	.140	.135	.078	.082	.167	.160	.165	.149	.152	.151	.169	.160	.151	.162	.156	.158	.158	.145	.154	.136	.025						
27FR541 pelingani PAL	.092	.094	.086	.098	.141	.144	.086	.090	.176	.169	.173	.152	.147	.154	.165	.156	.162	.163	.150	.159	.137	.068	.064								
28FR418 zetteli MDO	.160	.160	.160	.174	.147	.139	.158	.158	.139	.135	.137	.118	.124	.120	.12	.126	.120	.122	.122	.116	.114	.108	.104	.102	.165	.167	.163				
29FR522 zetteli BUS	.145	.148	.147	.160	.139	.137	.128	.134	.120	.116	.118	.114	.122	.116	.112	.132	.116	.108	.101	.099	.112	.098	.094	.090	.147	.158	.163	.057			
30FR534 zetteli LEY	.143	.145	.145	.163	.137	.135	.126	.132	.126	.122	.124	.116	.128	.118	.114	.135	.118	.114	.108	.106	.118	.100	.096	.092	.150	.161	.161	.055	.005		
31FR417 zetteli LUZ	.143	.145	.137	.156	.137	.133	.120	.126	.128	.124	.126	.112	.124	.114	.114	.135	.114	.108	.106	.118	.098	.094	.090	.145	.156	.154	.055	.012	.007		
32FR429 zetteli SAM	.150	.152	.152	.169	.143	.141	.132	.139	.130	.126	.128	.116	.130	.118	.116	.141	.118	.114	.110	.108	.124	.102	.098	.094	.156	.167	.163	.061	.011	.005	.012



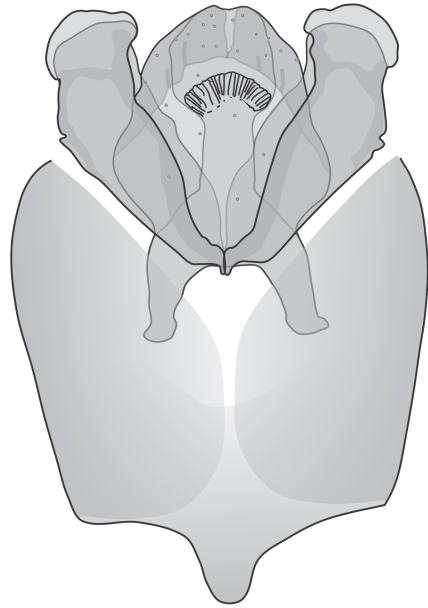
1



2

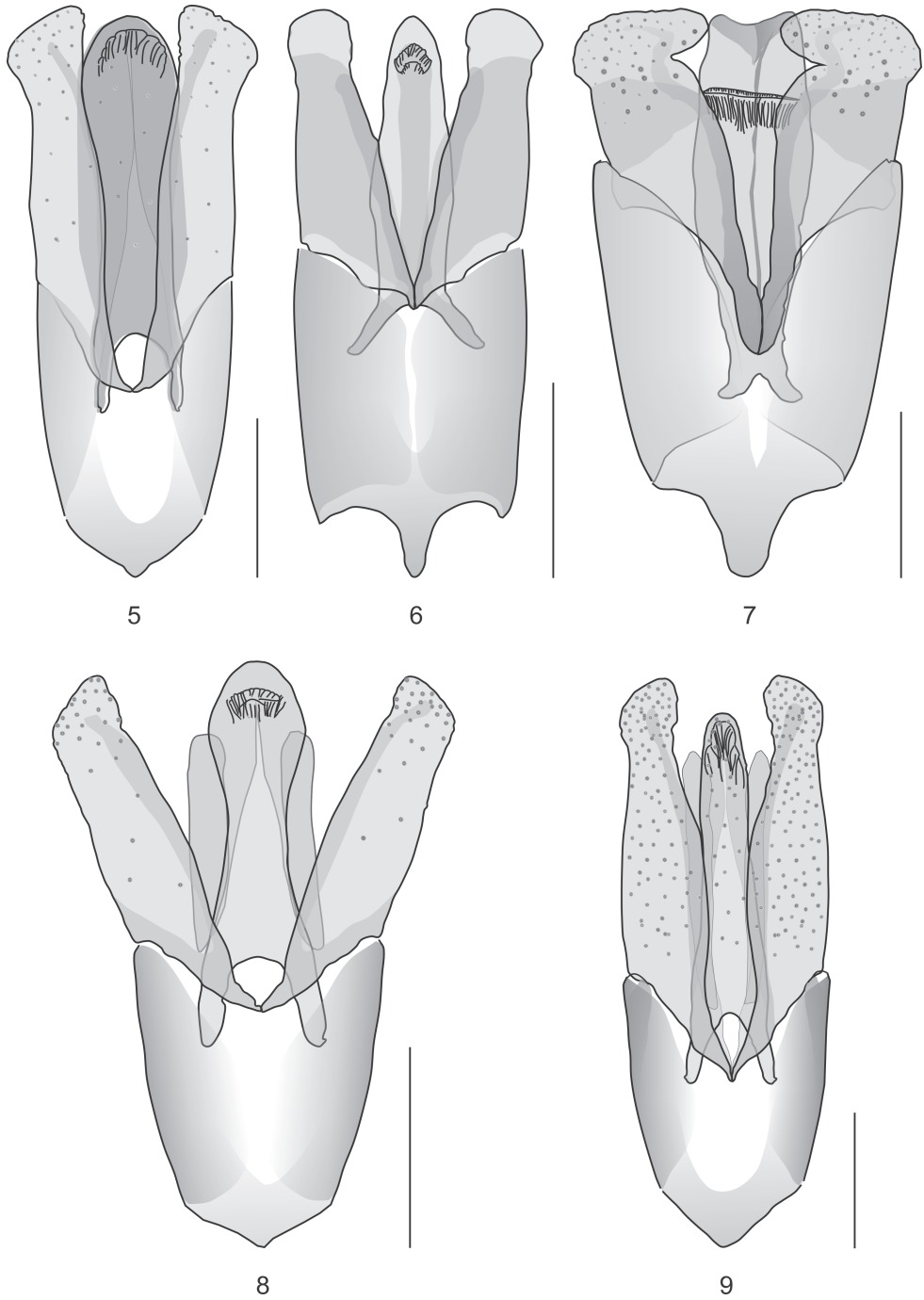


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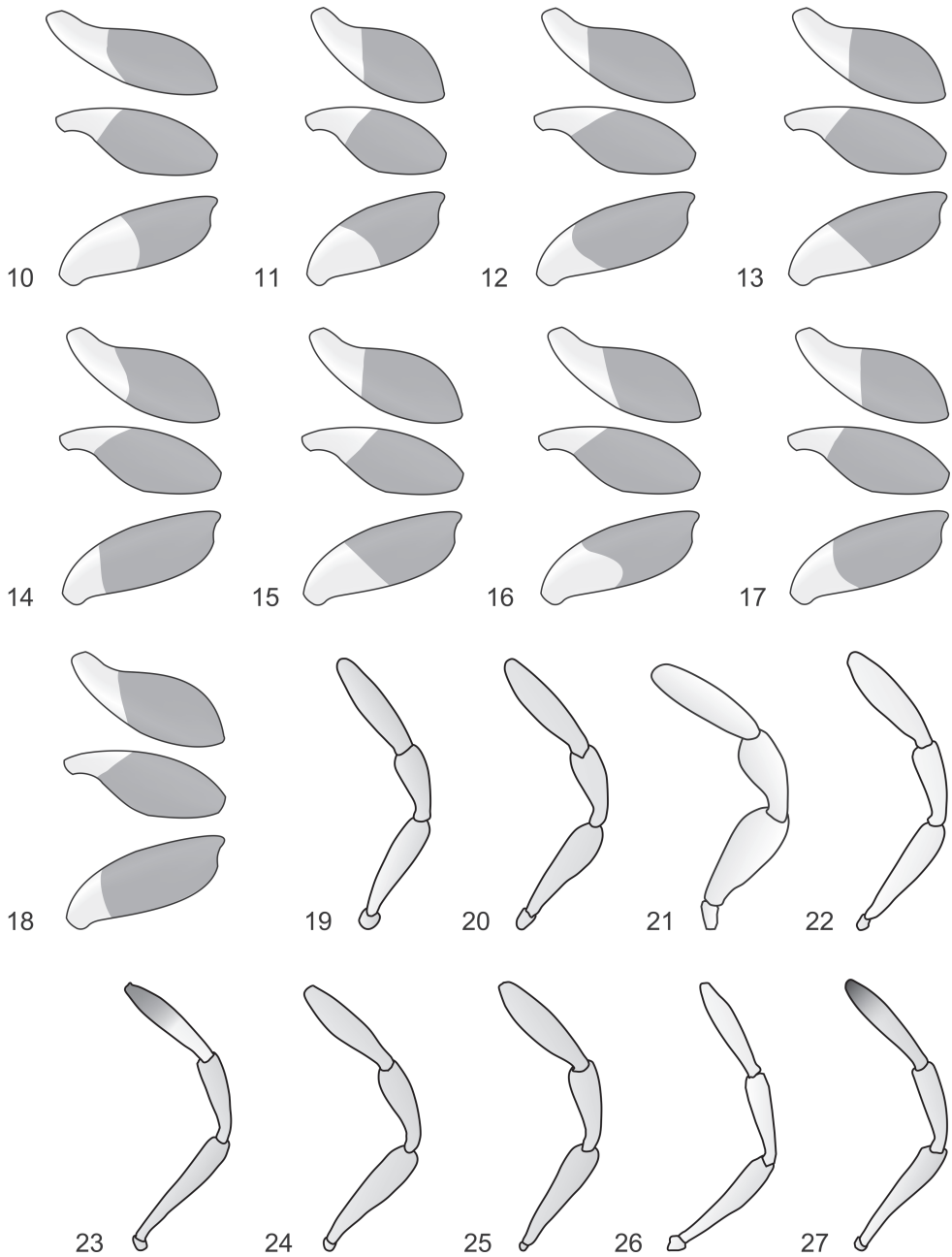


4

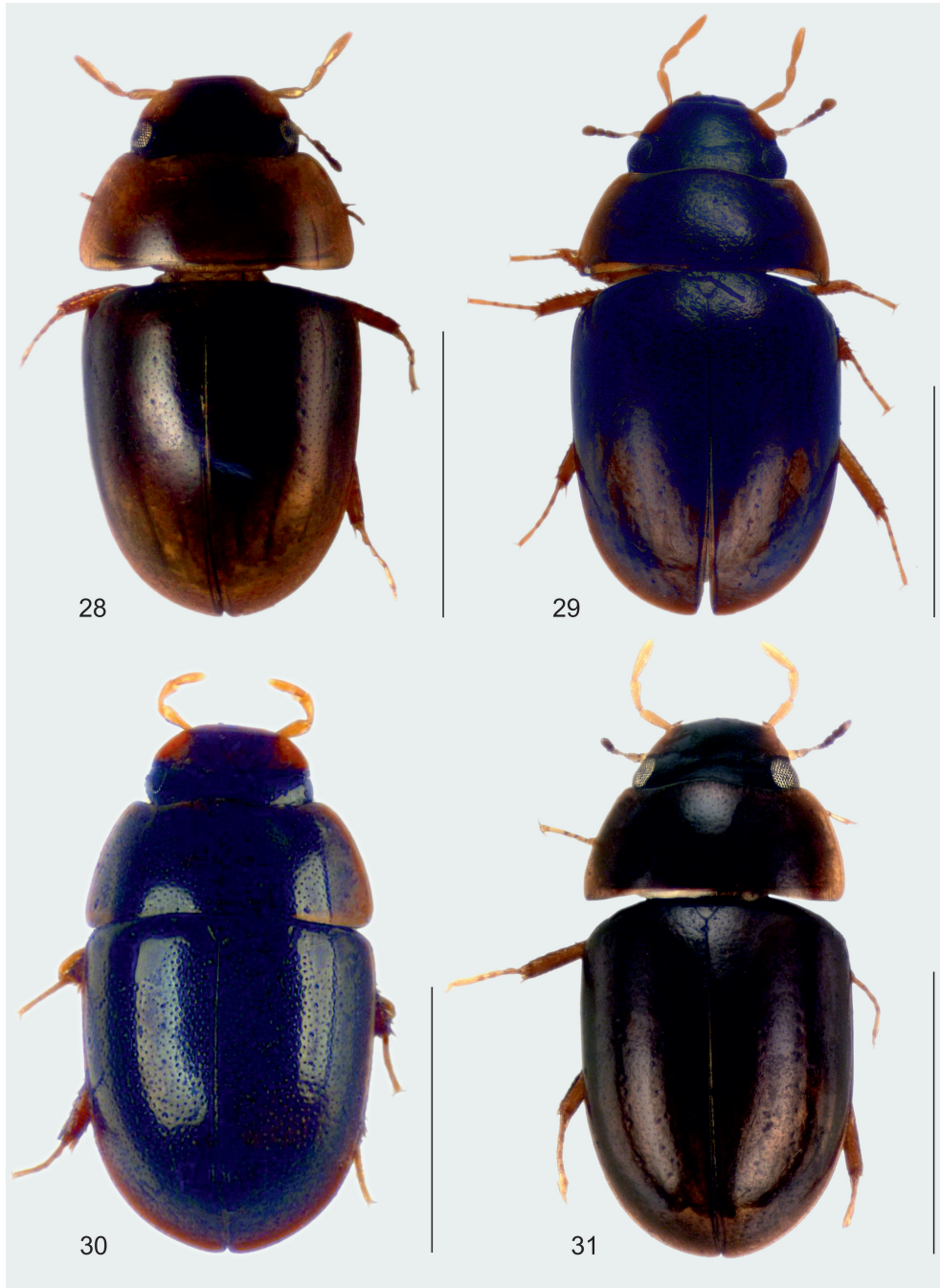
Figs. 1–4: Aedeagus; 1) *Agraphydrus abrasus*; 2) *A. ampullatus*; 3) *A. bataki*; 4) *A. brevilobatus*.



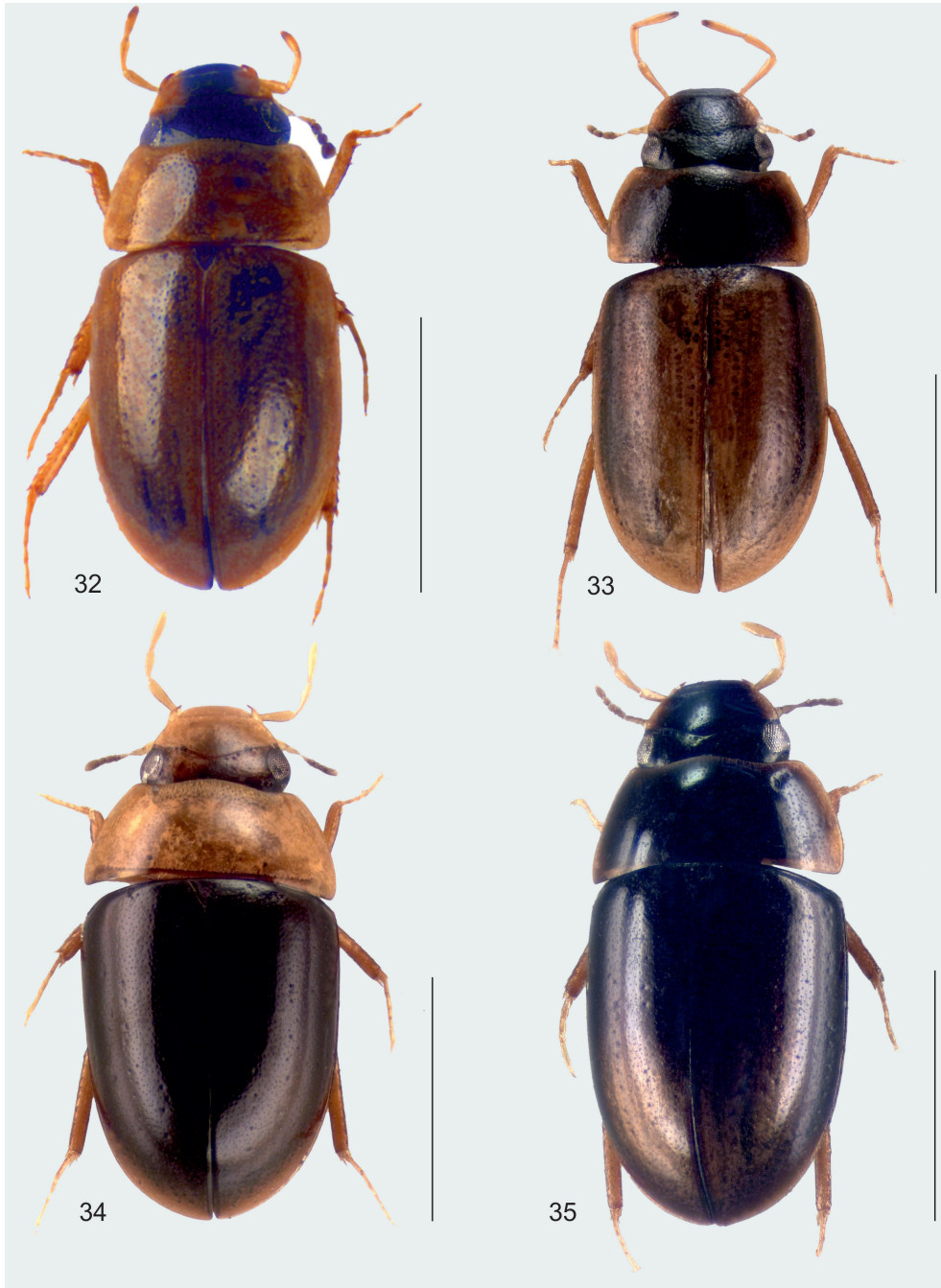
Figs. 5–9: Aedeagus; 5) *Agraphydrus occultus*; 6) *A. palawanensis*; 7) *A. pelingeni*; 8) *A. tenuipalpis*; 9) *A. zetteli*.



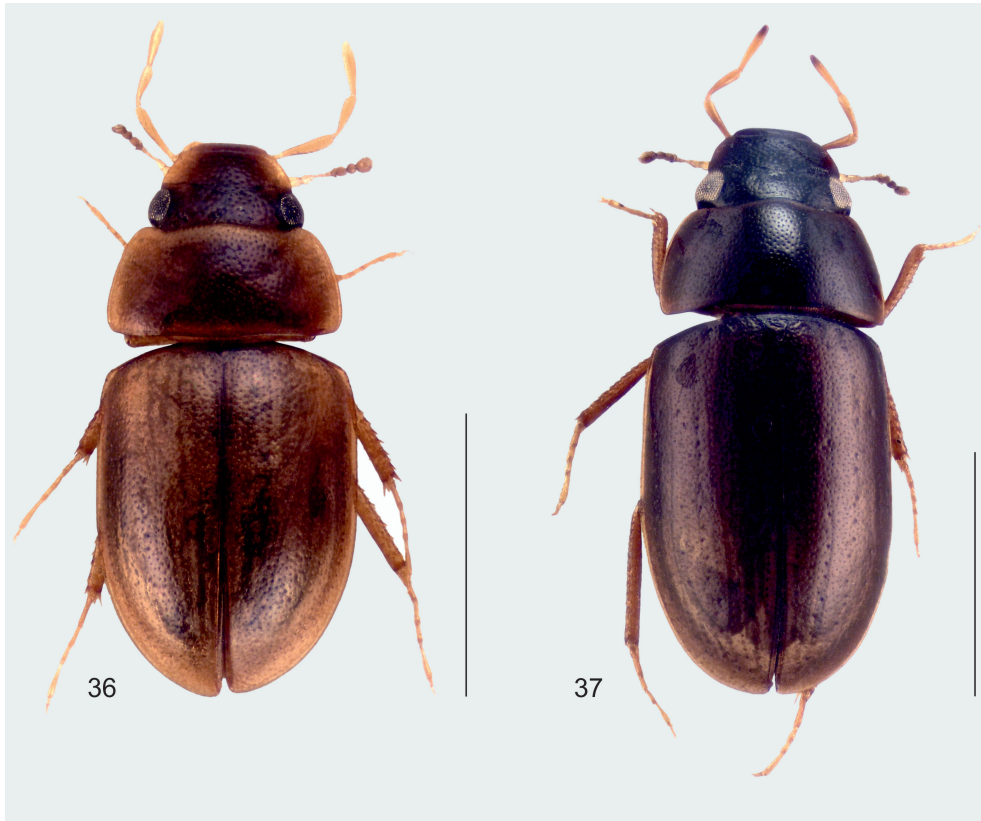
Figs. 10–27: Femora (10–18) and maxillary palpi (19–27): 10, 19) *Agraphydrus abrasus*; 11, 20) *A. ampullatus*; 12, 21) *A. batak*; 13, 22) *A. brevilobatus*; 14, 23) *A. occultus*; 15, 24) *A. palawanensis*; 16, 25) *A. pelingeni*; 17, 26) *A. tenuipalpis*; 18, 27) *A. zetteli*.



Figs. 28–31: Habitus; 28) *Agraphydrus abrasus* (paratype); 29) *A. ampullatus* (holotype); 30) *A. batak* (holotype); 31) *A. brevilobatus* (Panay). Scale = 1 mm.



Figs. 32–35: Habitus; 32) *Agraphydrus* cf. *coomani* (Palawan); 33) *A. occultus* (paratype); 34) *A. palawanensis* (paratype); 35) *A. pelingeni* (paratype). Scale = 1 mm.



Figs. 36–37: Habitus; 36) *Agraphydrus tenuipalpis* (holotype), 37) *A. zetteli* (paratype). Scale = 1 mm.

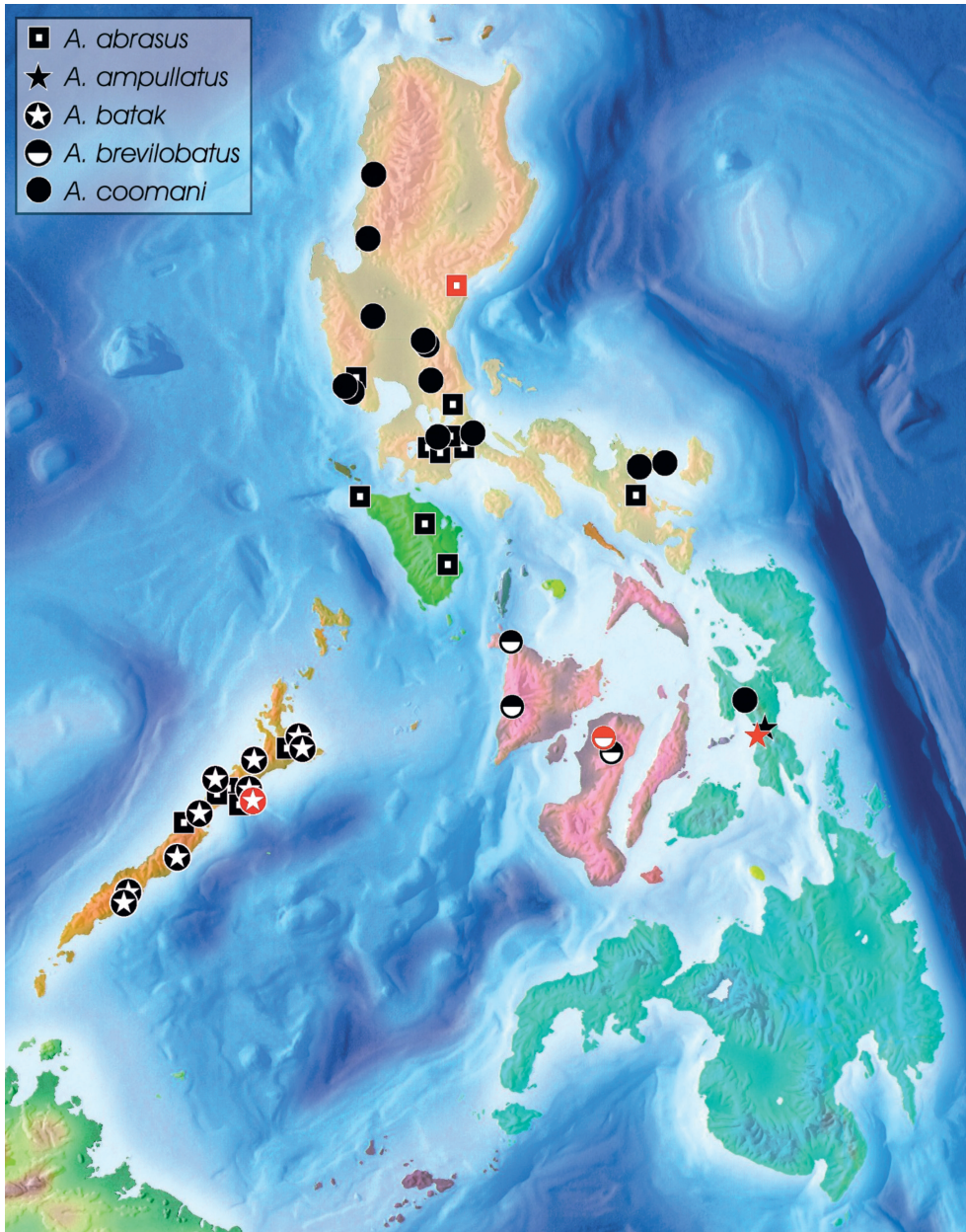


Fig. 38: Distribution of Philippine *Agraphydrus* species: *A. abrasus*, *A. ampullatus*, *A. batak*, *A. brevilobatus*, *A. coomani*. Type locality symbols in red color.

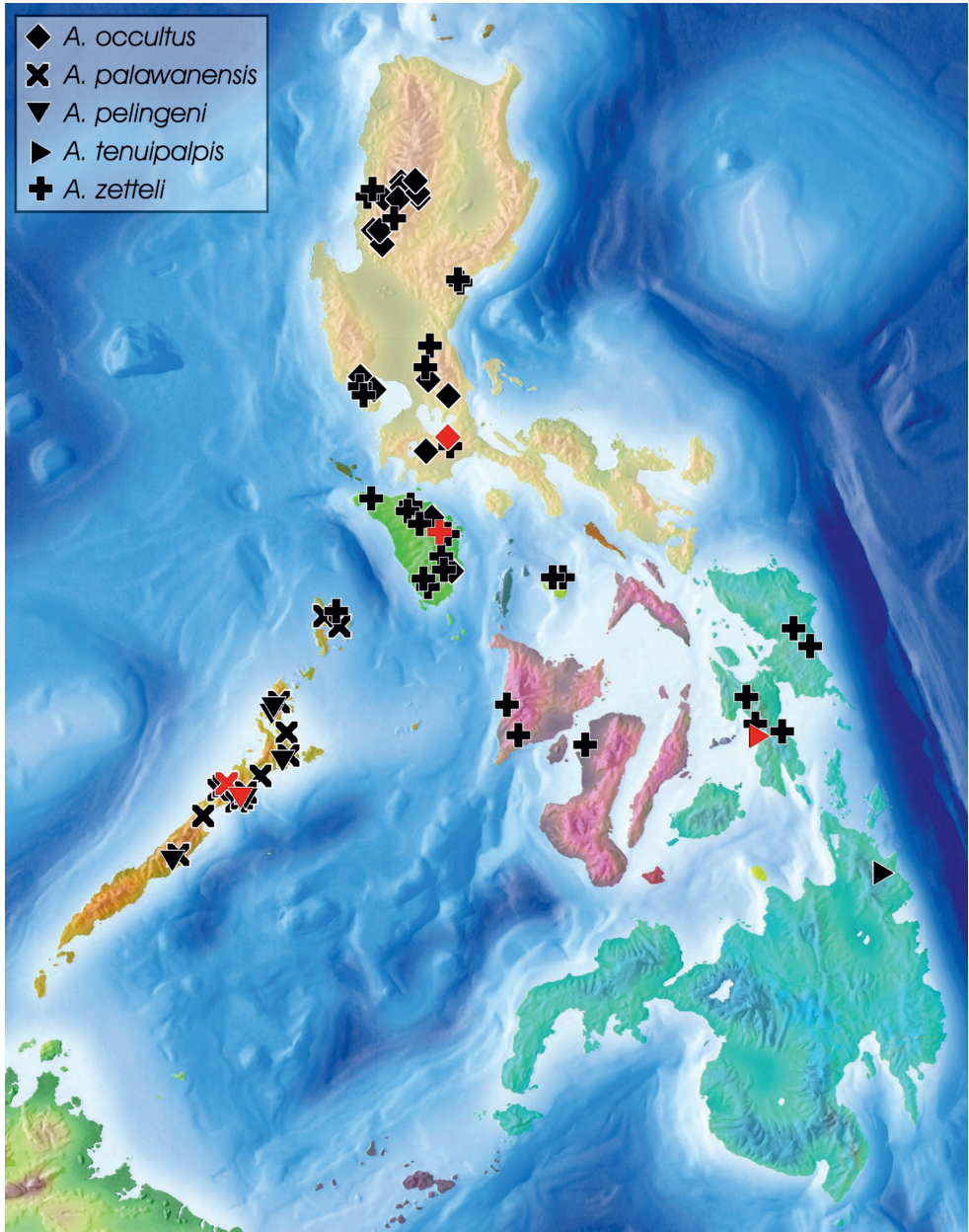


Fig. 39: Distribution of Philippine *Agraphydrus* species: *A. occultus*, *A. palawanensis*, *A. pelingeni*, *A. tenuipalpis*, *A. zetteli*. Type locality symbols in red color.

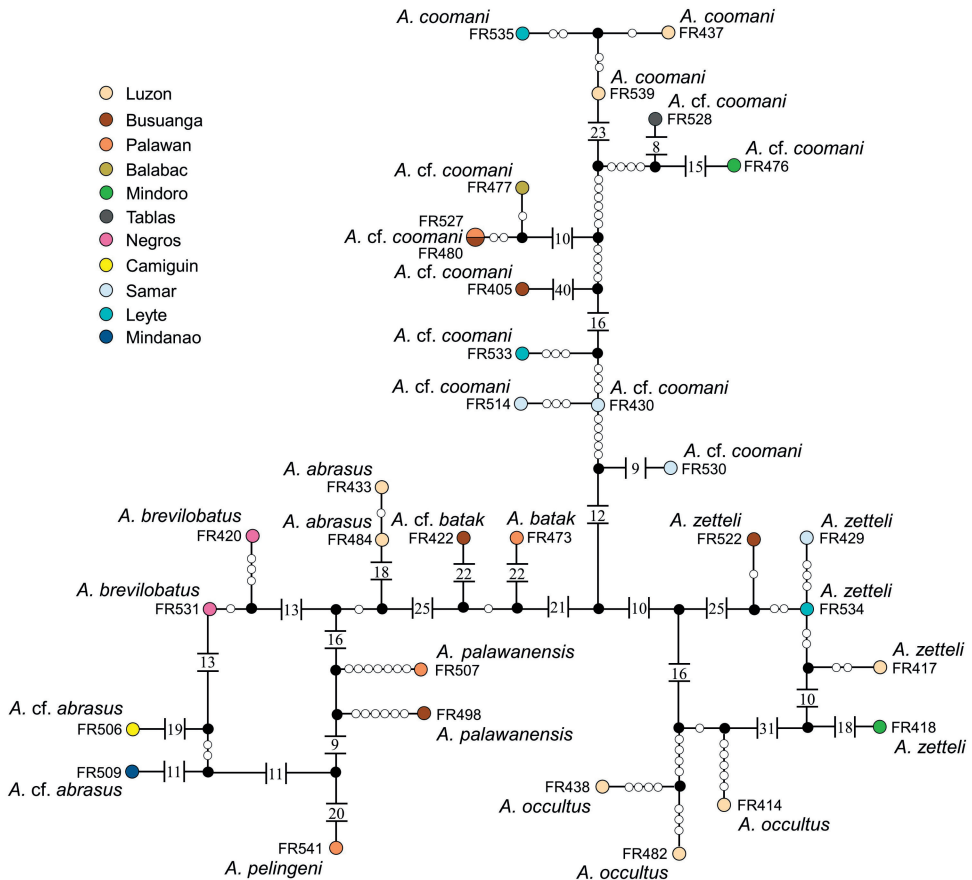


Fig. 40: Rescaled statistical parsimony network of Philippine *Agraphydrus* haplotypes generated from aligned 569 bp *COI* mtDNA sequences. Present haplotypes are indicated by colors that refer to their island of origin. Missing haplotypes / substitutions are indicated by empty circles or their number.

Overall, we observe a high nucleotide diversity, only two specimens (FR480, FR527) in one clade have identical haplotypes, which might be attributed to the higher dispersal abilities in the genus (see above).

Methodology: Only 32 out of 58 extracted specimens yielded useable DNA sequences. This is mainly due to older material that has initially not been preserved and/or subsequently not been stored under optimal conditions (freezers and 96 % or absolute ethanol) as advocated by several biodiversity initiatives (e.g., BALKE et al. 2013, FREITAG et al. 2016). However, even in fresh and well-preserved material barcoding with standard primers sometimes fails. The use of shorter fragments, taxon-specific primers (e.g., FREITAG & KODADA 2017b), or other mtDNA markers, such as *cob* (FREITAG & BALKE 2011, SABORDO et al. in press) might provide an alternative.



Figs. 41–44: Collection sites and type localities (TL) of: 41) *Agraphydrus batak* (TL), *A. pelingeni* (TL), *A. abrasus*; Tarabanan River, Puerto Princesa, Palawan; 42) *A. brevilobatus* (TL); Dumalabdad River, Silay, Negros; 43) *A. coomani*, *A. occultus*; upper Tapuacan River, Tuba, Benguet (Luzon); 44) *A. abrasus*, *A. occultus*, *A. zetteli*; Taugad Diit River, tributary of Baroc River, Mindoro, in the front: litorral gravel and sand in shallow calm water, the most typical *Agraphydrus* microhabitat. Photographs by C.V. Pangantihon, E. de la Calzada, and H. Freitag.



Figs. 45–50: Microhabitats of Philippine *Agraphydrus* species; 45) calm stream section ('pool') with leaf litter deposits; 46) dense root bunches and other CPOM in a river pool; 47) bottom gravel in shallow running water; 48) hygropetric rock with attached plant material; 49) residual pools with organic and mineral deposits of an ephemeral forest creek; 50) isolated sun-exposed shallow side pool along a river bank. Photographs by C.V. Pangantihon, and H. Freitag.

Difficulties in the use of mtDNA data for species delineation in radiating complexes are not unusual (MONAGHAN et al. 2006, BALKE et al. 2013). The genetic signal of *COI* can be unstructured among young species (MEYER & PAULAY 2005, HENDRICH et al. 2010), allowing only for delineation of species complexes rather than individual species. The integrative approach employed here has helped to recognize such complexes. It prevented us from designating cryptic material as types. On the other hand, it leaves several doubtful clades unnamed. When more sequencable material becomes available, including specimens of *Agraphydrus coomani* from the type locality, then an integrative taxonomic approach, where partial *COI* mtDNA sequences are used as an a priori clustering method, might help to delimit the remaining putative species (e.g., GARCES et al. 2020).

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Dr. Albrecht KOMAREK

Naturhistorisches Museum Wien, Burgring 7, A – 1010 Wien, Austria (albrecht.komarek@aon.at)

Prof. Dr. Hendrik FREITAG

Biodiversity Laboratory, Ateneo de Manila University, Katipunan Avenue, Quezon City, PH – 1108 Philippines (hfreitag@ateneo.edu)

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