

Integrative taxonomy of the genus *Onchidium* Buchanan, 1800 (Mollusca, Gastropoda, Pulmonata, Onchidiidae)

Benoît Dayrat¹, Tricia C. Goulding¹, Deepak Apte², Vishal Bhave²,
Joseph Comendador³, Ngô Xuân Quảng⁴, Siong Kiat Tan⁵, Shau Hwai Tan⁶

1 Department of Biology, Pennsylvania State University, University Park, PA 16802, USA **2** Bombay Natural History Society, Mumbai, Hornbill House, Opp. Lion Gate, Shaheed Bhagat Singh Road, Mumbai 400 001, Maharashtra, India **3** National Museum of the Philippines, Taft Ave, Ermita, Manila, 1000 Metro Manila, Philippines **4** Institute of Tropical Biology, Vietnam Academy of Science and Technology, 85 Tran Quoc Toan Str., District 3, Ho Chi Minh city, Vietnam **5** Lee Kong Chian Natural History Museum, 2 Conservatory Dr, National University of Singapore, 117377, Singapore **6** Marine Science Laboratory, School of Biological Sciences, Universiti Sains Malaysia, 11800 Minden Penang, Malaysia

Corresponding author: Benoît Dayrat (bad25@psu.edu)

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Abstract

In an effort to clarify the species diversity of onchidiid slugs, the taxonomy of the genus *Onchidium* Buchanan, 1800 is revised using an integrative approach. New, fresh specimens were collected in a large number of places, including type localities. The genus *Onchidium* is redefined here as a clade including only three species which are strongly supported by both morphological and molecular data. All three species were already named: the type species *O. typhae* Buchanan, 1800, *O. stuxbergi* (Westerlund, 1883), and *O. reevesii* (J.E. Gray, 1850). With the exception of a re-description of *O. typhae* published in 1869, all three species are re-described here for the first time. First-hand observations on the color variation of live animals in their natural habitat are provided. The anatomy of each species is described. Important nomenclatural issues are addressed. In particular, *Labella* Starobogatov, 1976 is regarded as a junior synonym of *Onchidium* and *Labella ajuthiae* (Labbé, 1935) and *O. nigrum* (Plate, 1893) are regarded as junior synonyms of *O. stuxbergi*. The nomenclatural status of several other species names is discussed as well. Many new records are provided across South-East Asia and precise ranges of geographic distributions are provided for the genus *Onchidium* and its three species. Distinctive features that help distinguish the genus *Onchidium* from other onchidiids are provided, as well as an identification key for the three species.

Keywords

Biodiversity, Euthyneura, Indo-West Pacific, mangroves, marine slugs, South-East Asia

Introduction

The systematics of the Onchidiidae, one of the higher clades of pulmonate gastropods, has been problematic for decades. Many species names were created up to the 1930s, and then the study of their diversity has been more or less abandoned. Identifications have remained nearly impossible at both generic and specific levels. As a result, there are 143 species names and 19 genus names in the literature but the actual species diversity is largely unknown (Dayrat 2009).

The taxonomy of onchidiid slugs has remained problematic primarily because no malacologist has dared to study it in the past 80 years, which in turn is explained by the fact that many serious issues have made onchidiids a nightmare for taxonomists (Dayrat 2009). For instance, most species were described based on preserved specimens with no information on the color and shape of live animals, which turns out to be critical for taxonomic identification; most species were described based on few specimens (and, in fact, a single specimen in many cases), denying individual variation; many type specimens are likely lost; even when types are available, they often were destroyed, with few internal organs left; and, finally, most specimens in museum collections are old and poorly-preserved.

A few years ago, the Dayrat lab embarked on a worldwide systematic revision of the Onchidiidae. Our goal has been to integrate both traditional taxonomy and modern molecular tools (Dayrat 2005). Thanks to local collaborators, thousands of slugs have been collected from 263 stations (as of September 2016) across the tropical Indo-West Pacific. These stations, which include a large number of type localities, are mangrove sites for the most part, although rocky shores and coral rubble areas (where some genera of onchidiids are found) were also visited. Hundreds of individually-numbered slugs were photographed and hundreds of DNA sequences obtained from tissue cuts of those individually-numbered specimens which were also preserved for anatomical dissection. In addition, all the types available were borrowed from museums as well as additional materials, and the most important collections in the world were visited.

Traditionally, especially in museum collections, any onchidiid slug from the tropical Indo-West Pacific was by default referred to as “*Onchidium*,” and any onchidiid slug from outside the tropical Indo-West Pacific was referred to as *Onchidella*. Still to this day, *Onchidella* has not been recorded in the tropical Indo-West Pacific but is found nearly everywhere else except for polar waters (Dayrat et al. 2011b). Also, most authors have agreed that *Onchidella* did not need to be divided into subgroups. Reciprocally, “*Onchidium*” slugs (in the broad sense of non-*Onchidella*) have not been recorded outside the tropical Indo-West Pacific. Because “*Onchidium*” was found to

be highly diverse, several generic names were proposed in addition to *Onchidium*, such as *Peronia*, *Paraperonia*, *Paraonchidium*, *Platevindex*, and *Semperoncis*. The application of all these names has remained ambiguous, to say the least (Dayrat 2009).

Our understanding of the onchidiid diversity in the tropical Indo-West Pacific has grown as new data were being gathered. Species diversity, distributions, and higher relationships have become clearer as more and more DNA sequences were obtained and more and more specimens were dissected from new places. As of November 2016, our data set for the onchidiid slugs in the tropical Indo-West Pacific includes approximately 70 species and ten clades of generic level. All species and genera are strongly supported by both DNA sequences and morphology.

After careful examination of all type materials, detailed comparisons between the original descriptions and our own observations, the nomenclatural status of nearly all existing species-group and generic-group names of the Onchidiidae is now known. In other words, it is clear which names are valid names, which names are junior synonyms, which names are *nomina dubia*, and which taxa require new names. So, results on the systematic revision of the Onchidiidae can now be shared.

In a first step, the nomenclature and the alpha-taxonomy of each of the clades of generic level in our data set must be clarified. The present contribution, which focuses on the genus *Onchidium*, marks the beginning of a series of taxonomic papers dedicated to each clade in our data set. Then, in a second step, a phylogenetic tree of the entire family will be provided (still an ongoing endeavor) and that tree used to address broader questions on onchidiid diversification, evolution, and biogeography.

The genus *Onchidium*, the type genus of the family, has been traditionally used by default for many onchidiid species from the tropical Indo-West Pacific. Therefore, it is important to give it a proper definition. The genus *Onchidium* is a clade including only three species, which were already named: the type species, *O. typhae* Buchanan, 1800, with a type locality in Bengal (Ganges delta); *O. stuxbergi* (Westermund, 1883), with a type locality from Brunei Bay, north-western Borneo; and *O. reevesii* (J.E. Gray, 1850), with a type locality from China (exact locality unknown). With the exception of a re-description of *O. typhae* by Stoliczka (1869), all three species are re-described here for the first time. New synonymies are proposed based on the examination of all available type materials and the careful study of all original descriptions, for the entirety of the Onchidiidae. New geographical records are provided.

Special attention has been given to type localities. Indeed, without going back to type localities to collect fresh specimens, it can be extremely challenging, and often impossible, to address the nomenclatural status of taxon names. For that reason, new specimens have been collected from type localities as far as possible. For the present study, for instance, new specimens of *O. typhae* were collected from the Sundarbans, in West Bengal, India, which corresponds to the type locality, and new specimens of *O. stuxbergi* were collected from Brunei Darussalam, north-western Borneo, extremely close to the type locality.

Materials and methods

Collecting. All specimens examined here were collected by our team, except for the types of existing species and a few specimens found in museum general collections. Local guides (local villagers or fishermen) also often accompanied us. Sites were accessed by car (if next to a road) or by boat (by hiring local fishermen). Local fishermen and villagers are a great source of information to find good collecting sites. They know where to find well-preserved mangroves with old trees and they also know about potential dangers (snakes, crocodiles, wasps, and even tigers in the case of the Sundarbans, West Bengal). Each site was explored for an average of two hours but the exact time spent at each site also depended on the time of the low tide, the weather, etc. At each site, many photographs were taken to keep track of the kind of mangrove being visited (e.g., thick forest of young *Rhizophora* trees, open forest of large *Avicennia* trees) as well as the diverse microhabitats where specimens were collected (e.g., surface of the mud, old and muddy log).

Specimens. All available types were examined. Some additional non-type material was collected by others and borrowed from museum collections. However, most specimens were collected by us and our new collections provided fresh material for DNA sequencing and invaluable natural history observations. All our new specimens were deposited in local institutions as vouchers. Acronyms of collections are:

BNHS	Bombay Natural History Society, Mumbai, India;
BDMNH	Brunei Museum, Natural History, Brunei Darussalam;
ITBZC	Institute of Tropical Biology, Zoology Collection, Vietnam Academy of Science and Technology, Ho Chi Minh City, Vietnam;
MNHN	Muséum national d'histoire naturelle, Paris, France;
NHMUK	Natural History Museum, London, United Kingdom;
PNM	National Museum of the Philippines, Manila, Philippines;
SMF	Naturmuseum Senckenberg, Frankfurt-am-Main, Germany;
SMNH	Swedish Museum of Natural History, Stockholm, Sweden;
USMMC	Universiti Sains Malaysia, Penang, Malaysia;
ZMB	Zoologisches Museum, Berlin, Germany;
ZMH	Zoologisches Museum, Hamburg, Germany;
ZRC	Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore.

Animal preparation and anatomical description. All anatomical observations were made under a dissecting microscope and drawn with a *camera lucida*. In addition, organs were prepared for scanning electron microscopy (SEM). Radulae were cleaned in 10% NaOH for a week, rinsed in distilled water for at least a week, briefly cleaned in an ultrasonic water bath (less than a minute), sputter-coated with gold-palladium, and examined by SEM. Soft parts (penis and penial hooks) were dehydrated in ethanol and critical point dried before coating. When a lot included several specimens, all

pieces of the dissected specimens were carefully numbered, both inside the jar and on the SEM stubs. A range of minimum to maximum animal size is provided for each lot of specimens. In addition, individualized numbers and measurements are provided for the specimens being illustrated here as well as for those comprising our molecular data set. The anatomical description of *O. typhae*, the type species, is fully detailed. The written description of the many anatomical features that are virtually the same between species (nervous system, heart, etc.) is not uselessly repeated three times.

DNA extraction and PCR amplification. DNA was extracted using the phenol-chloroform extraction protocol with cetyltrimethyl-ammonium bromide (CTAB). Portions of two mitochondrial genes (COI, 16S) were amplified using the following universal primers: COIF (5'-3') GGT CAA CAA ATC ATA AAG ATA TTG G, and COIR (5'-3') TAA ACT TCA GGG TGA CCA AAR AAY CA (Folmer et al. 1994); 16Sar (5'-3') CGC CTG TTT ATC AAA AAC AT, and 16S 972R (5'-3') CCG GTC TGA ACT CAG ATC ATG T (Klussmann-Kolb et al. 2008). The 25 µl PCR reactions contained 15.8 µl of water, 2.5 µl of 10X PCR Buffer, 1.5 µl of 25 mM MgCl₂, 0.5 µl of each 10 µM primer, 2 µl of dNTP Mixture, 0.2 µl (1 unit) of TaKaRa Taq (Code No. R001A), 1 µl of 20 ng/µl template DNA, and 1 µl of 100X BSA (Bovine Serum Albumin). The thermoprofile used for COI and 16S was: 5 minutes at 94°C; 30 cycles of 40 seconds at 94°C, 1 minute at 46°C, and 1 minute at 72°C; and 10 minutes at 72°C. The PCR products were cleaned with ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) prior to sequencing. Sequenced fragments represented ~680 bp of COI, and ~530 bp of 16S.

Phylogenetic analyses. Alignments were obtained using Clustal W in MEGA 6 (Tamura et al. 2013). Chromatograms were consulted to resolve rare ambiguous base calls. DNA sequences were all deposited in Genbank and vouchers clearly identifiable in museum collections (Table 1). The ends of each alignment were trimmed and sequences were concatenated. The concatenated alignment included 993 nucleotide positions: 582 (COI) and 411 (16S). In addition to analyses with the two concatenated markers, another set of analyses was performed with only COI sequences. Pairwise genetic distances between COI sequences were calculated in MEGA 6. Prior to phylogenetic analyses, the best-fitting evolutionary model was selected using the Model Selection option from Topali v2.5 (Milne et al. 2004). A GTR + G + I model was selected. Other (unpublished) analyses were performed using different models, which all yielded identical results. Maximum Likelihood analyses were performed using PhyML (Guindon and Gascuel 2003) as implemented in Topali v2.5. Node support was evaluated using bootstrapping with 100 replicates. Bayesian analyses were performed using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003) as implemented in Topali v2.5, with four simultaneous runs of 10⁶ generations each, sample frequency of 100, and burn in of 25% (and posterior probabilities were also calculated). Three other onchidiid species and their corresponding COI and 16S sequences were selected from previous studies from our lab as out-groups (Dayrat et al. 2011a: *Onchidella celtica* (Cuvier in Audouin and Milne-Edwards, 1832), *Peronia* sp. (Okinawa), and *Peronia* sp. (Hawaii)). Other (unpublished) analyses were performed using different combinations of outgroups, which all yielded identical results.

Table 1. GenBank accession numbers for COI and 16S DNA sequences. All sequences are new, except for the specimens from China (Sun et al. 2014) and the *Peronia* and *Onchidella* out-groups (Dayrat et al. 2011a). Sun et al. (2014) misidentified all specimens from China as *Onchidium* “*struma*” (*nomen nudum*). Information on individually-identified specimens can be found in the additional material examined (see Fig. 1). The individual numbers starting with “S” from China correspond to vouchers used by Sun et al. (2014).

Species	Individual (DNA)	Locality	GenBank COI	GenBank 16S
<i>Onchidella celtica</i>		Ceuta, Northern Africa	AY345048	AY345048
<i>Onchidella floridana</i>		Tobago	HQ660035	HQ659903
<i>Peronia</i> sp.		Okinawa, Japan	HQ660043	HQ659911
<i>Peronia</i> sp.		Hawaii, USA	HQ660038	HQ659906
<i>Onchidium typhae</i>	1064	West Bengal, India	---	KX179528
	1089	Andaman, India	KX179512	KX179529
	1109	Andaman, India	KX179513	KX179530
	967	Peninsular Malaysia	KX179510	KX179526
	965	Peninsular Malaysia	KX179509	KX179525
	1007	Singapore	KX179511	KX179527
<i>Onchidium stuxbergi</i>	971	Peninsular Malaysia	KX179514	KX179531
	1048	Brunei	KX179515	KX179532
	3251	Bohol, Philippines	KX179517	KX179534
	3363	Bohol, Philippines	KX179518	KX179535
	5602	Vietnam	KX179519	KX179536
	5605	Vietnam	KX179520	KX179537
	S891	China (19°56'N)	JN543155	JN543091
<i>Onchidium reevesii</i>	S871	China (22°30'N)	JN543161	JN543097
	S831	China (24°24'N)	JN543160	JN543096
	S853	China (27°29'N)	JN543164	JN543100
	S821	China (33°20'N)	JN543162	JN543098
	S802	China (34°46'N)	JN543157	JN543093

Phylogenetic results

Molecular phylogenetic analyses. Here, the primary purpose of using DNA sequences is to test the species limits within *Onchidium*. The phylogenetic analyses yielded three species units that are all reciprocally monophyletic and strongly supported (Fig. 1). Each species is supported by a bootstrap support of 100 and posterior probabilities of 1 (except for *O. stuxbergi* with a posterior probability of 0.97). Within *O. typhae* and *O. reevesii*, there is virtually no phylogenetic structure. Within *O. stuxbergi*, the specimens from Bohol (Philippines), cluster together in a well-supported (100/1.0) subunit. This, however, does not warrant any species status to the Bohol specimens because they are nested within *O. stuxbergi* which, without them, would not be monophyletic.

Pairwise genetic divergences. The pairwise genetic distances unambiguously support the existence of three species of *Onchidium* (Table 2). There is a wide gap between intra- and inter-specific distances. All intra-specific genetic distances are below 5.1%

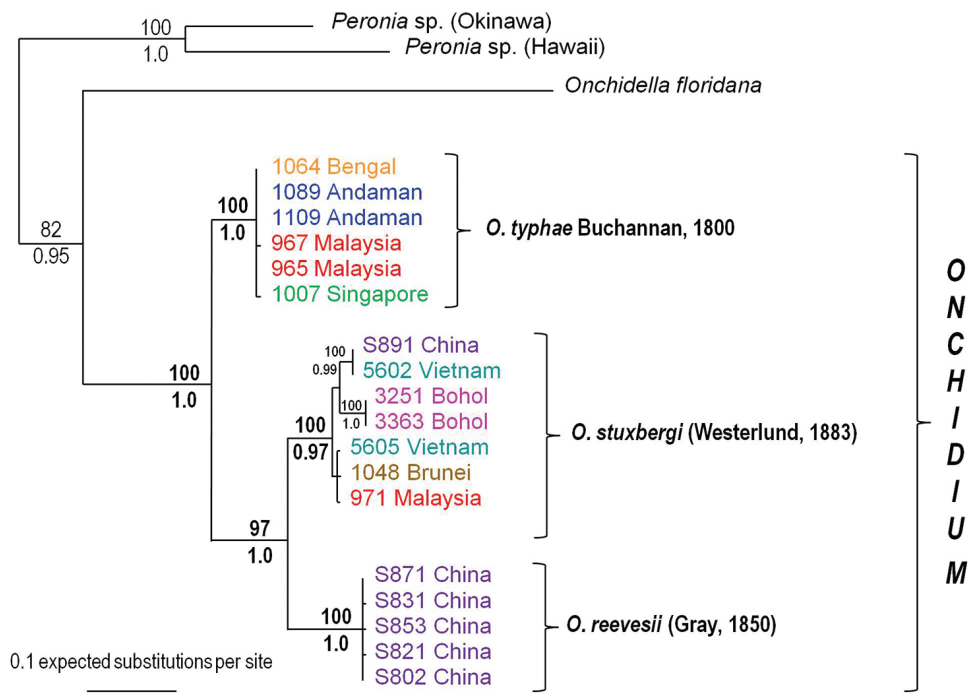


Figure 1. Phylogenetic tree. Relationships within the genus *Onchidium* based on COI and 16S sequences. Numbers above branches are the bootstrap values (Maximum Likelihood analysis) and below are the posterior probabilities (Bayesian analysis); only significant numbers (> 80% and > 0.9) are indicated. *Onchidella* and *Peronia* sequences serve as outgroups. Numbers for each individual correspond to unique identifiers in our DNA collection. All sequences of *Onchidium* specimens are new, with the exception of the specimens from China which were all misidentified as *Onchidium* “*struma*” by Sun et al. (2014). Information on individually-identified specimens can be found in the additional material examined and in Table 1.

Table 2. Intra- and inter-species pairwise genetic distances. Ranges of minimum to maximum distances are indicated (in percentage). For instance, within *O. typhae*, individual sequences are between 0% to 0.5% divergent, and individual sequences between *O. stuxbergi* and *O. typhae* are minimally 21.7% and maximally 26.2% divergent.

Species	<i>O. typhae</i>	<i>O. stuxbergi</i>	<i>O. reevesii</i>
<i>O. typhae</i>	0.0–0.5		
<i>O. stuxbergi</i>	21.7–26.2	0.0–5.1	
<i>O. reevesii</i>	26.9–28.3	15.0–18.1	0.0–0.7

(below 5.1% within *O. stuxbergi* and below 0.7% for the two other species). All inter-specific genetic distances are minimally 15% (between *O. stuxbergi* and *O. reevesii*) and as high as 28.3% (between *O. typhae* and *O. reevesii*).

Systematics and anatomical descriptions

Family Onchidiidae Rafinesque, 1815

Genus *Onchidium* Buchannan, 1800

Type species. *Onchidium typhae* Buchannan, 1800, by monotypy.

Labella Starobogatov, 1976: 211. **New synonym.** Type species, by monotypy, *Labella ajuthiae* (Labbé, 1935); replacement name of *Elophilus* Labbé, 1935, preoccupied by *Elophilus* Meigen, 1803 [Diptera].

Remarks. The synonymy of *Labella ajuthiae* (Labbé, 1935) with *Onchidium stuxbergi* (Westerlund, 1883) is discussed in the remarks on *O. stuxbergi*. *Labella* is a junior synonym of *Onchidium* because the two generic names *Labella* and *Onchidium* apply to the same clade. Baker (1938) provided a list of misspellings and unjustified emendations of *Onchidium*: *Onchidion*, *Onchyidium*, *Orchidium*, and *Oncidium*.

Diagnosis. Body not flattened. No marginal glands in the notum. No dorsal gills. Dorsal eyes present on notum. Fully retractable, central papilla (with three dorsal eyes) present. Long eye tentacles. Male opening inferior to the right ocular tentacle, slightly to its left. Pneumostome medial. Intestine of types II and III. Rectal gland present. Accessory penial gland and hollow spine present. Penis with hooks.

Distinctive diagnostic features. *Onchidium* differs from all other onchidiids by the presence of unmistakably, large, conical, pointed papillae on the dorsum of live animals. Disturbed live animals and preserved animals are retracted and their dorsal papillae are significantly smaller. The identification to the genus level can then be more challenging.

Distribution. From north-eastern India (West Bengal) to the Philippines, including the Strait of Malacca, Singapore, Thailand, Vietnam, eastern Borneo, and China (Fig. 2).

Onchidium typhae Buchannan, 1800

Figs 3–8

Onchidium typhae Buchannan, 1800: 132–134, plate V, figs 1–3; Stoliczka 1869: 90–103, plate xiv, figs 1–6.

Type locality. “Bengal.” Bengal is a vast region of eastern India (and Bangladesh) around the delta of the Ganges. Collecting specimens in West Bengal was the best that could be done to try to go back to the type locality.

Type material. The original type material could not be located and is likely lost. Given that the identity of *O. typhae* is no longer problematic, there is no need to designate a neotype.

Additional material dissected. **Bangladesh**, Sundarbans, delta, October 1927, 1 specimen [25/15 mm], leg. Konietzko, det. as *Onchidium* (ZMH 27506/2); **India**,

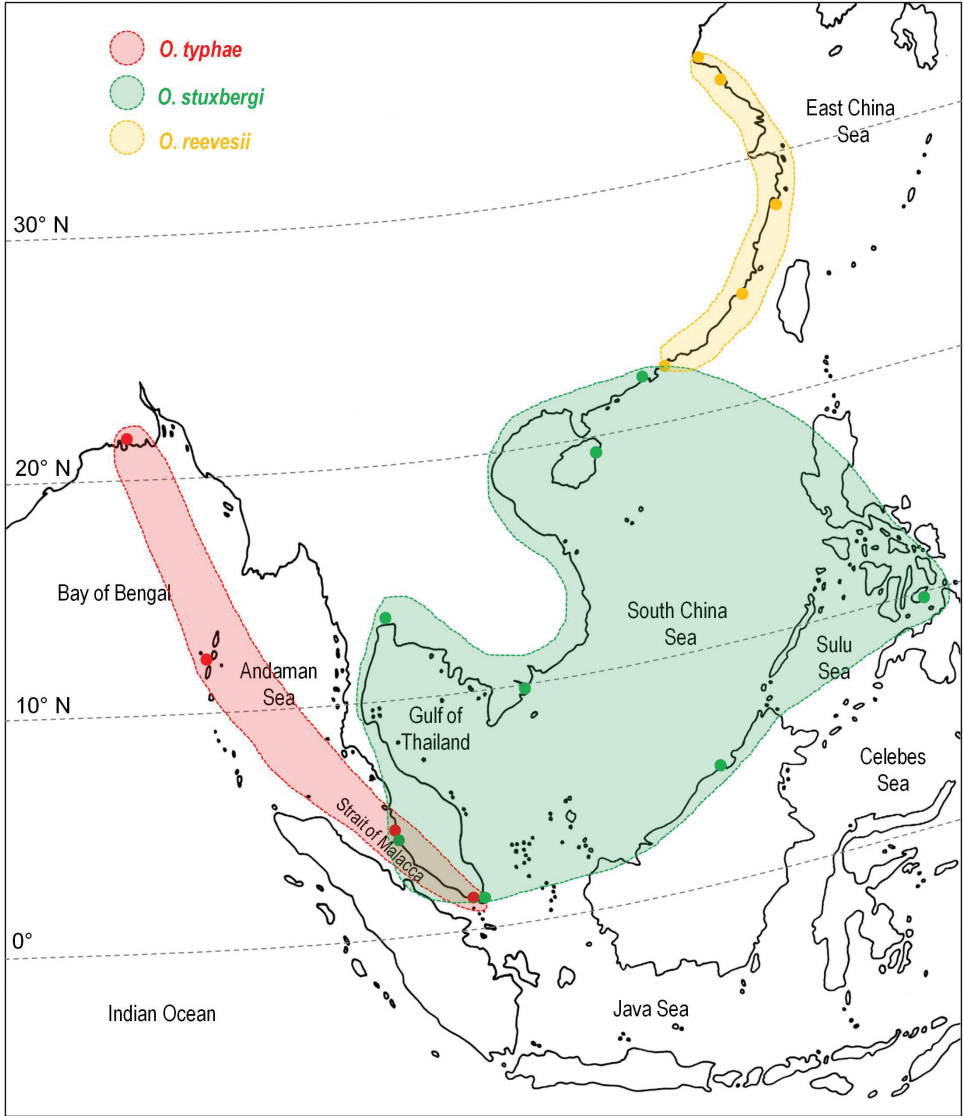


Figure 2. Geographic distribution of the genus *Onchidium* and its three valid species. The colored dots correspond to the known records for each species. Colored areas correspond to hypothetical ranges proposed based on those known records. Naturally, details about the distribution of each species remain uncertain. For instance, *O. typhae* may or may not be found on the western coasts of Thailand by the Andaman Sea.

West Bengal, Sundarbans, Bally, Datta River, 21°59.277'N, 088°45.213'E, 04 January 2011, 5 specimens (45/25 to 40/25 mm), leg. B. Dayrat & V. Bhawe, [station 48, very narrow band of mud with a few sparse *Avicennia* trees, between the edge of the river and the walls protecting the village, no old logs since firewood is a precious

resource] (BNHS); Sundarbans, Amlamethi Island, Bidyadhari River, 22°04.923'N, 088°41.882'E, 05 January 2011, 1 specimen (40/30 [DNA 1064] mm), leg. B. Dayrat & V. Bhawe, [station 49, very soft mud on the shore with recently-planted *Avicennia* trees; uninhabited island] (BNHS); **India, Andaman Islands**, Middle Andaman, Rangat, Yerrata, Saban, 12°27.451'N, 092°53.792'E, 10 January 2011, 3 specimens (45/20 to 35/20 mm), leg. B. Dayrat & V. Bhawe, [station 56, open, impacted mangrove patch by a creek, near village, with medium trees and old logs] (BNHS); Middle Andaman, Rangat, Shyamkund, 12°28.953'N, 092°50.638'E, 11 January 2011, 25 specimens (55/30 to 30/15 mm; 40/20 [DNA 1089] mm), leg. B. Dayrat & V. Bhawe, [station 57, by a large river, deep mangrove with tall trees, small creeks, and plenty of old muddy logs, next to a road and a small cemented bridge for creek] (BNHS); Middle Andaman, Shantipur, Kadamtala, 12°19.843'N, 092°46.377'E, 12 January 2011, 25 specimens (65/30 to 30/20 mm; 40/20 [DNA 1109]), leg. B. Dayrat & V. Bhawe, [station 58, open area with hard mud and many old logs, next to a mangrove with medium trees] (BNHS); South Andaman, Bamboo Flat, Shoal Bay, 11°47.531'N, 092°42.577'E, 13 January 2011, 7 specimens (50/35 to 40/25 mm), leg. B. Dayrat & V. Bhawe, [station 59, open mangrove with medium trees, hard mud, old logs, next to a road and a small cemented bridge for creek] (BNHS); **Malaysia**, Peninsular Malaysia, Merbok, 05°39.035'N, 100°25.782'E, 12 July 2011, 1 specimen (35/24 mm), leg. B. Dayrat & T. Goulding, [station 21, deep *Rhizophora* forest with old, tall trees, hard mud, many small creeks and many old logs] (USMMC 00001); Langkawi Island, Tanjung Rhu, 06°25.771'N, 099°49.436'E, 13 July 2011, 2 specimens (60/35 [#1] and 27/18 mm), leg. B. Dayrat, [station 23, dense forest with young trees, a few creeks] (USMMC 00002);, Langkawi Island, Tanjung Rhu, 06°25.317'N, 099°50.106'E, 15 July 2011, 2 specimens (45/40 and 27/17 [DNA 967] mm), leg. B. Dayrat, [station 26, open forest (mostly *Rhizophora*) with high mud lobster mounds] (USMMC 00003); Peninsular Malaysia, Matang, off Kuala Sepatang, Crocodile River, Sungai Babi Manpus, 04°49.097'N, 100°37.370'E, 19 July 2011, 4 specimens (32/20 to 20/17 mm), leg. B. Dayrat & T. Goulding, [station 28, old and open *Rhizophora* forest with tall trees, hard mud, creeks, and many old logs] (USMMC 00004); Matang, close to the jetty, facing fishermen's village on the other side of river, 04°50.154'N, 100°36.368'E, 20 July 2011, 18 specimens (42/24 [#1] to 28/18 [#2] and 15/10 [DNA 965] mm), leg. B. Dayrat & T. Goulding, [station 29, oldest and open *Rhizophora* forest of tallest and beautiful trees, with hard mud, many creeks, and many old logs] (USMMC 00005); **Singapore**, Semakau Island, 01°12.083'N, 103°45.585'E, 4 April 2010, 1 specimen (40/22 [DNA 1007] mm), leg. B. Dayrat & S. K. Tan, [station 8, artificial, landfill island with low and very dense newly-planted *Rhizophora* trees; muddy areas in between *Rhizophora* patches and coral rubble close to the shore] (ZRC.MOL.6396);, Lim Chu Kang, 01°26.785'N, 103° 42.531'E, 5 April 2010, 3 specimens (40/20, 38/22 [#1], and 19/10 mm), leg. B. Dayrat & S. K. Tan, [station 9, mangrove east of the jetty; open forest with medium trees and medium mud; ended on sun-exposed mudflat outside the mangrove with soft mud; very polluted with trash] (ZRC.MOL.6397).



Figure 3. Habitats for *O. typhae*. **A** India, West Bengal, very soft mud on the shore with recently-planted *Avicennia* trees (station 49) **B** India, Andaman Islands, by a large river, deep mangrove with tall trees, small creeks, and plenty of old muddy logs (station 57) **C** Malaysia, Matang, old and open *Rhizophora* forest with tall trees, hard mud, creeks, and many old logs (station 28) **D** Malaysia, Langkawi Island, open forest with high mud lobster (*Thalassina*) mounds (station 26).

Distribution (Fig. 2). India: Bengal (type locality; Stoliczka 1869; present study), Andaman Islands (present study). Bangladesh (present study). Singapore (present study). Malaysia (present study).

Habitat (Fig. 3). In West Bengal, *O. typhae* was collected at both sites on soft mud, just next to the river (brackish water) and a few sparse *Avicennia* trees. In the Andaman Islands, it was collected directly on the mud, on the muddy surface (most often at the base) of tree trunks and roots, and on muddy old logs, inside old and deep mangroves with tall trees as well as more open muddy areas; it was also found on the cemented walls of small bridges (under a road next to mangrove). In Singapore, it was collected on muddy old logs. In Malaysia, it was most often found on muddy old logs and on muddy tree trunks and roots, as well as on the surface of the mud (especially that of mud lobster mounds). *Onchidium typhae* is a very cryptic species, especially when it is on the surface of the mud, and one needs to patiently look for it to find it, especially because it is rarely abundant (see below).

Abundance. In the Sundarbans, *O. typhae* was found in two of the four mangrove sites that were visited, but for a total of only six specimens. In the Andaman Islands, it

was found in four of the five mangrove sites visited. The mangrove site where *O. typhae* was not found was not at all muddy but rather, comprised a sandy patch of *Avicennia* by a coral rubble sandy beach. It was especially abundant at two sites (many specimens were observed but not collected), mostly on or near old logs. In Malaysia, *O. typhae* was found in only five of the 18 mangroves that were visited and it was abundant (17 specimens collected) only at one site, which happens to be one of the best, oldest, most pristine, and most diverse mangrove forests we have ever seen anywhere. In Singapore, *O. typhae* was found in three of the five mangroves that were visited (the two sites mentioned above, and one site by the Mandai River where one specimen was collected but ultimately escaped). However, it is rare there (only five specimens collected in total).

Color and morphology of live animals (Fig. 4). Live animals are abundantly covered with mud and the color of their dorsum can hardly be seen at all. In fact, if it were not for their fecal pellets and their long ocular tentacles, they would be really difficult to find because they can be very cryptic. Once the mud is washed out, their dorsum is brownish, with no particular pattern. The color of the foot and of the hyponotum is important because it differs from the other species described here. The foot and the hyponotum vary from gray to yellow in color, and show sometimes even a greenish hue. The color of the foot and the hyponotum may or may not have the same color. It is remarkable that the color of the foot and of the hyponotum of a particular individual can change rapidly, especially when disturbed. The lateral sides of the foot remain dark grey. Distally, the long ocular tentacles are reddish brown. Proximally, they are darker brown and less reddish, speckled with many tiny white dots. The ocular tentacles are extremely long (easily 2 cm when the animal is undisturbed). The ocular tentacles of all *Onchidium* species described here are significantly longer than in other onchidiids, which is a useful character in the field to identify a slug as an *Onchidium*. The head is reddish brown to black, with many white dots evenly distributed.

When animals are not disturbed, the dorsum is typically covered by large pointed papillae that rest on larger, hemispherical bases. Those pointed papillae are unique to *Onchidium* and extremely useful for identification in the field. For a long time (before we realized those slugs were *Onchidium* in the strict sense), we called them the “spiky” slugs to refer to the unique pointed papillae. Those papillae may seem to be arranged in two to four longitudinal ridges (each with five to ten papillae), but this is not the rule. They bear from one to four black “dorsal eyes” at their tip but some papillae do not bear dorsal eyes (especially on the dorsum margin). As in many other onchidiids, there is a central peduncle entirely retractable within the notum. The central peduncle bears three or four “dorsal eyes” but its size is similar to the large pointed papillae (i.e., it is not significantly larger than the other large papillae). The large pointed papillae are surrounded by small papillae as well, which may be rounded or pointed. As soon as the animal is disturbed (by walking on the mud on which it crawls or by touching its dorsum), all dorsal papillae rapidly retract and the animal looks completely different. It then is evenly covered with minute pointed papillae. The body of disturbed animals also is more humped and their ocular tentacles are entirely retracted. One has to patiently wait for a long time for a disturbed slug to relax again (easily 10 or 15 minutes)

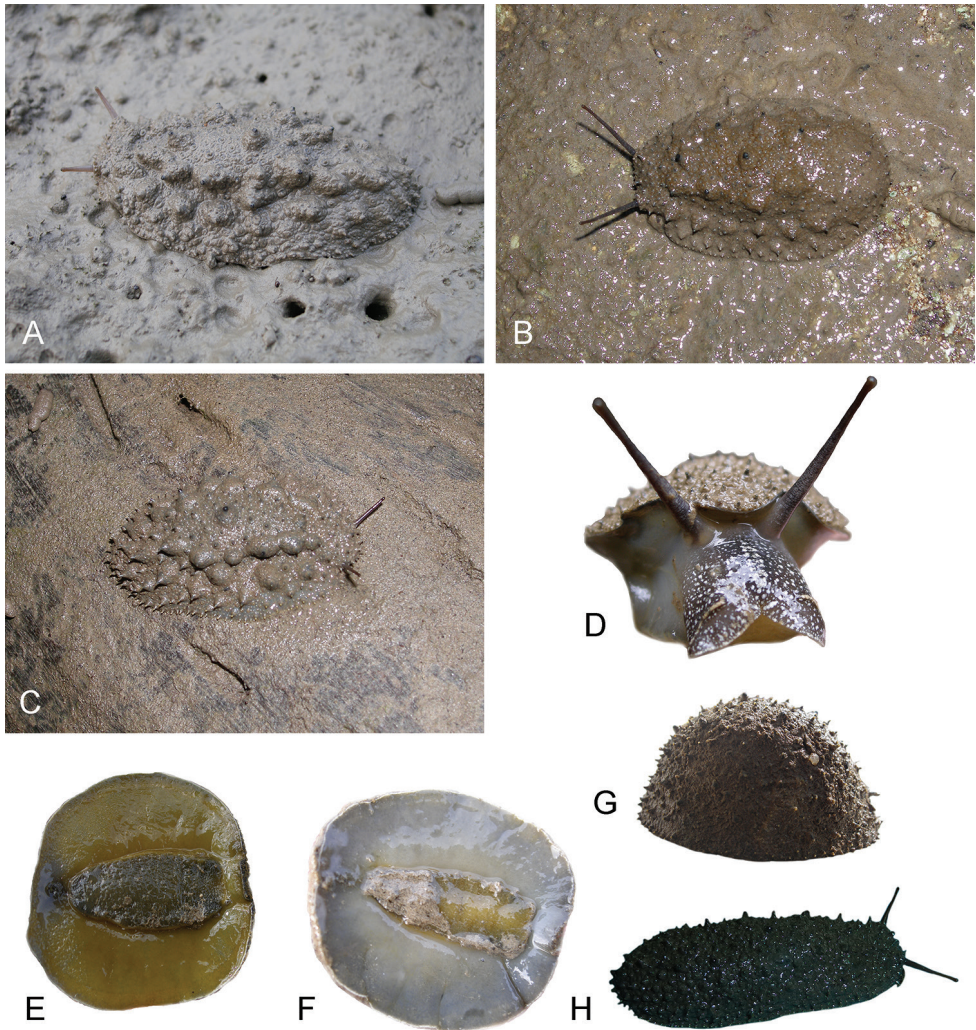


Figure 4. Live specimens, *O. typhae*. **A** Dorsal view, 45 mm long, India, West Bengal, station 48 (BNHS) **B** Dorsal view, 55 mm long, India, Andaman Islands, station 57 (BNHS) **C** Dorsal view, 40 mm long, Singapore (ZRC.MOL.6396) **D** Frontal view, 25 mm wide, India, Andaman Islands, station 57 (BNHS) **E** Ventral view, 50 mm long, India, Andaman Islands, station 59 (BNHS) **F** Ventral view, 40 mm long [DNA 1064], India, West Bengal, station 49 (BNHS) **G** Dorso-lateral view, 40 mm long, India, Andaman Islands, station 59 (BNHS) **H** Dorsal view, 42 mm long, Malaysia, Matang (USMMC 00005, #1).

so the rule is “take a picture first and then touch it!” Interestingly, the appearance of the dorsum of live, disturbed animals is very close to the appearance of preserved animals, which was quite useful when examining type materials of existing species and recognizing them as *Onchidium* species. Crawling individuals can easily measure 30 to 40 mm in length (largest individuals measured 65 mm).

External morphology (Figs. 5A–C). Preserved specimens no longer display the distinct color traits seen in live animals. The color of preserved animals is meaningless and uninformative. The body is not flattened. The notum is elongated, occasionally oval. Dorsal gills are absent. The notum is evenly covered by papillae. Large papillae with hemispherical bases are typical for live animals but, in preserved animals, those papillae are pointier and smaller. These larger papillae are surrounded by even smaller papillae. As in live animals, papillae with so-called ‘dorsal eyes’ are present. There is a central, retractable peduncle in the center of the notum, but it can only be seen in live animals in the field. The hyponotum is horizontal. The width of the hyponotum relative to the width of the pedal sole varies among individuals. The width of the hyponotum ranges from about 1/3 to 1/2 its total width, occasionally extending to 4/5 its total width. The anus is posterior, medial, close to the edge of the pedal sole. On the right side (to the left in ventral view), a peripodial groove is present at the junction between the pedal sole and the hyponotum, running longitudinally from the buccal area to the posterior end, a few millimeters from the anus and the pneumostome. The pneumostome is medial. Its position on the hyponotum relative to the notum margin and the edge of the pedal sole varies among individuals but averages in the middle. The position of the female pore (at the posterior end of the peripodial groove) does not vary much among individuals. In the anterior region, the left and right ocular tentacles are superior to the mouth. They are outside if specimens were relaxed before preservation. Otherwise they are retracted. Eyes are located at the tips of the ocular tentacles. Inferior to the ocular tentacles, superior to the mouth, the head bears a pair of oral lobes. On each oral lobe, there is an elongated bump, likely with sensitive receptors. The male aperture (opening of the copulatory complex) is inferior to the right ocular tentacle, slightly to its left (internal) side.

Visceral cavity and pallial complex (Fig. 5D). Marginal glands (found in *Onchidella*) are absent. The anterior pedal gland is oval and flattened, lying free on the floor of the visceral cavity below the buccal mass. The visceral cavity is not pigmented internally and not divided (the heart is not separated from the visceral organs by a thick, muscular membrane). The heart, enclosed in the pericardium, is on the right side of the visceral cavity, slightly posterior to the middle. The ventricle, anterior, gives an anterior vessel supporting several anterior organs such as the buccal mass, the nervous system, and the copulatory complex. The auricle is posterior. The kidney is more or less symmetrical, the right and left parts being equally developed. The kidney is intricately attached to the respiratory complex. The lung is in two left and right, equally-developed, more or less symmetrical parts.

Digestive system (Figs 5E–G, 6). There are no jaws. The left and right salivary glands, heavily branched, join the buccal mass dorsally, on either side of the esophagus. The radula is in between two large postero-lateral muscular masses. Each radular row contains a rachidian tooth and two half rows of lateral teeth of similar size and shape. Examples of radular formulae are: 58×73 -1-73 in USMMC 00005 #1 (42 mm long), 58×65 -1-65 in USMMC 00005 #2 (28 mm long), 53×80 -1-80 in USMMC 00002 #1 (60 mm long), and 65×70 -1-70 in ZRC.MOL.6397 #1 (38 mm long). The rachidian teeth are tricuspid: the medial cusp is always present; the two lateral

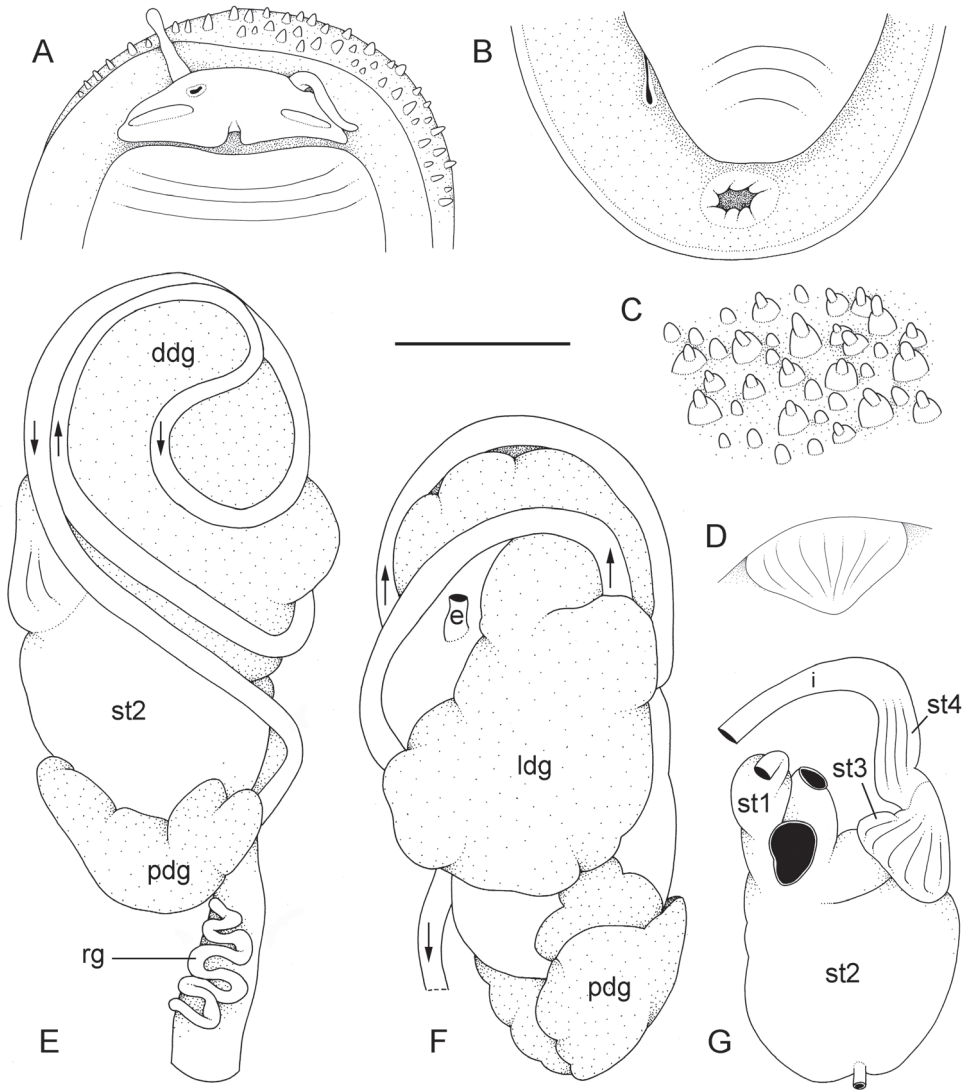


Figure 5. External morphology and digestive system, *O. typhae*. **A** Anterior region, ventral view, Singapore, scale bar 8 mm (ZRC.MOL.6396) **B** Posterior region, ventral view, Singapore, scale bar 7 mm (ZRC.MOL.6396) **C** Dorsal papillae (preserved), Singapore, station 8, scale bar 3.8 mm (ZRC.MOL.6396) **D** Buccal gland, Malaysia, Langkawi Island, scale bar 3 mm (USMMC 00002, #1) **E** Digestive system, dorsal view, Singapore, scale bar 5 mm (ZRC.MOL.6397, #1) **F** Digestive system, ventral view, Singapore, scale bar 5 mm (ZRC.MOL.6397, #1) **G** Stomach (digestive gland removed), ventral view, Singapore, scale bar 5 mm (ZRC.MOL.6397, #1). Abbreviations: **ddg**, dorsal lobe of digestive gland; **e**, esophagus; **i**, intestine; **ldg**, lateral lobe of the digestive gland; **pdg**, posterior lobe of the digestive gland; **rg**, rectal gland; **st1**, stomach chamber 1; **st2**, stomach chamber 2; **st3**, stomach chamber 3; **st4**, stomach chamber 4.

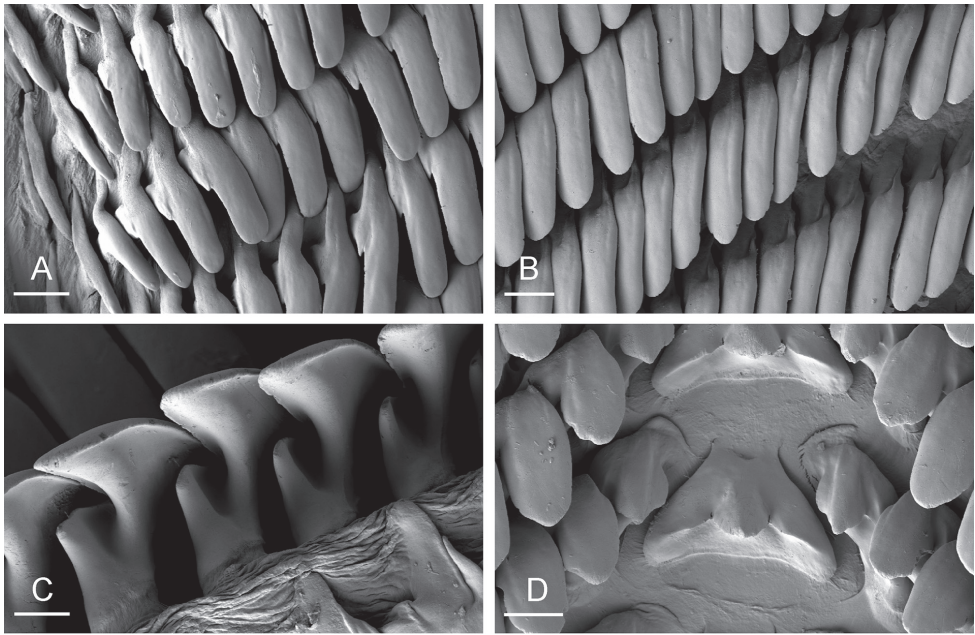


Figure 6. Radula, *O. typhae*, Malaysia, Matang (USMMC 00005, #1). **A** Outermost lateral teeth, scale bar 20 μ m **B** Lateral teeth, scale bar 20 μ m **C** Lateral teeth, inferior view, showing the additional outer spine of each tooth, scale bar 10 μ m **D** Rachidian and innermost lateral teeth, scale bar 20 μ m.

cusps, on the lateral sides of the base of the rachidian tooth, are small and inconspicuous. Rachidian teeth tend to be about half the size of the lateral teeth (with a length of the rachidian tooth usually not exceeding 40 μ m). The lateral aspect of the base of the rachidian teeth is straight (not concave). The half rows of lateral teeth form an angle of 45° with the rachidian axis. With the exception of the few innermost and few outermost lateral teeth, the size and shape of the lateral teeth do not vary along the half row, nor do they vary among half rows. The lateral teeth seem to be unicuspid with a flattened and curved hook with a rounded tip (the length of the hook is between 50 and 60 μ m), but there also is an outer pointed spine on the lateral expansion of the base. In most cases, the basal lateral spine cannot be observed because it is hidden below the hook of the next, outer lateral tooth. It can only be observed when the teeth are not too close (such as in the innermost and outermost regions) or when teeth are placed in an unusual position. The inner and outer lateral aspects of the hook of the lateral teeth are straight (i.e., not wavy and not forming any protuberance).

The esophagus is narrow and straight, with thin internal folds. The esophagus enters the stomach anteriorly. Only a portion of the posterior aspect of the stomach can be seen in dorsal view because it is partly covered by the lobes of the digestive gland. The dorsal lobe is mainly on the right. The left, lateral lobe is mainly ventral. The posterior lobe covers the posterior aspect of the stomach. The stomach is a U-shaped sac divided in four chambers. The first chamber, which receives the esophagus, is delimited

ited by a very thin layer of tissue, and receives the ducts of the dorsal and lateral lobes of the digestive gland. The second chamber, posterior, is delimited by a thick muscular tissue and receives the duct of the posterior lobe of the digestive gland. It appears divided externally but consists of only one internal chamber. The third, funnel-shaped chamber is delimited by a thin layer of tissue with high ridges internally. The fourth chamber is continuous and externally similar to the third, but it bears only low, thin ridges internally. The intestine is long, narrow, and of type II. A rectal gland is present. It is a long, narrow, and coiled tube that opens in the left portion of the pulmonary complex. Its function is unknown.

Nervous system (Fig. 7A). The circum-esophageal nerve ring is post-pharyngeal and pre-esophageal. The two cerebral ganglia touch and the cerebral commissure is short. However, the length of the cerebral commissure does vary among individuals. Pleural and pedal ganglia are also all distinct. The visceral commissure is short but distinctly present and the visceral ganglion is more or less medial. Cerebro-pleural and pleuro-pedal connectives are short and pleural and cerebral ganglia touch each other. Nerves from the cerebral ganglia innervate the buccal area and the ocular tentacles, and, on the right side, the penial complex. Nerves from the pedal ganglia innervate the foot. Nerves from the pleural ganglia innervate the lateral and dorsal regions of the mantle. Nerves from the visceral ganglia innervate the visceral organs.

Reproductive system (Fig. 7B). Sexual maturity is correlated with animal length. Mature individuals have large female organs (with a large female gland mass) and fully-developed, male, copulatory parts. Immature individuals may have inconspicuous female organs (or simply no female organs at all) and rudimentary anterior male parts. The hermaphroditic gland is a single mass, joining the spermoviduct through the hermaphroditic duct (which conveys the eggs and the autosperm). There is a large, bent, and approximately oval receptaculum seminalis (caecum) along the hermaphroditic duct. The female gland mass contains various glands (mucus and albumen) which can hardly be separated by dissection and of which the exact connections remain uncertain. The hermaphroditic duct becomes the spermoviduct (which conveys eggs, exosperm, and autosperm) which is not divided proximally, at least not externally. A prostate, not distinct externally, may be located within the walls of the spermoviduct. The spermoviduct is completely embedded within the female gland mass, at least proximally. Distally, the spermoviduct branches into the deferent duct (conveys the autosperm up to the anterior region, running through the body wall) and the oviduct. The free oviduct conveys the eggs up to the female opening and the exosperm from the female opening up to the fertilization chamber, which should be near the proximal end of the spermoviduct. The ovate-spherical spermatheca (for the storage of exosperm) connects to the oviduct through a wide and strong duct. The oviduct is narrow, only slightly elongated and convoluted. The vaginal gland is absent.

Copulatory apparatus (Figs 7C–D, 8). The male anterior organs consist of the penial complex (penis, penial sheath, vestibule, deferent duct, retractor muscle) and penial accessory gland (flagellum, and hollow spine). The penial complex and the penial accessory gland share the same vestibule and the same anterior male opening.

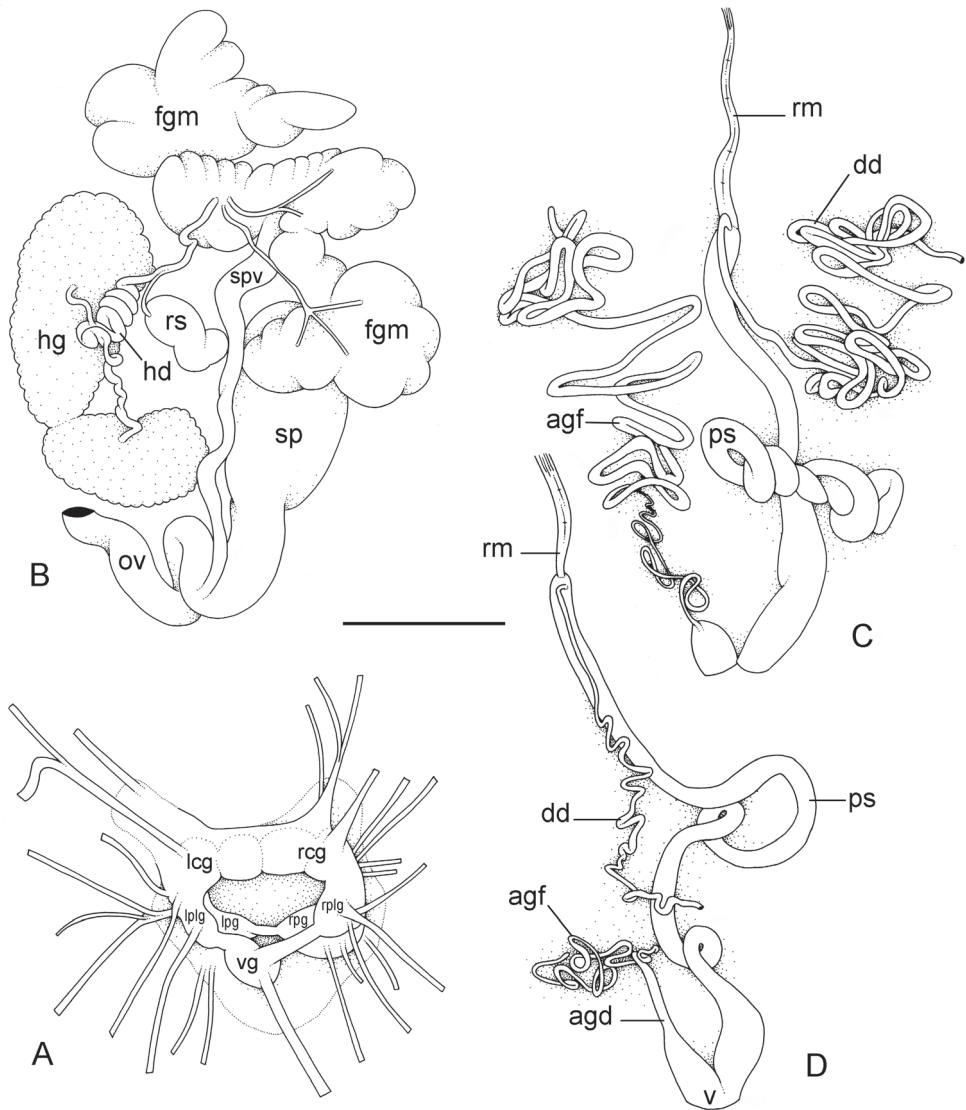


Figure 7. Nervous and reproductive systems, *O. typhae*. **A** Nervous system, Malaysia, Langkawi Island, scale bar 3.8 mm (USMMC 00002, #1) **B** Hermaphroditic (female), posterior parts, Singapore, scale bar 3.8 mm (ZRC.MOL.6397, #1) **C** Male, anterior, copulatory parts, Malaysia, Matang, scale bar 5 mm (USMMC 00005, #1) **D** Male, anterior, copulatory parts, Malaysia, Matang, scale bar 2.7 mm (USMMC 00005, #2). Abbreviations: **agf**, accessory gland flagellum; **dd**, deferent duct; **fgm**, female gland mass; **hd**, hermaphroditic duct; **hg**, hermaphroditic gland; **lcg**, left cerebral ganglion; **lpg**, left pedal ganglion; **lplg**, left pleural ganglion; **ov**, oviduct; **ps**, penial sheath; **rcg**, right cerebral ganglion; **rm**, retractor muscle; **rpg**, right pedal ganglion; **rplg**, right pleural ganglion; **rs**, receptaculum seminis; **sp**, spermatheca; **spv**, spermoviduct; **v**, vestibule; **vg**, visceral ganglion.

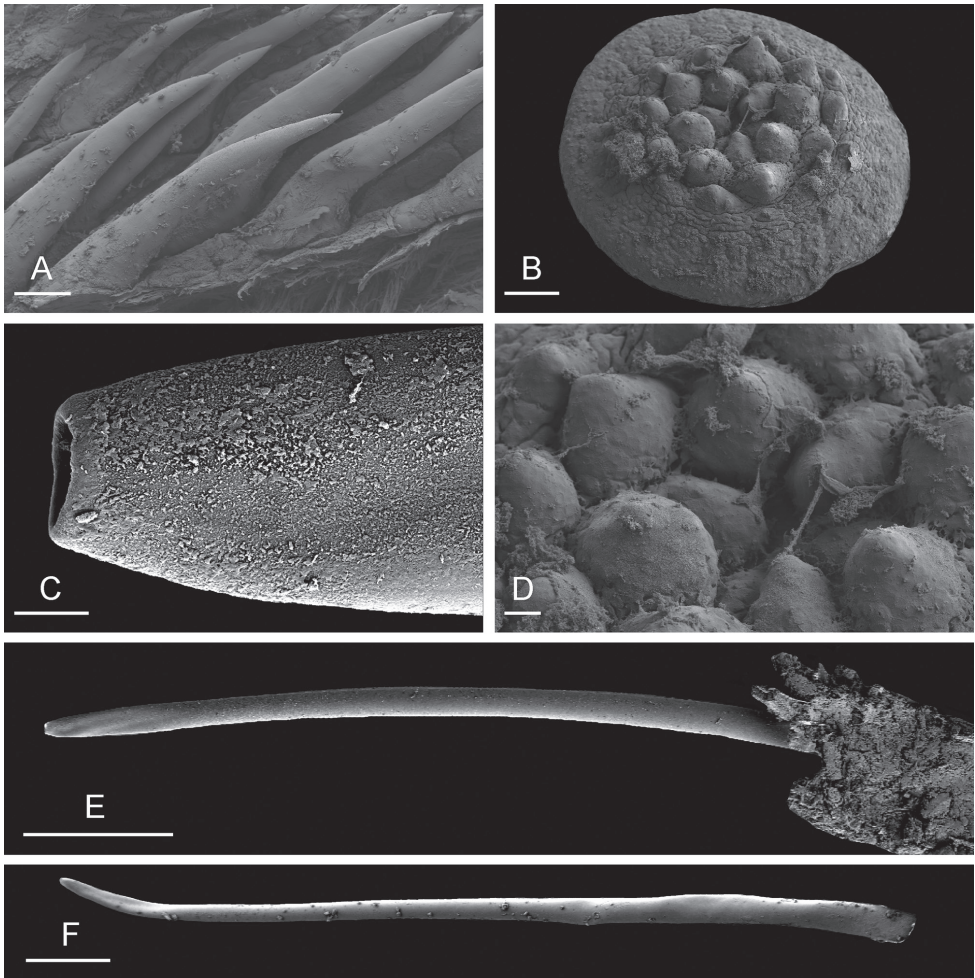


Figure 8. Male, anterior, copulatory parts, *O. typhae*. **A** Penial hooks, Malaysia, Matang, scale bar 30 μ m (USMMC 00005, #1) **B** Flat disc at distal end of flagellum of penial accessory gland, Malaysia, Langkawi Island, scale bar 100 μ m (USMMC 00002, #1) **C** Tip of hollow spine, penial accessory gland, Singapore, scale bar 4 μ m (ZRC.MOL.6397, #1) **D** Detail of B, scale bar 20 μ m (USMMC 00002, #1) **E** Hollow spine, penial accessory gland, Singapore, scale bar 100 μ m (ZRC.MOL.6397, #1) **F** Hollow spine, penial accessory gland, Malaysia, Langkawi Island, scale bar 100 μ m (USMMC 00002, #1).

The penial gland is a long, tube-like flagellum with a proximal dead end. The length of the flagellum of the penial gland varies among individuals but it is always heavily coiled. Distally, the flagellum ends in a hard, hollow spine protected by a sheath which is fused distally with the vestibule. The hollow spine is narrow and elongated, slightly curved. Its diameter is between 20 and 30 μ m but it narrows down distally. The diameter of the opening at its tip is between 4 and 6 μ m. Its length ranges from 0.7 mm (ZRC.MOL.6397 #1) to 1.2 mm (USMMC 00005 #1). The hollow

spine does not open directly into the vestibule. Instead, the end of the tube of the accessory gland is a disc which is more or less flat (between 0.4 and 0.6 mm in diameter) and bears approximately 20 conical papillae in its center. The hollow spine thus must go through that disc in order to be outside and shared with the partner.

The penial sheath is long and very strongly coiled in spirals. In less mature individuals, the coils may not be as strong and numerous but they are present. The penial sheath protects the penis for its entire length. The insertion of the retractor muscle marks the separation between the penial sheath (and the penis inside) and the deferent duct. The retractor muscle is shorter than the penial sheath and runs straight to the posterior half of the visceral cavity. The insertion of the retractor muscle varies among individuals: in the posterior half of the visceral cavity in all specimens but those from India; in the anterior half of the visceral cavity (just anterior to the heart) in the specimens from India. The deferent duct also is highly convoluted with many loops. In immature specimens, the deferent duct is significantly less coiled. The penis is elongated, round, narrow, and hollow; its diameter is less than 200 μm , and its distal part covered with hooks. When the penis is retracted inside the penial sheath, the hooks are inside the tube-like penis. During copulation, the penis is exerted like a glove and the hooks are then on the outside. Hooks are very densely packed inside the penis, with multiple, irregular rows of an average of 15 hooks around the circumference of the penis. Hooks are conical, slender, sharply pointed, and measure up to 300 μm in length.

Distinctive diagnostic features. Externally, *O. typhae* differs from other *Onchidium* species by the color of the hyponotum, which is not white but instead varies between grayish, yellowish, and even greenish (see below the dichotomous identification key, before the final conclusion). The color of the foot (yellowish, not bright orange) is not diagnostic. Internally, the spirally coiled penial sheath is not diagnostic. However, *O. typhae* is the only *Onchidium* species known so far with an intestine of type II.

Remarks. The original description of *O. typhae* by Buchannan was brief but it was based on first-hand observation of live animals, which is quite unusual for onchidiids since most onchidiid species were described based on preserved material with no information on shape and color of live animals. Even though the type material is likely lost, two features described and illustrated by Buchannan support the identification of the material described here as *O. typhae*. First, and most importantly, the long eye tentacles (only *Onchidium* species have such long eye tentacles) and the dorsal papillae of various sizes (Buchannan's "glandular tubercles"). Buchannan's (1800: fig. 2) illustration of an elongated body of a crawling slug is perfectly compatible with what we observed in the field. Buchannan originally described *O. typhae* as non-hermaphroditic; however, as pointed out by Cuvier (1804) shortly after Buchannan's article, onchidiid slugs are in fact hermaphroditic.

Stoliczka (1869) re-described *O. typhae* based on live animals that he collected himself near Calcutta. His identification is in agreement with Buchannan's original description. Stoliczka provided some information on the internal anatomy, which is compatible with our observations. Semper (1885) examined two specimens from Calcutta which he identified as *O. typhae*. According to Buchannan (1800), *O. typhae* is found

on leaves of *Typha elephantina* (hence the specific name), a common reed in brackish waters of the Ganges delta. Wild areas with reeds have become very rare because Bengal was heavily developed in the last century and most coastal areas were converted to rice fields. According to Stoliczka (1869), however, *O. typhae* is also found “about old bricks” and “in ditches.” Stoliczka also mentioned that it was the only species found near Calcutta, suggesting that in the past it could be found in brackish waters extending far inland. Finally, Stoliczka mentions *O. typhae* from the banks of the Hooghly River, which is very close to where our own specimens were collected in West Bengal.

Semper accepted Stoliczka’s anatomical re-description of *O. typhae* and added some detail on the anterior male parts. In particular, Semper illustrated some penial hooks and the spine of the penial accessory gland. However, the sizes described by Semper (a maximum size of 170 μm for the penial hooks and a length of 4.5 mm for the spine of the penial accessory gland) are not really compatible with the sizes observed for the present study (penial hooks up to 300 μm and a spine less than 1.2 mm long). Therefore, Semper likely examined individuals of a different species, which cannot be identified at this stage.

Hoffmann (1928) re-described a specimen that he identified as *O. typhae*. That identification as an *Onchidium* is possibly correct (because of the presence of a rectal gland and of a penial accessory gland). However, the specimen examined by Hoffmann came from an unknown locality and it remains unclear whether Hoffmann did actually examine *O. typhae*. Labbé (1934) simply mentions the name *O. typhae* with no additional description or records. Dey (2006) illustrated a preserved (and not relaxed) specimen identified as *O. typhae* from the Sundarbans. The identification is possibly correct (the photograph is fuzzy). However, it is unclear whether the brief comments on the natural history of *O. typhae* refer only to *O. typhae* or a mix of species because Dey claims that *O. typhae* is found climbing on the trees, which is uncertain. Based on our observations, *O. typhae* can be found on muddy old logs, but not actually climbing on trees.

Finally, a search for potential synonyms of *O. typhae* revealed no synonyms (the available type materials of all onchidiid species were personally examined) and it does seem that it was named only once.

***Onchidium stuxbergi* (Westerlund, 1883), comb. n.**

Figs 9–13

Vaginulus stuxbergi Westerlund, 1883: 165; Westerlund 1885, p.191–192, pl. 2, fig. 2a–c.

Oncidium nigrum Plate, 1893: 188–190, pl. 8, fig. 31a, pl. 10, fig. 53, pl. 11, fig. 75;

Hoffmann 1928: 78; Labbé 1934: 223–224, figs. 58–61. **New synonym.**

Elophilus ajuthiae Labbé, 1935: 312–317, figs 1–3. **New synonym.**

Type locality (*V. stuxbergi*). “Borneo in silva, ad flum Kalias” means that the slugs were found in forests by a river now called the Klias River. The latter runs into the Bru-

nei Bay, which is a small bay bordered by Brunei Darussalam in the South, by Sabah (Malaysia) in the north, and by the small island of the Labuan Territory (Malaysia) in the west. Several of the labels of the type material indicate Labuan as the locality. So, it is possible that the type material is a mix of specimens collected at Labuan Island itself and on the shore of Borneo, facing Labuan. Here is what the different labels read for the first jar: “*Vaginulus stuxbergi* Westerlund, 1885. Borneo, Labuan. On the beach, mangroves. Leg. Vega Exp 1878-1880, sta. 633. SMNH-Type-7523-syntype(s);” “*Oncidium*. Mangrover Sump, Labuan vid Borneo [i.e., meaning Labuan opposite (seeing) Borneo], Vega Exp. n° 633, 18/11 1879;” and “*Oncis stuxbergi* Wstld, 1883. Hab. Labuan b. Borneo (Mangrove - Sumpf). Leg Vega-Expedition (N°633) 18-xi-1879, Jena, Jan 1927, Hoffmann determ.” Here is what the different labels read for the second jar: “*Vaginulus stuxbergi* Westerlund, 1885. Borneo, Labuan. On the beach, mangroves. Leg. Vega Exp 1878-1880, sta. 633. SMNH-Type-1334-syntype(s);” “*Vaginulus Stuxbergi*,” “*Vaginulus Stuxbergi* Borneo Vega Exp, det. Westerlund;” and “*Oncis stuxbergi* Westerlund, 1883 [Typ fur Vaginula stuxbergi Wsterld]. Hab. Borneo. Leg. Vega-Expedition, Westerlund det. Jena, Jan 1927, Hoffmann determ.” Our specimens here were collected from Brunei Darussalam, which borders the Brunei Bay and faces the island of Labuan, i.e., from a locality that is extremely close to the type locality.

Type locality (*O. nigrum*). “Borneo” is the only geographic information provided by Plate (1893) in the original description as well as on the label of the type, which reads “*Oncidium nigrum* Plate. 22749. Borneo. Gera S.” The mention of “Gera S.” does not refer to Sungai Geras, a river near the city of Bintulu, on the west coast of Borneo, in Sarawak, Malaysia, but most likely to the fact that the specimen was collected by Gerard, as indicated in Plate’s (1893: 188) original description (“1 Exemplar von Borneo, durch Gerard gesammelt”). Thus, the type locality of *O. nigrum* could be anywhere in Borneo.

Type locality (*E. ajuthiae*). The “Province d’Ajuthia (Siam)” is the province of Ayutthaya, in Thailand, approximately 80 kilometers north of Bangkok, which used to be the capital of the Kingdom of Siam. Because that province is inland, Labbé assumed that the slugs had been collected in fresh water. However, the Chao Phraya River of the basin than runs through the province of Ayutthaya actually is under the influence of the tide year round. The salt front (brackish water) goes up to 75 and 175 kilometers from the river mouth in the wet and dry seasons, respectively, and it was even more so the case in the past when the river side was still not developed (syntypes collected by M. Bocourt in 1862 according to the label of the type material). In the province of Ayutthaya, the river is approximately at its kilometer 140 (Singkran 2015: 28). The label of the type specimens of *Elophilus ajuthiae* says that it lived in the “eaux dormantes de la province d’Ajuthia.” The French expression “eaux dormantes” means “swamps.” Given what is known of the basin of Chao Praya River, those swamps were brackish water under the influence of daily tides.

Type material (*V. stuxbergi*). One lectotype hereby designated (43/25 mm; entire and never dissected; SMNH 1334). All eleven other syntypes become paralectotypes with no name-bearing status. Originally, the type material included a total of

twelve specimens split in two different jars: five specimens (all paralectotypes) with catalog number SMNH 7523 (from 35/30 to 15/12 mm, all entire except one specimen opened by a previous investigator, with a vial including the male copulatory system); and seven specimens with catalog number SMNH 1334 (the lectotype 43/25 mm, entire, and six paralectotypes from 20/18 to 15/15 mm, all entire except for one specimen dissected by a previous investigator, with a vial including a male copulatory system). All paralectotypes are *Platevindex* and the lectotype clearly is an *Onchidium*. The only one *Onchidium* specimen was selected as the lectotype because it is the only specimen that Westerlund (1885) illustrated for his new species *Vaginulus stuxbergi*. In fact, Westerlund's figures are a perfect image of the lectotype and, most importantly, it is exactly how *Onchidium* slugs (in the strict sense) look like when they are preserved without relaxation or when they are alive but disturbed.

Type material (*O. nigrum*). Holotype, by monotypy (ZMB 22749). One specimen 40/30 mm, completely dissected (by Plate) and empty. There is a vial with destroyed pieces of the digestive system (mostly the digestive gland and the intestine).

Type material (*E. ajuthiae*). Three syntypes (MNHN 22965) 20/17, 20/15 and 20/14 mm. All three specimens, dissected by Labbé, are now empty. Only a few destroyed pieces of the digestive system remain in a vial.

Additional material examined. Malaysia, Peninsular Malaysia, Kuala Sepatang, 04°50.434'N, 100°38.176'E, 18 July 2011, 1 specimen (42/24 [DNA 971] mm), leg. B. Dayrat & T. Goulding, [station 27, old forest with tall, old *Rhizophora* trees, high in the tidal zone (ferns), following boardwalk in educational preserve, reached a creek lower in the tidal zone, with mud] (USMMC 00006); **Brunei Darussalam,** Mentiri, Jalan Batu Marang, 04°59.131'N, 115°01.820'E, 29 July 2011, 3 specimens (33/18 [#1], 20/16, and 16/13 [DNA 1048] mm), leg. T. Goulding & S. Calloway, [station 36, old mangrove with tall *Rhizophora* trees with high roots and *Thalassina* mounds] (BDMNH); **Philippines,** Bohol, Inabanga, 10°04.255'N, 124°04.416'E, 13 July 2014, 3 specimens (from 30/20 [DNA 3251] to 25/17 mm), leg. J. Comendador, B. Dayrat & T. Goulding, [station 187, mostly *Nypa* palms with *Thalassina* mounds] (PNM 041199); Inabanga, 10°04.432'N, 124°04.691'E, 13 July 2014, 1 specimen (27/17 mm), leg. J. Comendador, B. Dayrat & T. Goulding, [station 188, old forest, untouched for about 30 years, mostly *Avicennia*, many old logs] (PNM 041200); Mabini, 09°51.532'N, 124°31.685'E, 17 July 2014, 1 specimen (35/25 mm), leg. J. Comendador, B. Dayrat & T. Goulding, [station 194, narrow forest on the edge of fish ponds, tall *Rhizophora* and *Avicennia* trees, many old logs, muds of different types] (PNM 041201); Mabini, 09°51.402'N, 124°30.982'E, 18 July 2014, 4 specimens (from 35/28 [#1] and 35/22 [#2, DNA 3363] to 12/9 mm), leg. J. Comendador, B. Dayrat & T. Goulding, [station 195, narrow forest with tall trees on the edge of fish ponds, cemented ditches between the mangrove patches and the ponds] (PNM 041202); **Vietnam,** Can Gio, 10°24.171'N, 106°53.960'E, 10 July 2015, 1 specimen (30/20 [DNA 5602] mm), leg. T. & J. Goulding, [station 221, hard mud by a small road and then a steep bank to the soft, deep mud, *Avicennia* and some *Rhizophora* trees spread out] (ITBZC IM 00001); Can Gio, 10°26.703'N, 106°53.694'E, 12 July 2015,

7 specimens (from 55/35 to 25/16 mm; 44/30 [DNA 5605], 35/25 [#1] mm), leg. T. & J. Goulding, [station 223, margin of mangrove by creek, shrimp ponds behind the mangrove, fairly high intertidal] (ITBZC IM 00002); Can Gio, 10°27.620'N, 106°53.316'E, 17 July 2015, 3 specimens (from 28/18 to 12/8 mm), leg. T. & J. Goulding, [station 231, open mangrove with large *Avicennia* trees, soft mud, some old logs] (ITBZC IM 00003); Can Gio, 10°24.157'N, 106°53.950'E, 19 July 2015, 1 specimen (20/12 mm), leg. T. & J. Goulding, [station 233, hard mud by a small road and then a steep bank to the soft, deep mud, open forest of *Avicennia* and *Rhizophora*, rocks and gravel on side of mangrove] (ITBZC IM 00004); **China**, Macau, 3 specimens (42/28 to 32/28 mm), leg. Heynemann, (SMF 333591/3).

Distribution (Fig. 2). Malaysia, Sabah (type locality of *Vaginulus stuxbergi*); Brunei Darussalam (present study, new record); Malaysia, Peninsular Malaysia (present study, new record); Philippines, Bohol (present study, new record); Vietnam (present study, new record); Thailand (type locality of *Elophilus ajuthiae*); China (present study; Sun et al. 2014, one individual misidentified as “*Onchidium struma*” *nomen nudum*). A specimen of *O. stuxbergi* was found in Singapore (in the mangrove by the Mandai River) but was unfortunately lost. The presence of *O. stuxbergi* was also documented (as *Onchidium nigrum*, which is a spelling mistake) in a guide to the mangroves of Singapore (Ng and Sivasothi 2002: 115). The type locality of *Onchidium nigrum* simply was cited as “Borneo,” which could be anywhere on the island in Indonesia (Kalimantan) or Malaysia (Sabah or Sarawak). Our record in Macau is the northernmost (22°10'N) confirmed locality on the coast of southern China.

Habitat (Fig. 9). The habitat of *O. stuxbergi* is very similar to that of *O. typhae*: directly on mud (not soft, i.e. mud that is not very watery), on muddy trunks, old logs, lobster mounds, and even under *Nypa* leaves (Philippines). However, *O. stuxbergi* was not observed on mud as soft as the mud on which *O. typhae* was found in West Bengal.

Abundance. *Onchidium stuxbergi* is a rare species. Only one individual was found in Malaysia (where 18 mangrove sites were explored), three individuals at one site in Brunei Darussalam (7 sites), nine individuals at four sites in Bohol (17 sites), and 12 individuals at four sites in Vietnam (19 sites). Even though it will need to be confirmed in the future, it seems that *O. stuxbergi* tends to be slightly more common (although still rare, overall) in more northern latitudes (Vietnam and Philippines).

Color and morphology of live animals (Fig. 10). Live animals are not always covered with mud and the color of their dorsum can normally be seen. The dorsum is brown, with no particular pattern. Exceptionally, it can be almost black. The hypnotum varies between grayish and yellowish, and sometimes even greenish. It occasionally bears conspicuous black dots. The foot is bright orange, which is different from the two other species described here. In a tiny specimen (12 mm in length, St. 195/17), the foot was pale yellow. The long ocular tentacles are cream to brown distally, and darker proximally. The head is brown to black, with many evenly distributed white markings. The morphology of live specimens is similar to that of *O. typhae*. The only difference is that the central papilla with a few dorsal eyes is prominent in *O. stuxbergi*. Crawling individuals normally measure between 30 and 40 mm in length.



Figure 9. Habitats for *O. stuxbergi*. **A** Malaysia, Kuala Sepatang, old forest with tall, old *Rhizophora* trees, high in the tidal zone (station 27) **B** Philippines, Bohol, mostly *Nypa* palms with *Thalassina* mounds (station 187) **C** Vietnam, Can Gio, open mangrove with large *Avicennia* trees, soft mud, some old logs (station 231) **D** Vietnam, Can Gio, hard mud with trees spread out by a small road and then a steep bank to the soft, deep mud (station 221).

Preserved specimens no longer display the distinct color traits seen in live animals. The color of preserved animals is meaningless and uninformative. The background color of the notum is brown. Some individuals, including old ones (SMF 333491) bear a few irregular, darker markings. The hyponotum and the foot of preserved animals are homogenously white.

Internal anatomy (Figs 11–13). Examples of radular formulae are: 70×75 -1-75 in USMMC 00006 (42 mm long), 50×68 -1-68 in BDMNH #1 (33 mm long), and 70×80 -1-80 in PNM 041202 #1 (35 mm long). The intestine is long, narrow, and of the so-called “type III,” characterized by the fact that a transverse line can intersect the intestine eight times.

The oviduct is narrow, short, and straight. The hollow spine of the penial accessory gland is slender and slightly curved. It measures between 0.5 (USMMC 00006) and 1.4 mm (PNM 041202 #2) in length, and between 20 (USMMC 00006) and 35



Figure 10. Live specimens, *O. stuxbergi*. **A** Dorsal view, 33 mm long, Brunei Darussalam (BDMNH, #1) **B** Dorsal view, 27 mm long, Philippines, Bohol (PNM 041200) **C** Dorsal view, 35 mm long, Bohol, Philippines (PNM 041201) **D** Dorsal view, 35 mm long, Vietnam, Can Gio (ITBZC IM 00002, #1) **E** Dorsal view, 30 mm long [DNA 3251], Bohol, Philippines (PNM 041199) **F** Ventral view, 35 mm long [DNA 3363], Bohol, Philippines (PNM 041202, #2).

(PNM 041202 #2) μm in diameter. The diameter of the opening at its tip is nearly 10 μm . The hollow spine does not open directly into the vestibule. Instead, the end of the tube of the accessory gland is a disc which is more or less flat (approximately 0.3 mm in diameter) and does not seem to bear distinct conical papillae. The hollow spine must thus go through that disc in order to be outside and shared with the partner.

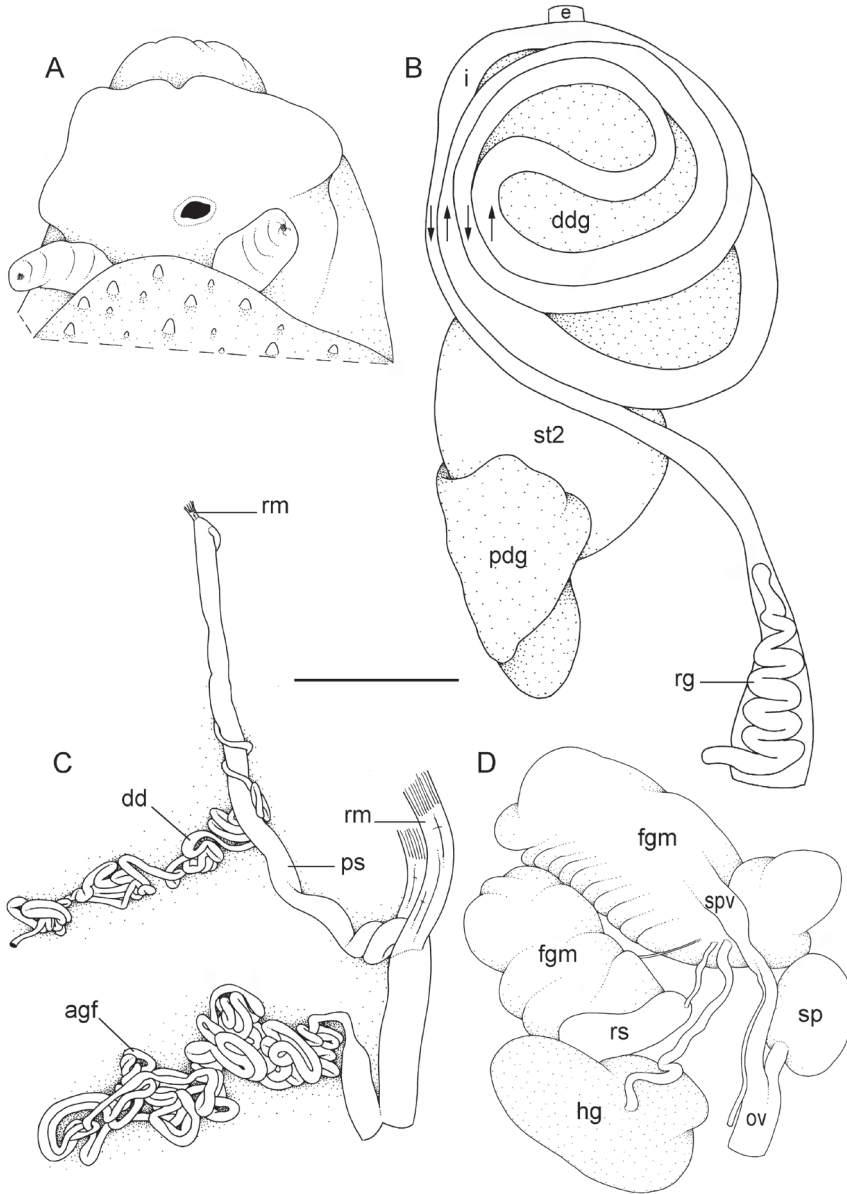


Figure 11. External morphology and internal anatomy, *O. stuxbergi*. **A** Anterior region, dorsal view, Malaysia, Kuala Sepatang, scale bar 4.4 mm [DNA 971] (USMMC 00006) **B** Digestive system, dorsal view, Philippines, Bohol, scale bar 5 mm [DNA 3363] (PNM 041199, #2) **C** Reproductive system, anterior, male, copulatory parts, Philippines, Bohol, scale bar 6.8 mm [DNA 3363] (PNM 041199, #2) **D** Reproductive system, hermaphroditic (female) posterior parts, Malaysia, Kuala Sepatang, scale bar 5 mm [DNA 971] (USMMC 00006). Abbreviations: **agf**, accessory gland flagellum; **dd**, deferent duct; **ddg**, dorsal lobe of digestive gland; **e**, esophagus; **fgm**, female gland mass; **hg**, hermaphroditic gland; **i**, intestine; **ov**, oviduct; **pdg**, posterior lobe of the digestive gland; **ps**, penial sheath; **rg**, rectal gland; **rm**, retractor muscle; **rs**, receptaculum seminis; **sp**, spermatheca; **spv**, spermoviduct; **st2**, stomach chamber 2.

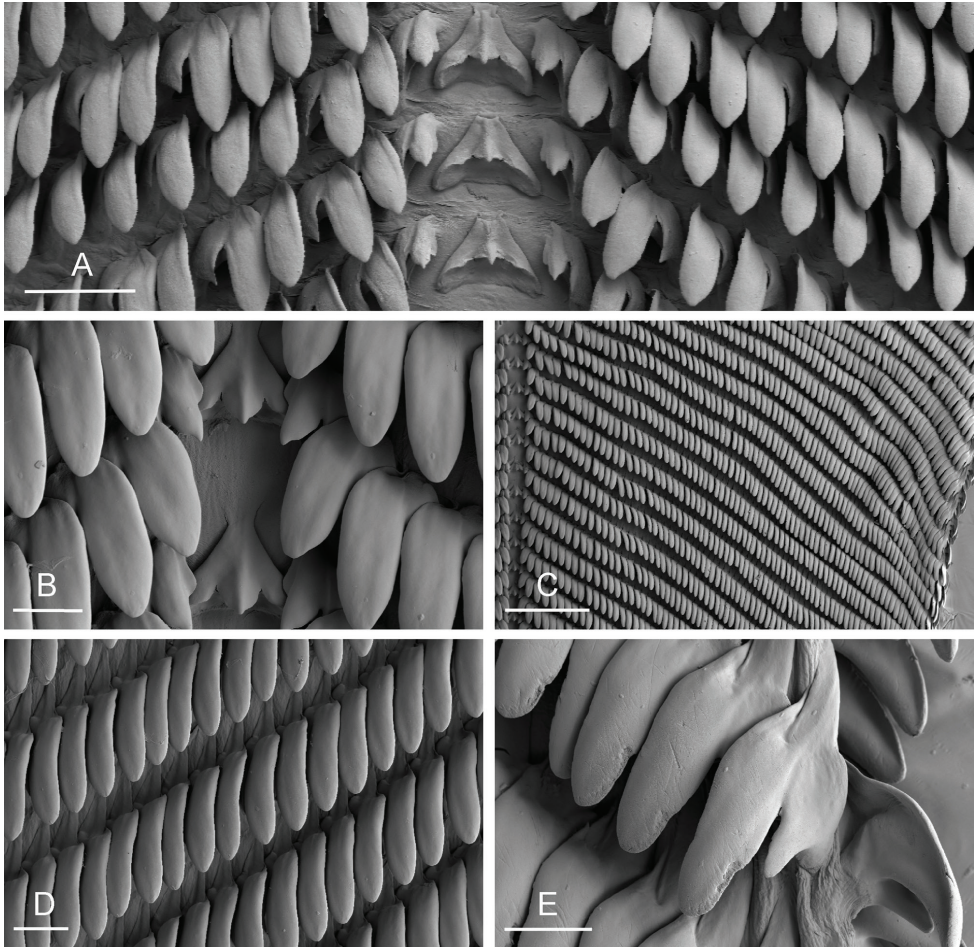


Figure 12. Radula, *O. stuxbergi*. **A** Rachidian and innermost lateral teeth, Brunei Darussalam, scale bar 40 μm (BDMNH # . **B** Rachidian and innermost lateral teeth, Philippines, Bohol, scale bar 20 μm (PNM 041202 #1) **C** Half rows, Philippines, Bohol, scale bar 200 μm (PNM 041202 #1) **D** Lateral teeth, Philippines, Bohol, scale bar 30 μm (PNM 041202 #1) **E** Outermost lateral teeth, Philippines, Bohol, scale bar 20 μm (PNM 041202 #1).

The penial sheath is long (to the posterior third of the visceral cavity) and coiled in a few spirals. In less mature individuals, the coils may not be as marked. The retractor muscle is short and inserts into the posterior third of the visceral cavity. There is an additional retractor muscle attaching the anterior portion of the penial sheath to the left wall of the visceral cavity, near the buccal mass. In some individuals, that left additional retractor muscle is very thick and strong. The deferent duct is highly convoluted with many loops, but less so in immature specimens. The penis is elongated, round, narrow, and hollow. Its diameter is less than 200 μm . Its distal part is covered with hooks. When the penis is retracted inside the penial sheath, the hooks are inside

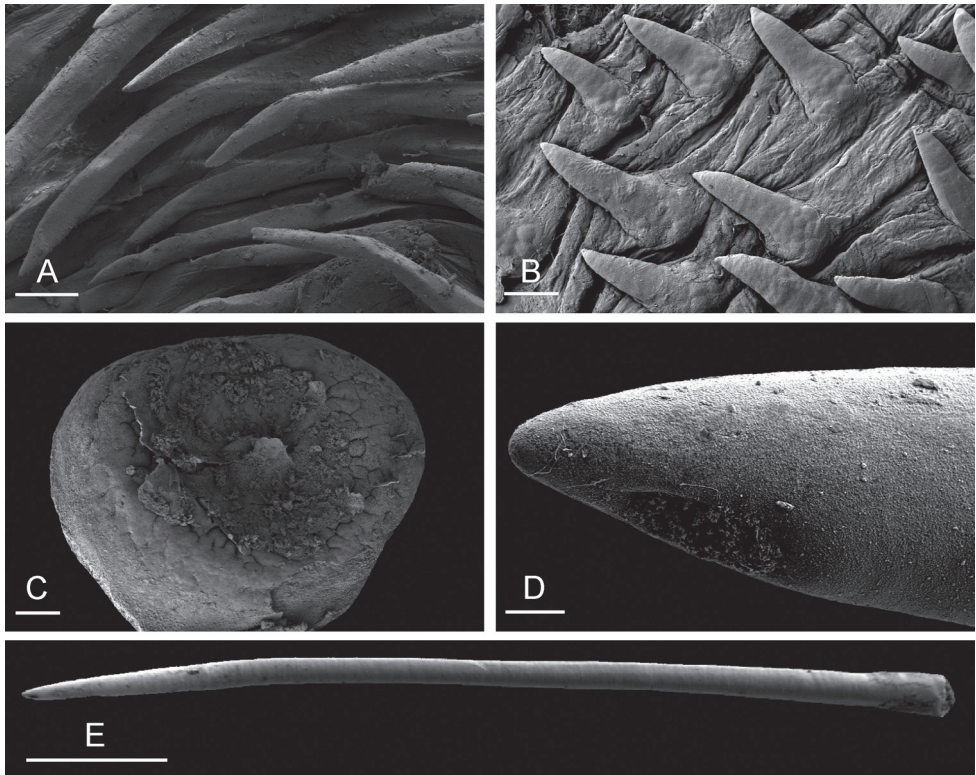


Figure 13. Male, anterior, copulatory parts, *O. stuxbergi*. **A** Penial hooks, Philippines, Bohol, scale bar 40 µm [DNA 3363] (PNM 041199, #2) **B** Penial hooks, Malaysia, Kuala Sepatang, scale bar 20 µm [DNA 971] (USMMC 00006) **C** Flat disc at distal end of flagellum of penial accessory gland, Malaysia, Kuala Sepatang, scale bar 40 µm [DNA 971] (USMMC 00006) **D** Tip, hollow spine, penial accessory gland, Philippines, Bohol, scale bar 3 µm [DNA 3363] (PNM 041199, #2) **E** Hollow spine, penial accessory gland, Philippines, Bohol, scale bar 200 µm [DNA 3363] (PNM 041199, #2).

the tube-like penis. During copulation, the penis is exerted like a glove and the hooks are then on the outside. Hooks are very densely packed inside the penis, with multiple, irregular rows of an average of 15 hooks around the circumference of the penis. Hooks are conical, slender, sharply pointed, and measure from 40 µm up to 300 µm in length. The longer they are the more slender they are.

Distinctive diagnostic features. Externally, *O. stuxbergi* differs from other *Onchidium* species by the color of the foot, which is bright orange (see below the dichotomous identification key, before the final conclusion). Internally, *O. stuxbergi* is the only *Onchidium* species known so far (and the only onchidiid species, for that matter) with a strong, additional retractor muscle attaching the anterior penial sheath to the left, anterior wall of the visceral mass, near the buccal mass.

Remarks. The status of *O. stuxbergi* has been problematic from the start because Westerlund unknowingly based his original description on specimens that are part

of two distinct species (see Type materials, above): eleven former syntypes (now paralectotypes) are *Platevindex* and another former syntype (now the lectotype) is an *Onchidium* (in the strict sense, as defined here). Two years after the original description, Westerlund (1885) again published the description of *Vaginulus stuxbergi*, as a new species again. Although that contribution is not the original description, its figure 2 helps confirm that *Vaginulus stuxbergi* is an onchidiid and, most importantly, illustrates the one former syntype (here designated as the lectotype) that is part of *Onchidium*. Therefore, even though the brief and vague description may be confusing (because it is based on two different species), the illustration makes the identification absolutely clear, hence our decision to designate the illustrated specimen as the lectotype. Note that Westerlund did not describe any internal characters.

However, as a direct consequence of Westerlund's ambiguous original description and type material, many authors have proposed synonymies between *O. stuxbergi* and some species names that clearly belong to *Platevindex*. Those cases are briefly discussed here, but they will be discussed in more detail in our revision of the genus *Platevindex*. Labbé (1934: 235) and Hoffmann (1928: 88) both regarded *O. stuxbergi* as a *Platevindex* (as *Oncis stuxbergi*) and suggested that *Onchidella condoriana* Rochebrune, 1882 and *Oncis inspectabilis* Plate, 1893, could be synonyms of *O. stuxbergi*. *Onchidium condoriana* and *O. inspectabilis* clearly belong to *Platevindex* (types were examined) and are not synonyms of *O. stuxbergi*. Hoffmann (1928: 88) also regarded *Onchidium coriaceum* Semper, 1885, as a synonym of *O. stuxbergi* but it actually is a valid name of the genus *Platevindex*. Finally, Hoffmann (1928: 88) suggested that *Onchidium ponsonbyi* Collinge, 1901, could possibly be a synonym of *O. stuxbergi* but it is very unlikely because *O. ponsonbyi* is a terrestrial species known from 850 to 1,050 meters high at Mt Penrissen, Borneo. *Onchidium ponsonbyi* likely belongs to the genus *Semperoncis* Starobogatov, 1976.

There is no doubt that *O. nigrum*, which is only known from the holotype, belongs to the genus *Onchidium* as re-defined here: the mantle of the preserved holotype bears the typical papillae of *Onchidium*. Also, Plate described both a rectal gland and an accessory gland, which are found in all three known *Onchidium* species. Plate did not mention the presence of an additional, left, retractor muscle for the penial sheath. He only mentioned that the insertion of the retractor muscle is of "type II" (i.e., near the pericardium). According to Plate, the penial hooks are from 14 to 87 μm long and the spine of the penial accessory gland is 1.2 mm long. The penial hooks observed here are from 40 to nearly 300 μm in length. It is possible that Plate, who observed only one specimen, could not fully evaluate the variation of penial hooks. Also, penial hooks are extremely challenging to extract and observe without SEM. However, Plate's description of the penial accessory gland spine is fully compatible with our observations (from 0.5 to 1.2 mm long). Finally, Plate described the intestine loops of *O. nigrum* as of a unique and exceptional pattern, which he referred to as "type III." The latter, as illustrated by Plate (1893: plate 8, fig. 31a) is slightly more coiled than what was observed for the present study, but they are basically identical patterns. That intestinal pattern is absent from *O. typhae* but it has also been observed in some species from

other genera. Given that Plate did not know the color of the live animal, it will never be known whether it matched the diagnostic color of the foot that was observed for our specimens (bright orange). According to our data, *O. stuxbergi* is distributed from Malaysia to Vietnam and the Philippines and therefore mostly encompasses Borneo. As a result, the synonymy of *O. nigrum* and *O. stuxbergi* is warranted, even though it cannot be completely excluded that *O. nigrum* could refer to an *Onchidium* species remotely endemic to the south east of Borneo.

The three syntypes described as *Elophilus ajuthiae* by Labbé (1935) were earlier identified by him as *O. nigrum* (Labbé, 1934). His first identification was supported by a pattern of intestinal loops (Plate's "type III") only known from *O. nigrum*. Labbé changed his mind after the observation of what he thought were tiny dorsal gills ("microbranchies") in those three syntypes from Thailand. Indeed, according to Labbé's (1934) onchidiid classification, dorsal gills are only found in the Dendrobranchiatae (which includes genera such as *Peronia*, *Paraperonia*, and *Scaphis*) while all other onchidiids (such as *Onchidium*, *Onchidella*, *Platevindex* and *Onchidina*), the Abranchiatae, lack dorsal gills. The three specimens from Thailand (with gills) could not belong to *Onchidium* (no gills) and, as a result, Labbé created a new species name and a new genus name for those specimens with an intestine of "type III" and dorsal gills. Labbé's new genus *Elophilus*, preoccupied, was replaced by Starobogatov (1976) by *Labella*. Those three syntypes from Thailand were re-examined for the present study; unfortunately, they are mostly empty. A few destroyed pieces of the intestine system remain but they are completely useless. However, the mantle clearly does not bear any "microbranchies" (i.e., microgills). It is very likely that Labbé's first intuition was correct and that he was just looking at large *Onchidium* papillae retracted within the mantle. Those three specimens from Thailand are part of *O. nigrum*, which means *O. stuxbergi*. Unfortunately, Labbé did not describe the male copulatory complex in detail and so the sizes and shapes of the penial accessory spine and of the penial hooks are unknown. However, our specimens from Vietnam suggest that there is only one species of *Onchidium* distributed in the region of the South China Sea, *O. stuxbergi*. Naturally, it cannot be excluded that the Gulf of Thailand actually hosts a distinct species; however, there is nothing in Labbé's description supporting that hypothesis. As a result, the synonymy of *Labella ajuthiae* with *O. stuxbergi* is warranted. Also, Labbé was confused about the type locality of *O. nigrum* because he claimed that "Plate's unique specimen came from Borneo (Guam)" (Labbé, 1934: 223, our translation) and that "Plate's unique specimen came from the Marianna Islands" (Labbé, 1935: 312, our translation). Borneo is with no doubt the type locality of *O. nigrum*. Finally, Labbé's claim that *L. ajuthiae* lived in fresh water was unfounded. Even though the specimens were collected far inland, it was still in brackish water and under the influence of the tides (see above, Type localities).

The name *Onchidium struma*, introduced by Qiu (1991) and used occasionally in the Chinese literature to refer to some onchidiids from the coast of China (e.g., Shen et al. 2006; Sun et al. 2014), is a *nomen nudum* (to our knowledge, *O. struma* has not been formally described as a new species). A survey of the diversity of onchidiids from China

based on molecular data was recently published (Sun et al. 2014). The sequences of the specimens identified as *Onchidium* “*struma*” by Sun et al. were all included in our analyses here, and that name appears in two distinct species units (Fig. 1), which demonstrates that the name *Onchidium* “*struma*” used by Sun et al. referred to two distinct species. One of their species, identified here as *O. reevesii*, is mostly subtropical and is distributed from 22°30' to 34°36' latitude north along the coast of China. So far, it seems to be endemic to China. In the data set of Sun et al., *O. reevesii* is represented by eight individuals (under the name *Onchidium* “*struma*”). Note that in that same contribution, Sun et al. (2014) apply the name *Paraoncidium reevesii* to a different species but that is also a misidentification. The species they refer to as *Paraoncidium reevesii* obviously cannot be *O. reevesii*, but it does not belong to *Paraoncidium* either. The other species referred to as *Onchidium* “*struma*”, identified here as *O. stuxbergi*, is tropical and, in China, is only found in the southernmost coastline. In the data set of Sun et al., only one individual from Hainan Island (19°56'N) can be safely referred to as *O. stuxbergi*. Another individual in their data set (from Hong Kong, at 22°28'N) is problematic because its CO1 and 16S sequences give contradictory results, and so it is likely that one of those sequences is a mistake. The three specimens examined for the present study from Macau (SMF 333591/3) are the northernmost confirmed locality of *O. stuxbergi* in China at 22°10'N.

***Onchidium reevesii* (J.E. Gray, 1850)**

Fig. 14

Onchidella reevesii J.E. Gray, 1850: 117, pl. 181, fig. 5–5a; Hoffmann 1928: 103.

Onchidium reevesii: Semper 1885: 290.

Type locality. China. *Onchidella reevesii* was not described by Gray. That name, which appears on page 117, simply referred to figures 5 and 5a of the plate 181). On page 117, there is no indication of the geographic origin, and there is no indication of geographic origin on the label of the holotype either. However, on page 36, those same figures are referred to as “*Onchidium* —. Mr. Reeve’s drawings. China,” clearly indicating that the animal illustrated on the fig. 5 (and 5a for the ventral side) of the plate 181 is from China. Hoffmann (1928) also accepted China as the type locality.

Type material. Holotype (43/25 mm), by monotypy (NHMUK 20160036). The label says “? Holotype *Onchidella reevesii* Gray 1850,” but there is no reason to think it is not the holotype because the specimen fits perfectly the original illustration and the label also does refer to “Gray, Figs. Moll. Anim., IV, 1850, p. 117” where the name *Onchidella reevesii* was first published. The holotype is in excellent condition. It was opened dorsally prior to the present study so several key features could easily be checked in the digestive system as well as the male anterior parts, which are all drawn here (Fig. 14). The posterior reproductive parts (far less critical for species identification) were not removed from the visceral cavity (because it would have required our destroying the posterior region of the holotype) and so they are not illustrated here.

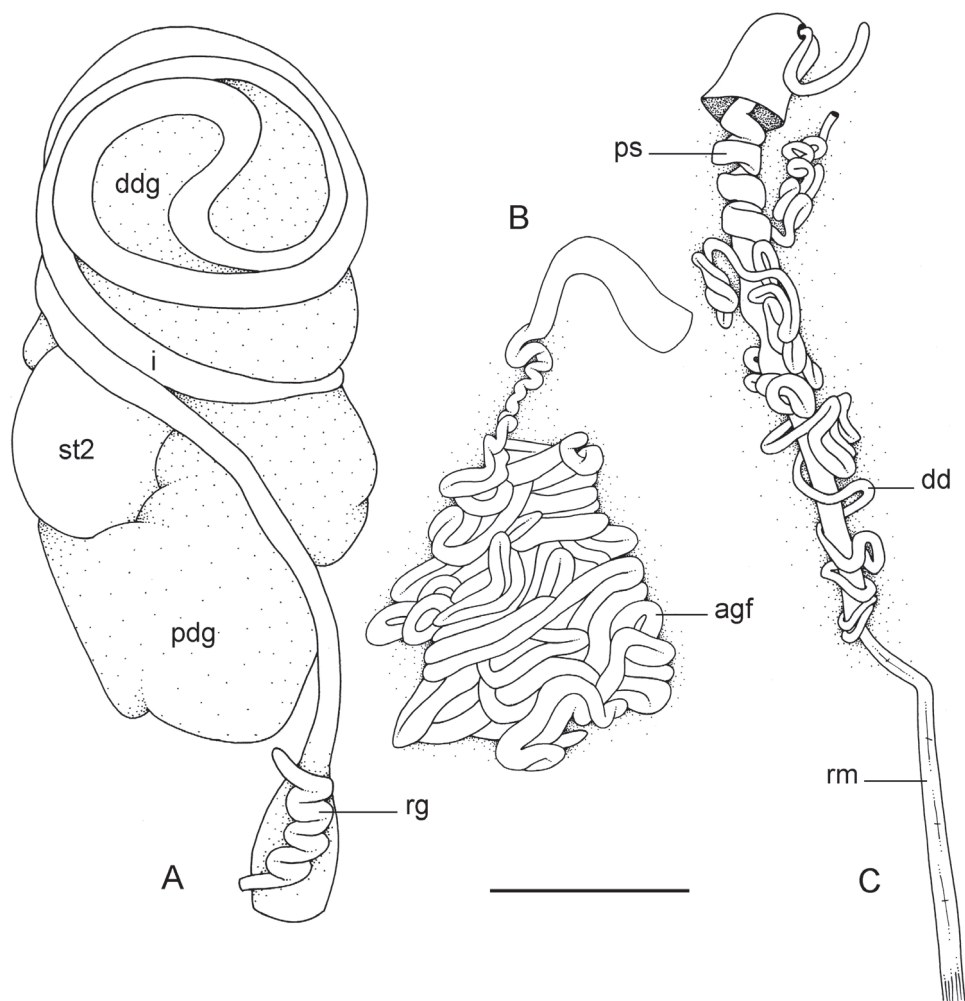


Figure 14. Internal anatomy, holotype, *O. reevesii* (NHMUK 20160036). **A** Digestive system, dorsal view, scale bar 7.5 mm **B** Reproductive system, anterior, penial accessory gland, scale bar 3 mm **C** Reproductive system, anterior, penial sheath, scale bar 5 mm. Abbreviations: **agf**, accessory gland flagellum; **dd**, deferent duct; **ddg**, dorsal lobe of digestive gland; **i**, intestine; **pdg**, posterior lobe of the digestive gland; **ps**, penial sheath; **rg**, rectal gland; **rm**, retractor muscle; **st2**, stomach chamber 2.

Distribution (Fig. 2). China (type locality). Based on sequences misidentified as *Onchidium "struma"* (a *nomen nudum*) by Sun et al. (2014) and re-analyzed here, *O. reevesii* is found on most of the coastline of mainland China (except for southernmost and northernmost latitudes), from 22°30' to 34°36' of latitude north.

Internal anatomy (Fig. 14). The intestine of the holotype is between a type II and a type III, because a transverse line can intersect the intestine six times (four times for the type II as in *O. typhae*, and eight times for the type III as in *O. stuxbergi*). Although observed, the hollow spine was not extracted. At the end of the flagellum of the accessory gland, there

is a flat disc which distally protects the hollow spine. The penial sheath is coiled in spirals. The retractor muscle is shorter than the penial sheath and inserts at the posterior end of the visceral cavity. There is no additional left retractor muscle. The deferent duct is highly convoluted with many loops. The penis of the holotype was not extracted for the present study.

Distinctive diagnostic features. Externally, *O. reevesii* differs from other *Onchidium* species by its ventral color, i.e., a whitish hyponotum and foot (see the dichotomous key below). Internally, the spirally coiled penial sheath of *O. reevesii* is not diagnostic (as in *O. stuxbergi* and *O. typhae*). However, *O. reevesii* lacks the additional, anterior, left retractor muscle of the penial sheath that is unique to *O. stuxbergi* (the only species with which *O. reevesii* may be shown later to overlap in the southernmost part of its distribution).

Remarks. Semper transferred *Onchidella reevesii* to *Onchidium* probably by default (i.e., as a non-*Onchidella* species) because he did not give any explanation and he did not examine any new material. At any rate, it just so happens that *Onchidium reevesii* is the correct combination, because the notum of the type specimen bears the long papillae that are typically found in *Onchidium* as defined here. The presence of a rectal gland and of an accessory penial gland also supports that *Onchidella reevesii* is an *Onchidium*, even though those traits are found in other genera and even though the accessory penial gland can be both present and absent within a genus. That being said, a rectal gland and an accessory gland are found in all other *Onchidium* species. There is a small disc at the distal end of the accessory gland of the holotype of *O. reevesii*, a structure which we found so far only in *Onchidium*.

Hoffmann (1928: 69) placed *O. reevesii* in the genus *Oncis* (i.e., *Platevindex*) with a question mark but, in the same publication (Hoffmann 1928: 103), accepted it as an *Onchidella* also. Hoffmann did not have access to new material and he does not seem to have examined the type because he did not comment on it. Britton (1984) then used the new combination *Paraonchidium reevesii* based on material that was sent to him from Hong Kong but without examining the type material of *O. reevesii*. However, Britton's identification was erroneous because he described *Paraonchidium reevesii* as lacking both a rectal gland and an accessory penial gland, while both glands are actually present in the holotype of *O. reevesii*. Also, *Paraonchidium* Labbé, 1934 actually is a junior synonym of *Onchidina* Semper, 1885, and thus refers to a different clade.

Sun et al. (2014) adopted Britton's (1984) work and their use of the name *Paraonchidium reevesii* is a misidentification because it refers to a species with no rectal gland and no accessory penial gland, based on our own dissections of that species. The molecular study of Sun et al. (2014) shows that there are eight onchidiid species in China. Unfortunately, their identifications are erroneous (at the specific and/or generic levels). However, by including their sequences in our comprehensive regional data set and due to our own dissections it is possible to know what those species are as well as their internal anatomy.

There are actually only two species in China with both a rectal gland and an accessory penial gland, and both species belong to the genus *Onchidium*. In the study

by Sun et al. (2014), those two species are confused under a single name, *Onchidium* “*struma*”, which is a *nomen nudum*. One of those two species, *O. stuxbergi*, is restricted to the extreme southernmost latitudes of the coast of China (up to 22°10'N) but is also distributed in Malaysia (Sabah, Peninsula), Vietnam, Brunei, and the Philippines (see above *O. stuxbergi*). The other species, *O. reevesii*, seems to be endemic to China and is distributed along nearly the entire coast of China (from 22°30' to 34°36'), except for the southernmost and northernmost latitudes. It makes sense that *Onchidium reevesii* applies to the species that is the most widely distributed in China because its type locality (“China”) had a much higher chance to fall within the range of *O. reevesii* compared to that of *O. stuxbergi*.

Onchidium reevesii and *O. stuxbergi*, of which the distribution ranges do not seem to overlap, differ externally and internally. A few pictures of live animals of *O. “struma”* from Shangai, northern China (Shen et al. 2006: fig. 1), show that the foot of *O. reevesii* is whitish (the foot of *O. stuxbergi* is bright orange). Internally, the holotype of *O. reevesii* is lacking the additional, left, retractor muscle that is exclusively diagnostic of *O. stuxbergi*. The spiral coils of the penial sheath of the holotype of *O. reevesii* are compatible with the illustration (although fuzzy) of the anterior male apparatus of specimens misidentified as *O. “struma”* from Shangai (Wu et al. 2007: fig. 1). However, spiral coils of the penial sheath are not diagnostic of *O. reevesii* because they are also found in *O. typhae*. Finally, there are fewer loops in the intestine of the holotype of *O. reevesii* than in *O. stuxbergi* (of type III) and, based on our data, the intestine of a species cannot be of different types.

Identification key

A key is provided here to help identify the three known species of *Onchidium*. The key is based on external characters because they are the most readily available. However, internal diagnostic features also distinguish the species (see species descriptions). DNA sequences provided in the present contribution can also help clear any potential confusion, because, to date, DNA sequences of *Onchidium* have yielded unambiguous results.

- 1 The foot is bright orange..... ***O. stuxbergi***
(known distribution: Peninsular Malaysia, Thailand (Gulf of Thailand),
Vietnam, eastern Borneo, Philippines, southernmost tropical China).
- The foot is not bright orange **2**
- 2 The hyponotum is white and the foot is whitish..... ***O. reevesii***
(known distribution: subtropical China, from 22°30' to 34°36')
- The hyponotum (and the foot) is not white but varies between grayish and
yellowish, and sometimes even greenish ***O. typhae***
(known distribution: Bengal, Andaman Islands, Malaysia, Singapore).

Discussion

Naturally, new species of *Onchidium* may be discovered in the future. However, our data currently support the existence of only three species. It is worth pointing out that *Onchidium* is not found in eastern Indonesia and is also absent in recent collections from Madang, Papua New Guinea, by the Paris Museum (MNHN). *Onchidium* were not found either on the western coast of India, Madagascar, or Mauritius. Its geographic distribution, as suggested by the present results, thus ranges from north-eastern India to the Philippines, including the Strait of Malacca, Singapore, Thailand, Vietnam, eastern Borneo, and China. So, even though *Onchidium* may be found from additional localities in the future (e.g., *Onchidium stuxbergi* should occur in Palawan, Philippines), the distribution of *Onchidium* proposed here may be close to its actual distribution.

Based on current data, the distribution ranges of *O. stuxbergi* and *O. reevesii* do not overlap. If they do overlap, it may simply be over a very small area around Hong Kong. The geographic distribution of *O. reevesii* is typically subtropical (from 22°30' to 34°36'N) and tolerance for different water temperatures may have largely participated in the speciation between *O. stuxbergi* and *O. reevesii*, which are most closely related in our phylogenetic analysis (Fig. 1). That the individuals of *O. stuxbergi* in the Philippines (Bohol) show some genetic divergence from the rest of the species can be easily explained due to their relative isolation from the rest of the species, centered about the South China Sea.

Several authors in the past (e.g., Plate 1893; Hoffmann 1928; Labbé 1934; Britton 1984) have commented on the variation of some of the anatomical traits that seem important for the higher classification of the Onchidiidae (e.g., rectal gland, penial accessory gland, position of the male aperture, and pattern of the intestinal loops). However, all those comments have been confusing because both genus and species identifications have remained highly problematic. Even though it still is too early to draw some general conclusions regarding the variation of anatomical characters across all onchidiids, it is appropriate to comment on their variation within the genus *Onchidium*. The rectal gland and the penial accessory gland (and its hollow spine) are present in all three species. This does not mean that the presence/absence of these two structures do not vary within other genera, it simply means that these structures are always present in *Onchidium*. The male aperture is always inferior to the right eye tentacle, slightly to its left (i.e., in dorsal view, which means that the male aperture actually is in between the two eye tentacles). The patterns for the loops of the intestine (the types I, II, III, etc., as defined by Plate and Labbé) need to be commented upon. Labbé created a distinct genus name (*Labella*, here a synonym of *Onchidium*) almost exclusively based on the presence of an intestine of type III in *Labella ajuthiae* (here a synonym of *O. stuxbergi*). However, our results show that both the type II and the type III are found in *Onchidium* (type II in *O. typhae*, type III in *O. stuxbergi*). The intestine of the holotype of *O. reevesii* is intermediary between a type II and a type III. However, the intestine type does not seem to vary within each species. It will certainly be very interesting to look at the distribution of these characters across all onchidiids, and map them onto a general phylogeny.

Because the new limits to the genus *Onchidium* are much more restricted than its traditional meaning, many specific names traditionally combined with *Onchidium* must be combined with different generic names (Dayrat 2009). Those names will be dealt with the systematic revision of each clade of Onchidiidae in our future contributions. Here, however, comments are being provided on existing *Onchidium* species names that are regarded as *nomina dubia*, i.e., names which have been validly published but that should simply be ignored because their application is doubtful.

Onchidium aberrans Semper, 1885 is a *nomen dubium* because its type locality (Singapore) was mentioned as uncertain in the original description. Also, no type material could be located. *Onchidium griseo-fuscum* (Tapparone-Canefri, 1874), originally described as *Onchidella griseo-fusca* from Singapore and for which no type material could be located, could not be associated with any of the species we collected in Singapore. It could belong to *Peronia* but it is uncertain. As a result, it is here regarded as a *nomen dubium*. *Onchidium hardwickii* (J. E. Gray, 1850) was originally described as *Onchidella hardwickii* from an unknown locality and is thus regarded here as a *nomen dubium*. The holotype (by monotypy, MNHN) of *Onchidium harmandianum* Rochebrune, 1882, originally described from the Côn Đảo archipelago, off southern Vietnam, is a piece of tissue that may not even be part of an onchidiid slug. Because its original description is too brief and uninformative, it is regarded as a *nomen dubium*. We explored this archipelago and no species could be associated with that name. *Onchidium planatum* Quoy and Gaimard, 1824, originally described from Guam, is a *nomen dubium*: the lack of type material (not located), a vague original description, and the lack of illustration make it nearly impossible for it to be re-identified. More importantly, it is not even sure, based on the original description, that it actually was an onchidiid (after all, *Onchidium secatum*, from the same publication and by the same authors, is clearly not an onchidiid). *Onchidium tabularis* (Tapparone-Canefri, 1883), originally described as an *Onchidella tabularis* from Wokam, Aru Islands, Indonesia, is a *nomen dubium* due to the lack of type material (not located), the lack of illustration, and a useless written description. Tapparone-Canefri suggested that *O. tabularis* might refer to the same species as *Onchidium planatum*, but the latter is also a *nomen dubium*. Additionally, none of the species that we collected from Kei Islands (which is very close to Aru Islands) could be linked to *O. tabularis*. *Onchidium tricolor* Simroth, 1918, also described from Aru Islands, is a *nomen dubium* because the type material could not be located, there is no internal description, and the drawings of the external morphology are not informative enough. Finally, *Onchidium trapezoideum* Semper, 1885 is a *nomen dubium* because the type locality is unknown.

The present contribution illustrates well some of the complicated and relatively common issues faced in taxonomy and the possible ways to address them within an integrative approach. Integrative taxonomy is more than simply comparing morphological data and molecular data: nomenclatural issues are at the core of integrative taxonomy (Dayrat 2005). Nomenclatural issues are not something one can think about after species units have been delineated. Nomenclatural issues need to be considered from the very beginning of a taxonomic study. For instance, as our field work was being planned, type localities were included as our top priorities and were actually visited as often as possible. That allowed us to include specimens from type localities in our mo-

lecular and morphological data sets, and easily find available names for the species units being delineated. Specimens from type localities are not indispensable to obtain well-delineated species units, but they are critical to name them. For instance, in the present study, it would have been very challenging to determine the status of the names *O. typhae* and *O. stuxbergi* without newly-collected specimens from West Bengal and Brunei Darussalam, their respective type localities. The good news is that taxonomic work becomes possible and much easier if type materials are examined, original descriptions are carefully studied, and new specimens are collected from (as many) type localities (as possible). The not-so-good news is that there is no such thing as a quick taxonomic study because addressing all these issues can take a great deal of time and expertise.

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A new species of *Lasiosmylus* from the Early Cretaceous, China clarifies its genus-group placement in Ithonidae (Neuroptera)

Bingyu Zheng¹, Dong Ren¹, Yongjie Wang¹

¹ College of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China

Corresponding author: Yongjie Wang (wangyjosmy@gmail.com)

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Abstract

A new species, *Lasiosmylus longus* **sp. n.**, is described from the Early Cretaceous Yixian Formation of Huangbanjigou Village, Liaoning Province, China. Based on the characters of the new species and nine new specimens of *Lasiosmylus newi* Ren & Guo, 1996, the generic diagnosis of *Lasiosmylus* is emended and the taxonomic position of *Lasiosmylus* Ren & Guo, 1996 is re-evaluated, and *Lasiosmylus* should be assigned to the ithonid genus-group.

Keywords

Fossil, Huangbanjigou, ithonid genus-group, taxonomy, Yixian Formation

Introduction

The genus *Lasiosmylus* Ren & Guo, 1996 was initially assigned to the subfamily Spilomylinae in Osmylidae. Makarkin et al. (2012, 2014) then transferred it to Ithonidae *sensu lato*, but without discussing the relationship of the genus to other genera within the family. It is evident that the original assignment of *Lasiosmylus* to Osmylidae is questionable since the shared osmylid-like features discussed by the authors (i.e., absence of r1-rs crossvein, fewer crossveins throughout wing, and absence

of gradate series) are not actual synapomorphies of Osmylidae. *Lasiosmylus* rather displays more typical ithonid-like characters, e.g., stout body, retracted head, distinctively narrowed costal space towards the pterostigma area and strongly recurrent humeral crossvein in forewing; undoubtedly, it is more suitable to attribute this genus to Ithonidae. At present, although it is widely accepted that Ithonidae comprise three lineages: ithonid genus-group (moth-lacewings), polystoechotid genus-group (giant lacewings), and rapismatid genus-group (montane lacewings), the interrelationships among these groups, especially for fossil taxa, are still not fully resolved (Winterton and Makarkin 2010, Makarkin et al. 2014, Zheng et al. 2016). As a result, most fossil taxa have been simply attributed to Ithonidae *sensu lato* without further systematic placement (Archibald and Makarkin 2006, Makarkin et al. 2014). Recently Zheng et al. (2016) proposed diagnostic features for the three lineages of Ithonidae, incorporating the extant and fossil taxa, which could form the basis for assignment of additional Ithonidae fossils.

In this study a distinctive new species of Ithonidae, *Lasiosmylus longus* sp. n., is described from the Early Cretaceous of Yixian Formation, China. Additionally, nine new fossil specimens assignable to *Lasiosmylus newi* Ren & Guo, 1996 were collected from the same locality, which allow us to re-evaluate the systematic position of the genus within Ithonidae. Based on this new information, the genus *Lasiosmylus* is attributed to the ithonid genus-group and the diagnostic characters of *Lasiosmylus* are amended.

Materials and methods

This study is based on ten specimens, which are deposited in the Key Lab of Insect Evolution and Environmental Change, Capital Normal University, Beijing, China. Draft drawings were produced using LEICA MZ75 dissecting microscope equipped with a drawing tube. Drawings were finalized using Adobe Illustrator CC. Photographs were taken by Leica Digital Camera DFC500 (Figs 1A, C) and Nikon Digital Camera SMZ25 (Fig. 3A), and produced with Adobe Photoshop CC. Additionally, the part of one specimen (CNU-NEU-LB2015001P) was fragmented and glued loosely during collecting, the counterpart of the specimen (CNU-NEU-LB2015001C) is complete. A composite photograph of the part and counterpart is shown on Fig. 1A, which is the combination of two photos from both parts of the specimen in dry condition. The technique of the composite photograph in this study follows that of Béthoux (2015).

The terminology of venation in general follows Barnard (1981), except the terminology of humeral plate follows Oswald (1993):

Sc	Subcosta;	CuA	anterior Cubitus (Cu);
R1	first branch of Radius (R);	CuP	posterior Cubitus;
Rs	Radial sector;	1A–3A	Anal veins;
MA	anterior branches of Media (M);	hp	humeral plate;
MP	posterior branches of Media;	hv	humeral veinlet.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Ithonidae Newman, 1853 *sensu* Winterton & Makarkin, 2010

Genus *Laiosmylus* Ren & Guo, 1996

Type species. *Laiosmylus newi* Ren & Guo, 1996.

Species included. *Laiosmylus newi* Ren & Guo, 1996, *Laiosmylus longus* sp. n.

Amended diagnosis. Body stout (ca. 11–17 mm long), covered with dense setae; head hypognathous, protruding from pronotum partly; antenna filiform (ca. 2–5 mm, incompletely preserved); compound eye large, ocelli absent; thorax robust, long setae concentrated on pronotum. Forewing ca. 12–23 mm long, 5–8 mm wide, membranous area with many fuscous spots; humeral plate distinct; dense setae along the veins, especially on the wing margin; trichosors and nygmata undetectable; costal space dilated basally and narrowed distally; humeral veinlet recurrent, with several simple branches; costal cross-veins simple, moderately curved distally in the apical half of the costal space; Sc and R1 separate distally, entering the margin before the wing apex; one or two sc-r1 crossveins; R1 with four to eleven pectinate branches distally; the origin of Rs distant from the wing base, with seven to thirteen branches regularly arranged; relatively few crossveins present in radial area; MA simple, dichotomously branched terminally; MP first fork distant from wing base. Hind wing ca. 11–18 mm long, 4–8 mm wide, partly preserved, venation similar to forewing except for the following characters: costal space narrow, only slightly expand in proximal portion.

Remarks. *Laiosmylus* shows a superficial similarity with osmylids, sharing plesiomorphic features such as the fork of MP in forewing usually between the separation of MA and first Rs branch, sometimes opposite the separation of MA; wings not falcate, with few crossveins (Ren and Guo 1996). However, all these characters do not well support the assignment of *Laiosmylus* to Spilosmylinae, or Osmylidae in general because they also frequently occur in other families (e.g., Ithonidae, Berothidae, some Mantispidae). The subsequent transfer to Ithonidae by Makarkin et al. (2012, 2014) seems reasonable; moreover, recently it was classified further as belonging to the polystoechotid genus-group by Zheng et al. (2016).

Herein, nine new-collected specimens are examined in this study. All these specimens are placed in *Laiosmylus* based on the following characters: numerous dispersed spots on the forewing, simple costal crossveins, two subcostal crossveins, Rs less than ten branches (about six to eight branches), MP distant from the wing base and beyond MA fork, MP1 and MP2 simple, one mp1–mp2 crossvein, CuA dichotomously branched distally (in particular, obs. CNU-NEU-LB2015001P/C and CNU-NEU-LB2015002, see Figs 1, 2; and Ren and Guo 1996: fig. 5, fig. 10, pl. 3, fig. 11, pl. 2). Noticeably, during checking the specimens, we found some variable characters that are distinctly different from the type specimen, e.g., humeral veinlet and separated Sc and R1. A recurrent humeral veinlet is considered as a synapomorphy for Ithonidae

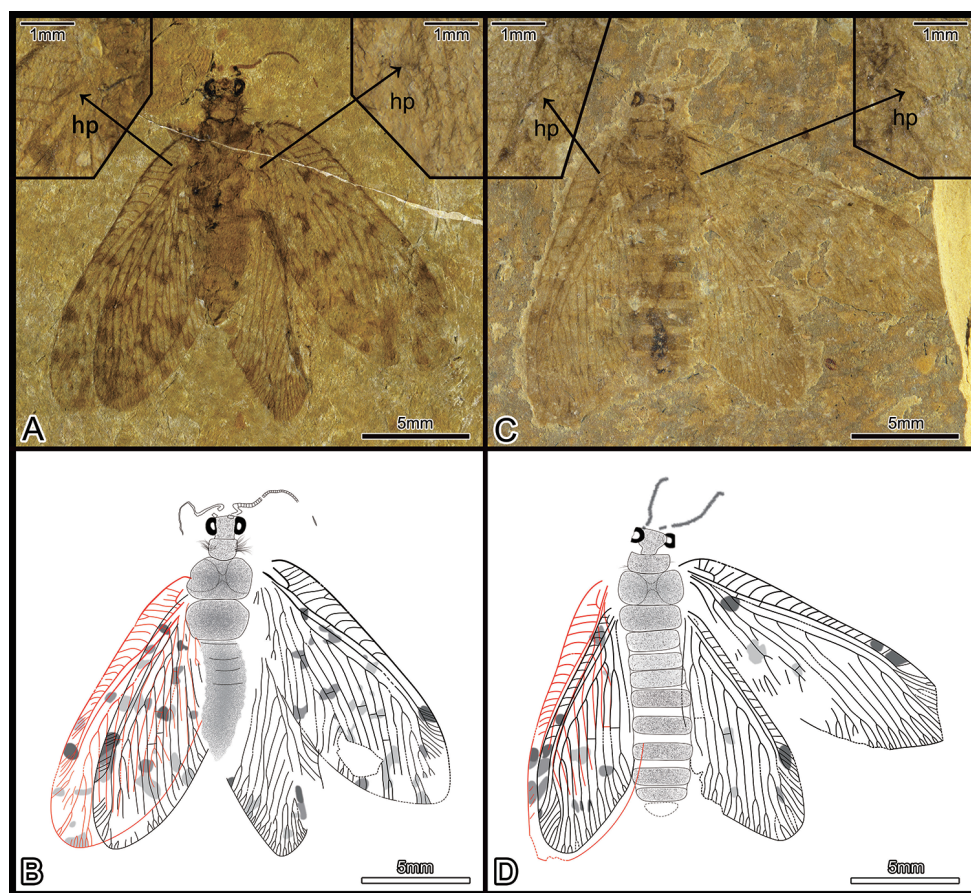


Figure 1. New materials of *Lasiosmylus newi*: CNU-NEU-LB2015001P/C, CNU-NEU-LB2015002. **A** composite photographs of habitus of part and counterpart (CNU-NEU-LB2015001P/C) hp, humeral plate (CNU-NEU-LB2015001C) **B** line drawing (CNU-NEU-LB2015001C) **C** habitus photograph, hp, humeral plate (CNU-NEU-LB2015002) **D** line drawing (CNU-NEU-LB2015002). Scale bars: 5 mm (**A–D**).

(Yang et al. 2012, Makarkin et al. 2013, Zheng et al. 2016). However, this character is absent in the line drawing of *L. newi* (Ren and Guo 1996: fig. 5), although some trace of recurrent humeral veinlet can be detected in the photograph of *Lasiosmylus* (Ren and Guo 1996: fig. 11, pl. 4). Regretfully, the holotype of *L. newi* was not available for examination during this study (possibly lost). However, it is reasonable to assume now that the recurrent humeral veinlet occurs in *Lasiosmylus newi* according to these new specimens.

In addition, the distally separated Sc and R1 were regarded as a synapomorphic character of Ithonidae (Zheng et al. 2016). In the original illustration of *L. newi*, Sc and R1 were drawn with fused termination. Unfortunately, the photograph of *L. newi* is too obscure for us to discern the condition of Sc and R1 (Ren and Guo 1996: fig. 10,

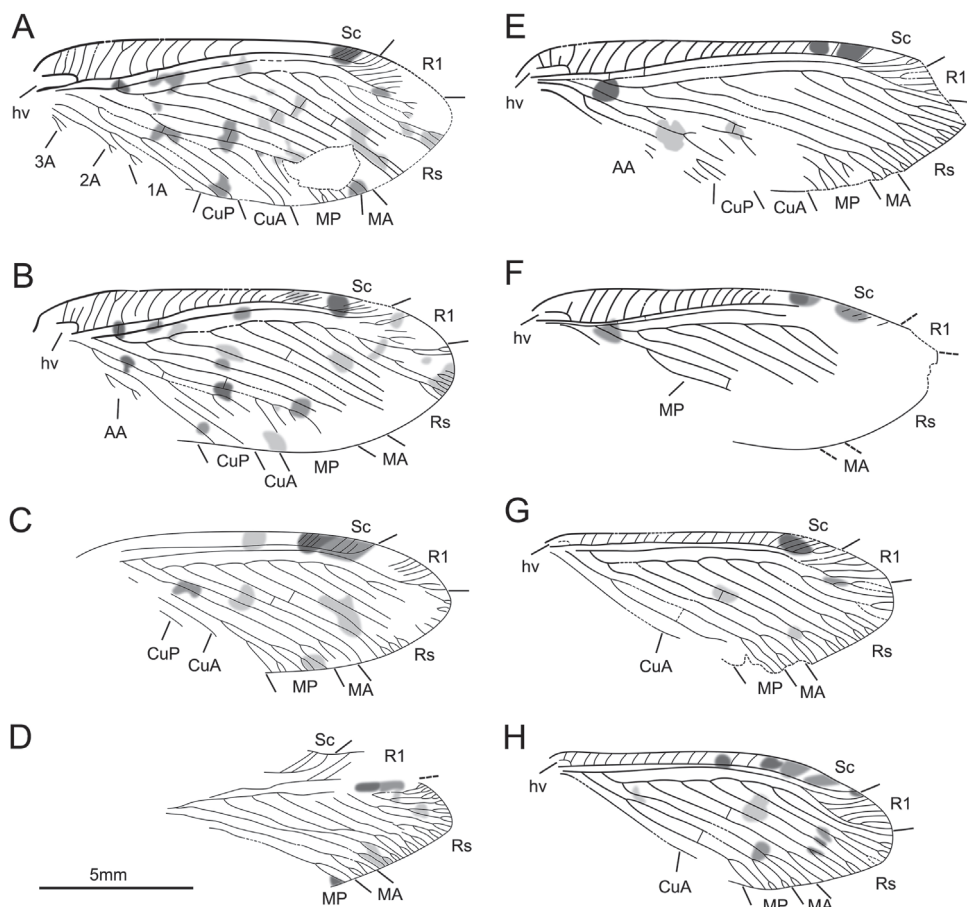


Figure 2. New materials of *Lasiosmylus newi*. Line drawings of CNU-NEU-LB2015001P/C, **A** left forewing **B** right forewing **C** right hind wing **D** left hind wing. Line drawings of CNU-NEU-LB2015002 **E** left forewing **F** right forewing **G** left hind wing **H** right hind wing. Scale bars: 5 mm (**A–H**).

pl. 3, fig. 11, pl. 2). In extant members of the polystoechotid genus-group Sc and R1 are closely approximated but are actually not fused, e.g., *Fontecilla* Navás, 1931, *Platystoechotes* Carpenter, 1940, *Polystoechotes* Burmeister, 1839 (see Winterton and Makarkin 2010). While this character was not fully investigated in the fossil lineages, most fossil polystoechotid genera were illustrated with the fused Sc and R1.

During the examination of the new materials, it is clear that all specimens assigned to *Lasiosmylus* (Figs 1, 2) show a separate Sc and R1. Furthermore, nine specimens (CNU-NEU-LB2015001P/C, CNU-NEU-LB2015002, CNU-NEU-LB2016001P/C, CNU-NEU-LB2016002, CNU-NEU-LB2016003, CNU-NEU-LB2016004, CNU-NEU-LB2016005, CNU-NEU-LB2016006, CNU-NEU-LB2016007) exhibit the typically venation with *L. newi* with exception for the incompatible conditions of Sc and R1. These nine specimens are considered to be *L. newi*.

It is concluded here that the genus *Lasiosmylus* most commonly has the separated Sc and R1 that is consistent with other moth lacewings. The exception of Sc and R1 in the holotype of *L. newi* possibly represents a particularly individual variation, inaccuracy in line drawing or obscurity in the specimen. Based on this we consider *Lasiosmylus* is unquestionably assigned to the ithonid genus-group by the following combination of characters: robust and hairy body, retracted head under pronotum, costal space dilated basally and narrowed disproportionately distally, separated Sc and R1 reaching the anterior margin straightly before the wing apex, MP first fork distant from the wing base and beyond the divergence of MA.

***Lasiosmylus longus* sp. n.**

<http://zoobank.org/66865D0B-21B0-42C4-BDD5-98CE8AE31A2D>

Figs 3, 4

Material. Holotype, CNU-NEU-LB2015003, a partly preserved specimen. Body barely preserved, but four overlapping, sub-complete wings, partially folded, with visible features.

Diagnosis. Humeral veinlet recurrent, with a few branches; numerous markings present on the forewing; a distinct oblique stripe parallel to the outer margin; costal crossveins simple; one basal subcostal crossvein; Sc and R1 separate distally, Sc terminating in costal margin 2/3 length of wing; R1 with numerous anteriorly directed branches; Rs with more than ten branches; MP fork level with origin of MA; CuA pectinately branched, CuP with three distal branches.

Description. *Body:* ca. 16.3 mm long; head hypognathous, retracted into pronotum partly; antenna filiform (ca. 4.0 mm) and incompletely preserved; compound eye large, ocelli absent; pronotum quadrate, numerous long setae concentrated laterally; mesonotum and metanotum stout; abdomen and legs indiscernible. *Fore wing:* ca. 22.7 mm long, 7.9 mm wide; slender and membranous with numerous fuscous spots; humeral plate discernible (Fig 3A); veins covered by dense setae, particular along wing margin; trichosors and nygmata undetectable; costal space broad basally (maximum width = 2.1 mm), narrowed distally; recurrent humeral veinlet with several branches; costal crossveins simple and with the occasional distal dichotomous forks, densely arranged distally; Sc and R1 separated distally; one subcostal crossvein close to the origin of Rs; R1 with many pectinately branches distally, entering the anterior margin; Rs branches regularly arranged with about thirteen branches; few crossveins present between branches of Rs; MA simple; MP first fork distant from wing base, close to the MA divergence from Rs; one mp1-mp2 crossvein detected; CuA branched near the middle of wing, with ten pectinate branches; CuP with three simple branches; anal veins partly preserved, 1A with three branches and forked proximally, 2A proximally forked. *Hind wing:* ca. 18.0 mm long, 7.3 mm wide, partly preserved, venation similar to forewing except costal space narrow; cubitus veins and anal veins not well preserved (Figs 3, 4).

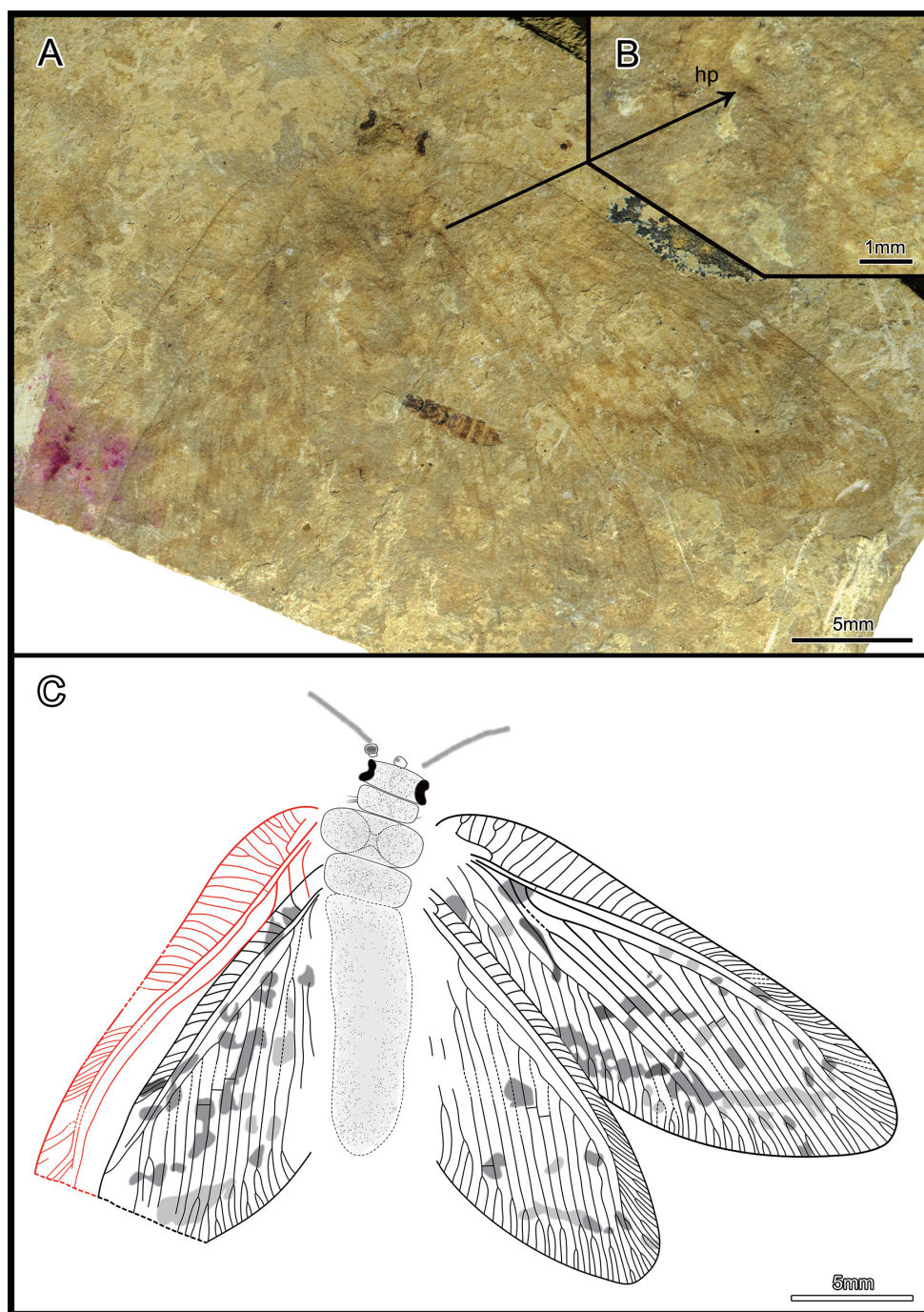


Figure 3. *Laiosmylus longus* sp. n. (holotype CNU-NEU-LB2015003). **A** habitus photograph **B** hp, humeral plate (left hindwing) **C** line drawing. Scale bars: 5 mm (**A**, **C**), 1 mm (**B**).

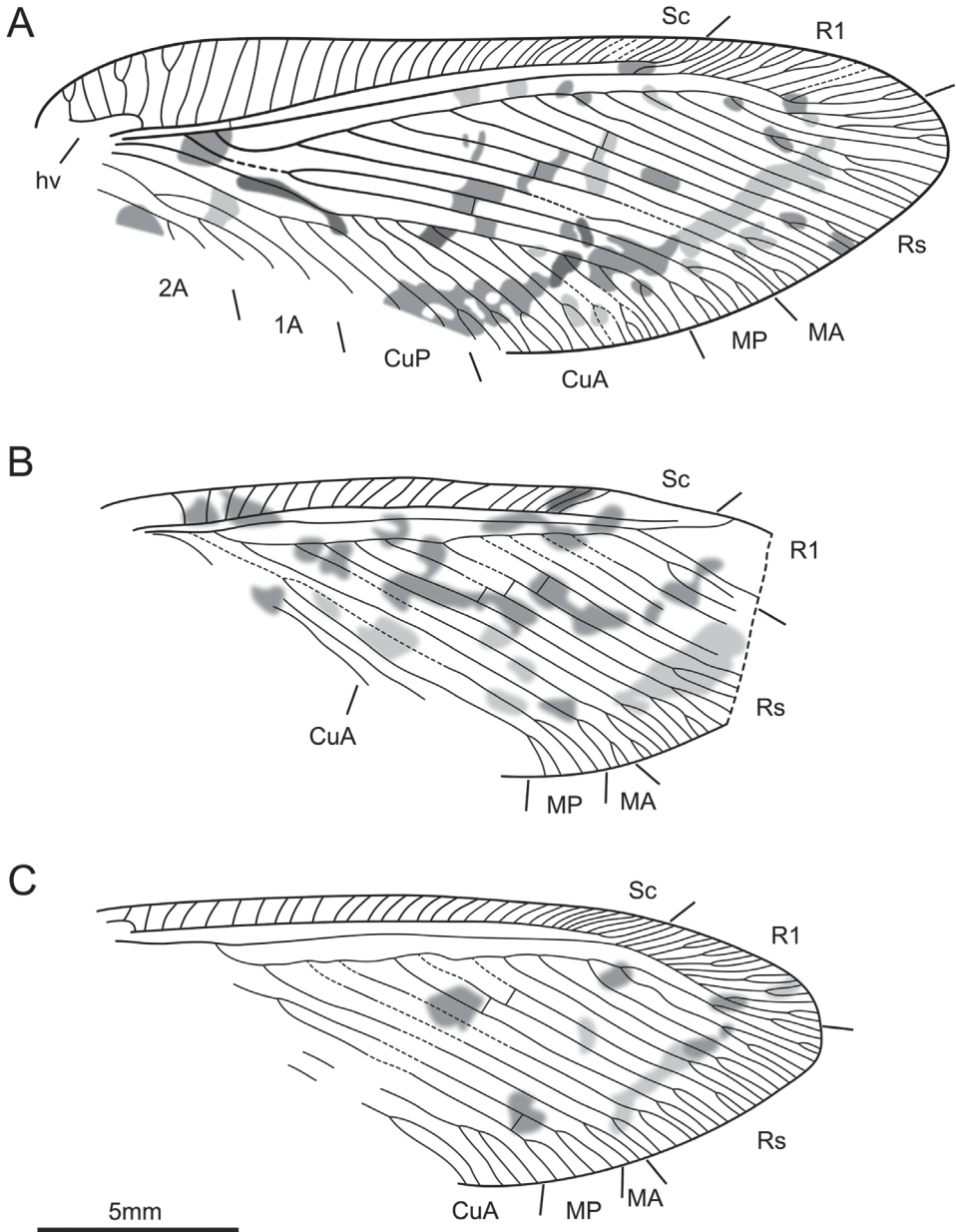


Figure 4. *Laiosmylus longus* sp. n. (holotype CNU-NEU-LB2015003), line drawings. **A** right forewing **B** left hind wing **C** right hind wing. Scale bars: 5 mm (**A–C**).

Etymology. The species name is from the Latin ‘*longus*’, referring to the slender wing of this moth lacewing.

Type locality. Huangbanjigou Village, Beipiao City, Liaoning Province, China.

Type horizon. Yixian Formation, Barremian-early Aptian (129.7–122.1 Ma), Early Cretaceous.

Remarks. *Laiosmylus longus* sp. n. can be distinguished from *L. newi* by the distinct oblique stripe close to the outer margin, multiple Rs branches, and pectinate CuA branches.

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We thank for Dr. Chungkun Shih (College of Life Sciences, Capital Normal University) for improving the manuscript. This work was supported by National Science Foundation of China (grants 31230065, 31272352, 31301905, 31672323, 41372013 and 41272006), Research Fund for the Doctoral Program of Higher Education of China (grant 20131108120005), Beijing Natural Science Foundation (grant 5132008), and Program for Changjiang Scholars and Innovative Research Team in University (IRT13081).

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A new earwig of the genus *Echinosoma* from Penang Island, Peninsular Malaysia, with notes on the taxonomic and nomenclatural problems of the genus *Cranopygia* (Insecta, Dermaptera, Pygidicranidae)

Yoshitaka Kamimura^{1,2}, Masaru Nishikawa³, Chow-Yang Lee²

1 Department of Biology, Keio University, 4-1-1 Hiyoshi, Yokohama 223-8521, Japan **2** Urban Entomology Laboratory, Vector Control Research Unit, School of Biological Sciences, Universiti Sains Malaysia, Minden 11800, Penang, Malaysia **3** Entomological Laboratory, Faculty of Agriculture, Ehime University, Matsuyama, 790-8566, Japan

Corresponding author: Yoshitaka Kamimura (kamimura@fbc.keio.ac.jp)

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Abstract

The pygidicranid earwigs (Dermaptera) of Penang Island, Peninsular Malaysia were re-examined based on material collected in extensive field surveys in 2012–2013 and 2015. *Echinosoma roseiventre* Kamimura & Nishikawa, **sp. n.** is described and illustrated, and *Cranopygia pallidipennis* (de Haan, 1842) is reported from the island for the first time. The taxonomic and nomenclatural problems of the genus *Cranopygia sensu* Hincks (1959) [A Systematic Monograph of the Dermaptera of the World. Part II. Pygidicranidae excluding Diplatyinae. British Museum (Natural History)] are also discussed. For the members of the subfamily Pygidicraninae from Indo-Austral and Oriental regions, the system, definitions of genera, and key of Hincks (1959) are followed. The genus *Mucrocranopygia* Steinmann, 1986 is synonymized with *Cranopygia* Burr, 1908. A key to the males of small *Echinosoma* from the Oriental region is provided.

Keywords

Cranopygia pallidipennis, *Cranopygia similis*, *Echinosoma roseiventre*, south-east Asia

Introduction

Penang Island (Pulau Pinang) is a 299-km² island located in the Straits of Malacca, approximately 5 km from the western coast of the mainland of Peninsular Malaysia. Thirty-one species of Dermaptera (earwigs) from this small tropical island are reported, based on an extensive field survey conducted in 2012–2013 (Kamimura et al. 2016), including an undescribed species of the genus *Echinosoma* Audinet-Serville, 1839 (Pygidicranidae). An additional field survey by the first author (YK) in 2014 resulted in the discovery of a species from the genus *Cranopygia* Burr, 1908 (Pygidicranidae) *sensu* Hincks (1959), which was not collected during the 2012–2013 survey (Kamimura et al. 2016). *Cranopygia similis* (Zacher, 1911) was recorded from “Penang” (Burr 1910, Hincks 1959) in the early 20th century, although whether it was collected on the island or from the mainland state of Penang is unclear. Based on a comparison of the samples collected during our surveys with material preserved in museums, the identity of *Cranopygia* from Penang Island is discussed, as well as the taxonomic and nomenclatural problems of the genus *Cranopygia sensu* Hincks (1959).

Methods

An extensive field survey of earwigs was conducted on Penang Island from March 2012 to March 2013 (see Kamimura et al. 2016 for details). Based on the samples collected during this survey a new species of *Echinosoma* is described. The type material of the new species and some representative samples collected during this study will be deposited in the collections of the Osaka Museum of Natural History (OMNH; Osaka, Japan) and the Lee Kong Chian Natural History Museum (LKC-NHM; Singapore).

An additional field survey was conducted by YK on 9–13 March, 2015, during which time two *Cranopygia* samples were collected from Bukit Jambul (5.348821N, 100.285692E). The site is a hill with a maximum elevation of approximately 200 m a.s.l that is covered with plantations of rubber, durian, banana, and other fruit trees, and is surrounded by secondary forests. A nymphal sample collected this location was reared to adulthood in the laboratory. For comparison, we examined specimens of *Cranopygia* species from Manchester Museum (MM) and the Natural History Museum (NHM), UK, and the entomological specimen collections of the School of Biological Sciences, Univerisiti Sains Malaysia, Penang, Malaysia.

Male and female genitalia removed from the examined specimens were mounted in Euparal (Waldeck GmbH & Co. KG, Münster, Germany) between two cover slips, and attached to the pin of the respective specimen. The terminologies of Klass (2003) and Kamimura (2014) are used for female and male genital structures, respectively.

Taxonomy

Genus *Echinosoma* Audinet-Serville, 1839

Echinosoma roseiventre Kamimura & Nishikawa, sp. n.

<http://zoobank.org/A1DA37A5-838E-4B46-A5A1-977893C9460A>

Figs 1a, 2–9

Echinosoma sp.: Kamimura et al. 2016: 240, figs 9, 10.

Diagnosis. *Echinosoma roseiventre* sp. n. is a small species less than 8 mm including the forceps. This species differs from all other similar sized species of *Echinosoma* with the combination of the following characters: abdomen uniformly reddish brown or rosy without a distinct pattern; ultimate tergite not pubescent, but with small rounded swellings; pygidium broader than long; virga very long, more than five times longer than parameres, tubular and simple.

Description. Holotype (male): length of body (without forceps): 7 mm. Length of forceps: 0.9 mm. Head width: 1.5 mm. Pronotum width: 1.6 mm. Pronotum length: 1.1 mm.

Color: General body color dull smoky black but abdomen, especially caudal part, pygidium, and forceps reddish brown or rosy (Fig. 1a). Mouth parts brownish. Antennae dark brown except for first three segments dirty white. Legs dirty white but femora with a broad fuscous band near the base. Caudal margin of tegmina with distinct, narrow whitish band. First abdominal segment whitish. *Body* covered with obtuse bristles sparsely. *Head* (Fig. 2) slightly broader than long; frons convex; transverse and median suture indistinct; caudal margin feebly emarginated in middle. Antennae (Fig. 3); 17 segments (left side partly broken, 16 segments remaining), segments mostly stout; 1st expanded apically, nearly half long as the distance between antennal bases; 2nd short, quadrate, almost as long as broad; 3rd long, twice as long as broad; 4th and 5th short, as long as broad; 6th and beyond gradually becoming longer and narrowing basally rendering some segments subpyriform. Eyes long, approx. as long as the post-ocular length. Post-ocular margin with a row of five long bristles. *Pronotum* (Fig. 2) broader than long; surface rough; sides rounded; frontal and caudal angles weakly and strongly rounded, respectively; caudal margin convex with distinct emargination in middle; prozona distinctively raised; median sulcus weak but visible; row of long bristles on frontal and lateral margins. *Tegmina* almost as long as pronotum; surface rough; humeral angle weak and anal angle shortly rounded off to show a small, triangular scutellum; caudal margin obliquely truncate, outer and caudal margins with long bristles. *Hind wings* wanting. *Legs* stout; femora not compressed, ecarinate; arolium small; hind tarsi with 1st segment longer than the third. *Abdomen* stout, more or less parallel-sided, except first three segments narrowed; sides of segments almost straight; tergites with scattered granules or very short obtuse bristles with whitish apex; first two tergites and lateral sides of 3rd tergites onward with long bristles near caudal margins. Penultimate

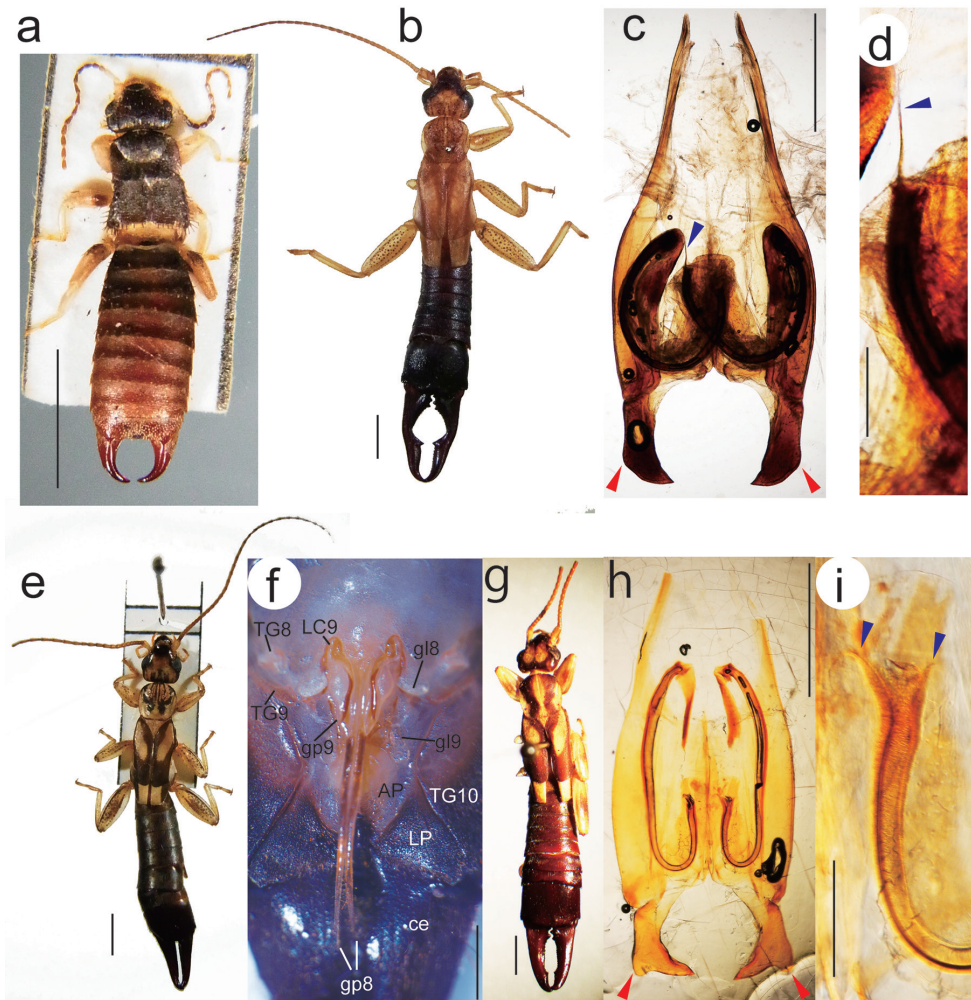
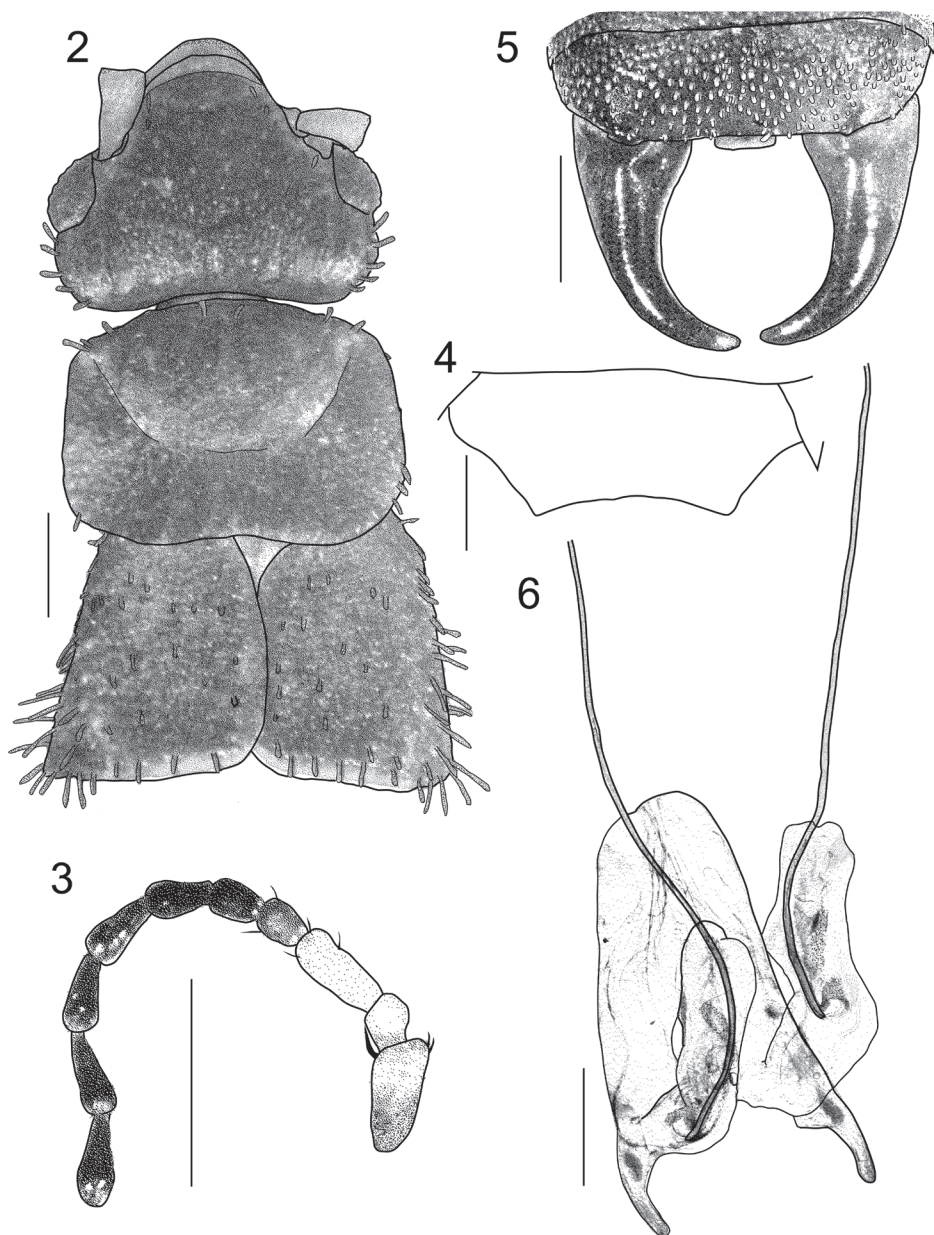


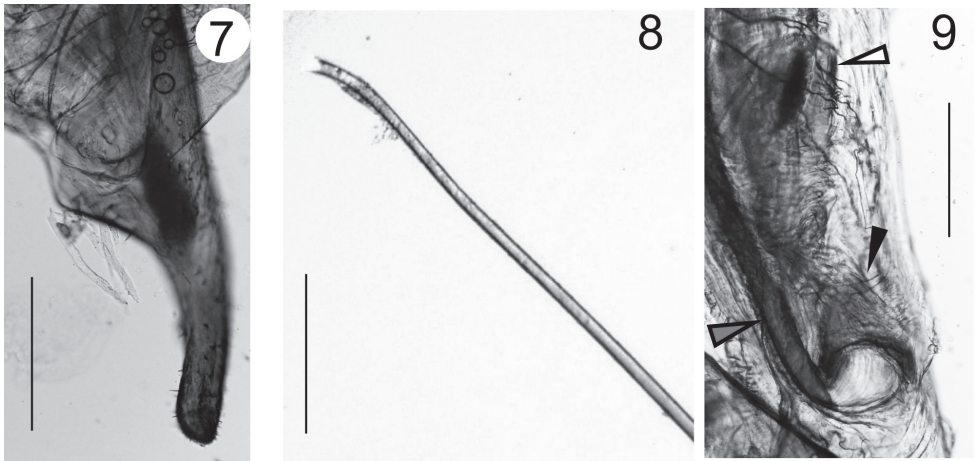
Figure 1. Holotype (male) of *Echinotoma roseiventris* sp. n. (a), a male (b–d) and a female (e–f) of *Cranopygia pallidipennis* from Penang Island, and a male of *Cranopygia similis* from Java (MM No. 3639) (g–i). (a, b, e, g) habitus; (c, d, h, i) male genitalia; (f) female genitalic region and ovipositor. The red and blue arrowheads indicate the expanded outer angle of the parameres (c) and the distal process of the virgae (c, d, i), respectively. Abbreviations: AP, anal plate; ce, cercus (=forceps); gl8, gonoplac (=coxal lobe) VIII; gl9, gonoplac (=coxal lobe) IX; gp8, gonapophysis VIII; gp9, gonapophysis IX; LC9, laterocoxa IX; LP, lateral plate; TG8–TG10, tergum VIII–X. Scale bars: 3 mm in a, b, e, and g; 1 mm in c, f and h; 200 µm in d and i.

sternite (Fig. 4) transverse, narrowed posteriorly with caudal margin being nearly half of the anterior, widely emarginated. Ultimate tergite (Fig. 5) transverse, with small rounded swellings above the base of forceps; caudal margin almost straight. *Pygidium* short, rectangular, transverse. *Forceps* (Fig. 5) short, strongly curving inwards, tapering apically; surface, smooth at tips. *Genitalia* (Figs. 6–9) with slender, finger-like parameres with obtuse tips and broad base (Fig. 7); penis lobe almost twice length of



Figures 2–6. *Echinotoma roseiventris* sp. n. Holotype (male) **2** Head and thorax **3** The basal part of left antenna **4** Penultimate sternite (pubescence omitted) **5** Ultimate tergite and forceps **6** Genitalia (before mounting in Euparal). Scale bars: 0.5 mm.

parameres; virga very long, more than five times longer than parameres, tubular and simple (Figs 6, 8); penis lobes also enclose a funnel-shaped sclerite at the base of virga, and a long ellipse sclerite distally (Fig. 9).



Figures 7–9. *Echinotoma roseiventris* sp. n. Holotype (male). **7** Right paramere **8** The tip of right virga **9** The base of right virga (indicated by the gray arrowhead) with the funnel-shaped sclerite (indicated by the solid arrowhead) and the long ellipse sclerite (indicated by the open arrowhead). Scale bars: 200 µm.

Paratype (male). Length of body (without forceps), 6.5 mm; length of forceps, 0.8 mm; head width, 1.2 mm; pronotum width, 1.2 mm; pronotum length, 0.8 mm. Antennae broken, five (right) and eleven (left) segments remaining. Tegmina longer, approx. 1.5 times longer than pronotum. Penultimate sternite not strongly narrows posteriorly, almost rectangular.

Female. Unknown.

Type series. Holotype: 1 male (genitalia mounted in Euparal between two coverslips and attached to the pin of the specimen), Bukit Jambul, Penang Island, West Malaysia, 27.XI.2012, Y. Kamimura leg. [OMNH]. Paratype: 1 male (genitalia mounted in Euparal between two coverslips and attached to the pin of the specimen), same locality as holotype, 24.VI.2012 (8.VII.2012 emerged from a nymph), Y. Kamimura leg. [LKCNHM].

Distribution. Penang Island, Peninsular Malaysia

Etymology. The specific epithet refers to the characteristic rosy abdomen of this new species.

Remarks. *Echinotoma roseiventris* sp. n. is very close to *E. andamanensis* Srivastava, 1988, described from India. Currently these two species can only be distinguished by differences in the length of the virgae (shorter than five times the parameres in *E. andamanensis*), the shape of the pygidium (longer than broad in *E. andamanensis*), and body coloration (*E. andamanensis* is generally dull smoky black but the abdomen, pygidium, and forceps are shiny; Srivastava 1988).

In addition to the species listed in the key below, *E. rufomarginatum* Borelli, 1931, which Hincks (1959), Steinmann (1986) and Srivastava (1988) treated as a doubtful species, also has a small body size (body length with forceps of ~11 mm; Hincks 1959). However, according to the original description by Borelli (1931), the male penultimate sternite of this species has a very deep emargination on the caudal margin.

The male genitalia of *E. burri* Hincks, 1959, recorded from Java and Sumatra, are very similar to those of *E. roseiventre* sp. n., but the body size is much larger (male body length with forceps of 18–20 mm; Hincks 1959).

Key to the small *Echinosoma* species (body length + forceps = 10 mm or less) from the Oriental Region (males only)

- 1 Abdomen with distinct pattern consisting of three light longitudinal stripes or series of spots.....2
- Abdomen more or less uniformly colored, without distinct pattern4
- 2 Sides of pronotum rounded. Virga almost straight... *E. affine* Hincks, 1959
- Sides of pronotum straight, parallel.....3
- 3 Virga slightly undulate..... *E. trilineatum* Borelli, 1921
- Virga very long, convoluted *E. sarawacense* Borelli, 1959
- 4 Pygidium characteristic, forming a large rounded lobe, filling the space between forceps, produced into a sharp pointed spine above posteriorly.....
.....*E. maai* Srivastava, 2003
- Pygidium normal, without a sharp pointed spine above posteriorly5
- 5 Ultimate tergite with long pubescence6
- Ultimate tergite setose or with very short, sparse, adpressed setae.....8
- 6 Virga not longer than penis lobe.....*E. sumatranum* (de Haan, 1842)
- Virga longer than penis lobe7
- 7 Virga convoluted *E. convolutum* Hincks, 1959
- Virga almost straight, not convoluted *E. komodense* Bey-Bienko, 1970
- 8 Virga not longer than penis lobe.....9
- Virga longer than penis lobe10
- 9 Penis lobe with long strong bristles (or toothed pad) beside virga
.....*E. setulosum* Hincks, 1959
- Penis lobes without long strong bristles (or toothed pad)
.....*E. parvulum* Dohrn, 1863
- 10 Virgae shorter than five times of parameres in length. Pygidium longer than broad.....*E. andamanensis* Srivastava, 1988
- Virgae longer than five times of parameres in length. Pygidium broader than long *E. roseiventre* sp. n.

Genus *Cranopygia* Burr *sensu* Hincks (1955)

Cranopygia pallidipennis (de Haan, 1842)

Material examined. Male, preserved in the collection of the laboratory of entomology (Makmal Entomologi), School of Biological Sciences, Universiti Sains Malaysia: Ta-

man Rimba (Teluk Bahang Recreational Park), Penang Island, 9 XII 2009, Tan Chia Chi leg. The specimen has now been transferred to the entomological specimen collections of the School of Biological Sciences, Universiti Sains Malaysia. Two females (one emerged from nymph on 30 III 2015): Bukit Jambul (secondary forest of a rubber plantation), Penang Island, 11 III 2015, Y. Kamimura leg.

Comparative material examined. *Cranopygia similis* (Zacher, 1911): Male, preserved in the collection of the Manchester Museum, the University of Manchester, England: “H. LUCHT, K. O. Blawan, 900/1500 Mr., Idjan Plateau [with unreadable handwritten characters: ? 205.39] / 3639 / *Cranopygia similis* (Zacher) ♂, det W. D. Hinks” [MM No. 3639].

Known distribution. Malaysia (Kuala Lumpur, Bukit Kuru), Myanmar, Indonesia (Java, Sumatra, Borneo).

Remarks. First record for Penang Island.

Discussion

Problems in the taxonomic treatment of *Cranopygia* Burr *sensu* Hincks (1955)

Within the family Pygidicranidae, the subfamily Pygidicraninae Verhoeff, 1902 is characterized by a medium to large body size (rarely less than 20 mm), antennae with 25 segments or more in which the 4th and 5th are wider than they are long, depressed femora, and equally developed right and left penis lobes (Burr 1915a, Hincks 1955, Steinmann 1986, Srivastava 1988). Indo–Austral and Oriental species of this subfamily are usually classified in the genus *Tagalina* Dohrn, 1863, in which the second tarsal segments are characteristically enlarged, or the genus *Cranopygia* Burr, 1908 *sensu* Hincks (1955). The taxonomy of the latter is rather unstable and unsettled. Including this group, for several species that were formerly in the genus *Pygidicrana* Audinet-Serville, 1831, Burr (1908) erected the following four genera based on differences in the shapes of the penultimate sternite, pronotum, and elytra: *Cranopygia* (type species, *Pygidicrana cumingi* Dohrn, 1863), *Pyge* (type species, *Pygidicrana modesta* de Bormans, 1894), *Dicrana* (type species, *Pygidicrana frontalis* Kirby, 1903), and *Picrania* (type species, *Pygidicrana liturata* Stål, 1855). Subsequently, Zacher (1911) established the genus *Kalocrania* (type species: *Pygidicrana marmoricrura* Audinet-Serville, 1839), to which two additional species of Oriental *Pygidicrana* were transferred, with the description of a new species. However, the species of *Cranopygia sensu* Burr (1908) were apparently unknown to Zacher, which resulted in a lack of agreement as to how to distinguish between *Cranopygia* and *Kalocrania* (see Hincks 1955 for more details). To settle this problem, Burr (1915a) consistently examined the male genitalia of this group for the first time, and redefined the genus *Cranopygia* based on the shape of the virga. Simultaneously, *Pyge* was synonymized with *Kalocrania*, and a new genus *Acrania* was established (type species, *Pygidicrana picta* Guérin-Ménéville, 1838). Hincks (1955), who examined the genital armatures for many more species in this group, concluded

that *Cranopygia*, *Kalocrania*, and *Acrania* could not consistently be distinguished based on their genital morphologies, and he later synonymized the latter two genera with *Cranopygia*, with the formation of five species groups (Hincks 1959). Several species formerly in the genus *Dicrana* were also included in *Cranopygia* by Hincks (1959).

Nearly 25 years later, Steinmann (1986) erected three new genera, *Epicranopygia* (type species: *Pygidicrana picta* Guérin-Méneville, 1838), *Mucrocranopygia* (type species: *Pygidicrana horsfieldi* Kirby, 1891), and *Paracranopygia* (type species: *Forficula pallidipennis* de Haan, 1842), for the species of *Cranopygia sensu* Hincks (1959) with virgae that were not straight. Srivastava (1993a) considered that the traits for diagnosing these genera (i.e., the shapes of the penis lobes and the virgae) were unstable and therefore unsuitable for generic classification. Instead, he focused on the shape of the parameres, which are robust and resistant to the artifacts of mounting, and reinstated *Acrania* for species with parameres that are neither knobbed nor hooked externally or internally (but occasionally with a slight convexity of the external apical angle).

Engel and Haas (2007), who omitted to cite Srivastava (1993a), noted that the generic names *Acrania* and *Pyge*, which Steinmann (1986) considered invalid, were available for the group containing the respective type species. Accordingly, they reinstated *Acrania* and *Pyge*, making *Epicranopygia* and *Paracranopygia* junior objective synonyms. Although they did not provide the species lists for *Cranopygia* and *Mucrocranopygia sensu* Steinmann 1986, Engel and Haas (2007) followed Steinmann's (1986) taxonomic system for the subfamily, except for the abovementioned changes in generic names.

Srivastava's (1993a) taxonomic treatment is also problematic. He reinstated *Acrania*, the type species of which is *Pygidicrana picta* Guérin-Méneville, 1838. However, he simultaneously synonymized *Epicranopygia*, which was created with the same type species (*P. picta*), with *Cranopygia*. According to his list of new combinations, Srivastava (1993a) transferred three species of *Epicranopygia* to *Cranopygia*, but transferred three others, including *E. picta*, to *Acrania*. Thus, the declaration of synonyms in Srivastava (1993a), and those cited in subsequent papers (Srivastava 1993b, 1995) are incorrect: Srivastava (1993a) synonymized *Epicranopygia* (**pars**) and *Paracranopygia* (**pars**) with *Acrania* and *Cranopygia*.

Subsequently, Sakai (1996, 2000) generally followed Srivastava's (1993a) system (and possibly the identification key), but concurrently adopted Hincks's (1959) species-group level classification. However, instead of using the *C. siamensis* species group (Hincks 1959), he treated *Paracranopygia* as a valid subgenus for most species of *Paracranopygia sensu* Steinmann (1986), as well as including *C. tianshanskyi* and *C. chirurga*, which were originally described by Gorochoy and Anisutkin (1993) under the genus *Paracranopygia*.

In addition to these nomenclatural problems, recent studies have shown that the morphology of earwig virgae, particularly the length, evolves rapidly due to sperm competition, resulting in considerable variation even among very closely related congeners (Kamimura 2000, 2014, Lieshout and Elgar 2011). Therefore, although useful for species diagnosis, generic classification systems based primarily on virgal characteristics

(e.g., length, convolution) likely do not reflect accurately the phylogenetic relationships. In contrast, the functional significance of male genital parameres is largely unknown for earwigs (Kamimura 2014). Nevertheless, the presence or absence of a tooth or process of the parameres, which Srivastava (1993a) proposed to distinguish *Cranopygia* and *Acrania*, is also likely an unreliable trait for the generic classification of this group. For example, male *Cranopygia vittipennis* Hincks, 1955 have a tiny process at the outer angle of the paramere, whereas a similar but weaker process is found in *Acrania luzonica* (Brindle, 1955) in the equivalent position (compare figs. 2 and 12 of Srivastava 1993a). A similar observation was made for *Cranopygia pallidipennis* from Penang Island, which is described below. Therefore, for the taxonomy of pygidicranine earwigs, we propose to follow the system, definitions of the genera, and key of Hincks (1959); that is, all of the species from Indo–Austral and Oriental regions (except for some species of *Dacnodes*) are classified either in the genera *Tagalina* (species with an enlarged second tarsal segment) or *Cranopygia* (species with a simple second tarsal segment). Accordingly, we propose to place all of the following species in the genus *Cranopygia*.

Genus *Cranopygia* Burr and its synonyms

Cranopygia Burr, 1908: 384, 389 [type-species: *Pygidicrana cumingi* Dohrn, 1868 (original designation)]; 1910: 53, 61; 1911: 16, 19; 1915a: 432, 435 (*Pyge* Burr, proposed synonymy with *Cranopygia* Burr). – Townes 1945: 346 (catalogue). – Hincks 1955: 809 (*Kalocrania* Zacher and *Acrania* Burr, proposed synonymy with *Cranopygia*); 1959: 52 (revision). – Popham 1965: 132 (in key). – Brindle 1970: 647. – Sakai 1971: 12 (catalogue); 1982: 15 (list of species); 1996: 3 (list of species); 2000: 89 (in key). – Steinmann 1973a: 148 (list); 1973b: 396 (in key); 1975: 202 (in key); 1983: 56 (synopsis); 1986: 240 (revision); 1989: 122 (catalogue). – Srivastava 1988: 37 (classification same as Hincks 1959); 1993a (1992): 43 (*Epicranopygia* Steinmann and *Paracranopygia* Steinmann, proposed synonymy with *Cranopygia*); 1995: 293 (*Epicranopygia* Steinmann and *Paracranopygia* Steinmann, as synonyms of *Cranopygia*).

Pygidicrana (*pars*) Audinet-Serville, 1831: 30 [type-species: *Pygidicrana v-nigrum* Audinet-Serville, 1831 (Monobasic)]; 1839: 19. – Dohrn 1863: 46. – Scudder 1876: 298. – de Bormans and Kraus 1900: 15. – Kirby 1904: 4. – Burr 1908: 384; 1910: 53.

Pyge (*pars*) Burr, 1908: 384, 390 [type-species: *Pygidicrana modesta* de Bormans, 1894 (original designation)]; 1910: 53, 65; 1911: 16, 20; 1915a: 435. – Shiraki 1928: 3. – Townes 1945: 354 (catalogue). – Engel and Haas 2007: 19 (*Paracranopygia* Steinmann, proposed synonymy with *Pyge*).

Dicrana (*pars*) Burr, 1908: 384, 387 [type-species: *Pygidicrana frontalis* Kirby, 1903 (original designation)]; 1910: 53, 60; 1911: 16, 19. – Townes 1945: 347 (catalogue).

Picrania (*pars*) Burr, 1908: 390 [type-species: *Pygidicrana liturata* Stål, 1855 (original designation)]; 1910: 53, 63; 1911: 16, 19. – Townes 1945: 353 (catalogue).

- Kalocrania* Zacher, 1910: 105 [type-species: *Pygidicrana marmoricrura* Audinet-Serville, 1839 (original designation)]. – Zacher 1911: 335, 336. – Burr 1911: 16, 18 (*pars*), pl. 8, fig. 18 (opisthomeres); 1915a: 432, 435; 1915b: 258, fig. 1 (opisthomeres), fig. 19 (gonapophyses). – Townes 1945: 350 (catalogue).
- Acrania* Burr, 1915a: 432, 436 [Type species: *Pygidicrana picta* Guérin-Méneville, 1838 (original designation)]. – Townes 1945: 343 (catalogue). – Srivastava 1993a (1992): 44 (*Mucrocranopygia* Steinmann, proposed synonymy with *Acrania*); 1993b: 373 (*Mucrocranopygia* Steinmann and *Epicranopygia* Steinmann (*pars*), as synonyms of *Acrania*); 1995: 293 (*Mucrocranopygia* Steinmann, as synonym of *Acrania*). – Sakai 1996: 2 (list of species); 2000: 100 (in key). – Engel and Haas 2007: 19 (*Epicranopygia* Steinmann, proposed synonymy with *Acrania*).
- Epicranopygia* Steinmann, 1986: 269 (proposed new name for *Acrania* Burr, 1915) [type-species: *Pygidicrana picta* Guérin-Méneville, 1838 (original designation)]; 1989: 146 (catalogue). – Sakai 1982: 16 (list of species).
- Paracranopygia* Steinmann, 1986: 277 [type-species: *Forficula pallidipennis* de Haan, 1842 (original designation)]; 1989: 150 (catalogue). – Sakai 1982: 15 (list of species).
- Cranopygia* (*Paracranopygia*) Sakai, 1996: 4 [= *siamensis*-group, Hincks (1959)] (list of species); 2000: 104 (in key).
- Mucrocranopygia* Steinmann, 1986: 266 [type-species: *Pygidicrana horsfieldi* Kirby, 1891 (original designation)]; 1989: 149 (catalogue). – Sakai 1982: 15 (list of species). **New synonym.**

List of species to be included in the genus *Cranopygia*

- C. angustata* (Dohrn, 1862); *C. appendiculata* Hincks, 1955; *C. assamensis* Hincks, 1955; *C. bakeri* (Borelli, 1921); *C. beybienkoi* Gorochof & Anisyutkin, 1993; *C. bhallaie* Kapoor, 1966; *C. bifurcata* Srivastava, 1980; *C. brindlei* Srivastava, 1988; *C. burmensis* Hincks, 1955; *C. burri* Hincks, 1955; *C. carinata* Hincks, 1959; *C. celebensis* (de Bormans, 1903); *C. chirurga* (Gorochof & Anisyutkin, 1993); *C. comata* Hincks, 1955; *C. constricta* Hincks, 1955; *C. corymbifera* Anisyutkin, 1997; *C. crockeri* Anisyutkin, 2014; *C. cumingi* (Dohrn, 1862); *C. curtula* Hincks, 1955; *C. daemeli* (Dohrn, 1869); *C. dravidia* (Burr, 1914); *C. eximia* (Dohrn, 1862); *C. fletcheri* Bharadwaj & Kapoor, 1967; *C. formosa* Hincks, 1955; *C. gialaiensis* Gorochof & Anisyutkin, 1993; *C. guttata* (Kirby, 1903); *C. horsfieldi* (Kirby, 1891); *C. imperatrix* (Burr, 1899); *C. jacobsoni* (Boeseman, 1954); *C. javana* Hincks, 1955; *C. kallipygos* (Dohrn, 1862); *C. lueddemanni* Srivastava, 1984; *C. luzonica* Brindle, 1967; *C. maculipes* Hincks, 1955; *C. manipurensis* Srivastava, 1975; *C. marmoricrura* (Audinet-Serville, 1839); *C. modesta* (de Bormans, 1894); *C. nietneri* (Dohrn, 1862); *C. nova* Anisyutkin, 2015; *C. okunii* (Shiraki, 1928); *C. ophthalmica* (Dohrn, 1862); *C. pallidipennis* (de Haan, 1842); *C. parva* Brindle, 1975; *C. philippinica* Burr, 1914; *C. picta* (Guerin-Méneville, 1838); *C. pluto* Hebard, 1923; *C. proxima* Hincks, 1959; *C. raja* (Burr, 1911); *C. rostrata* Brindle, 1970;

C. sarawacensis Hincks, 1959; *C. sauteri* (Burr, 1912); *C. semenoffi* (Burr, 1912); *C. siamensis* (Dohrn, 1862); *C. similis* (Zacher, 1911); *C. spenceri* Srivastava, 2003; *C. steineri* Srivastava, 1993; *C. steinmanni* Srivastava, 1988; *C. tianshanskyi* (Gorochov & Anisytukin, 1993); *C. tonkinensis* Hincks, 1955; *C. tumida* Borelli, 1931; *C. valida* (Dohrn, 1867); *C. vanderdoesi* Boeseman, 1954; *C. variegata* Brindle, 1965; *C. vicina* Hincks, 1959; *C. vietnamensis* Gorochov & Anisytukin, 1993; *C. vitticollis* (Stål, 1855); *C. vittipennis* Hincks, 1955.

Identification of specimens of *Cranopygia* from Penang

The external morphology, coloration, and genitalia of the male specimen collected at Taman Rimba (Teluk Bahang Recreational Park), Penang Island are very similar to those of *C. pallidipennis* (de Haan, 1842) described by de Haan (1842), Burr (1910), Zacher (1911), and Hincks (1959) (Fig. 1b–d). The external morphologies and coloration of the female specimens from Bukit Jambul, Penang Island also match the descriptions of *C. pallidipennis* (de Haan 1842, de Bormans and Kraus 1900, Zacher 1911, Hincks 1959). The female genital region was also examined for a female specimen that emerged in the laboratory (Fig. 1f). Although the female genitalia are rarely described for the genus (but see Zacher 1911; Anisytukin 2014) and thus diagnostic features have not been established, the observed morphology (Fig. 1f) matches that described by Zacher (1911) for *C. pallidipennis*.

A male specimen of *Cranopygia* was recorded from “Penang” in the early 20th century (Burr 1910; Hincks 1959). Burr (1910) identified it as *C. siamensis* (Dohrn, 1863). Later, Hincks (1959) tentatively identified the specimen as *C. similis* (Zacher, 1911) based on features of the genitalia. However, according to Hincks (1959), the large body size (36 mm) of the specimen and the following external morphology are not typical of *C. similis*; “In the Penang male the pronotum is as broad as long, and the sides are strongly rounded; the occiput is marmorated with fuscous dots and streaks; the pronotum has the dark bands much more broken; the femora are dotted with fuscous and not longitudinally streaked; the forceps are rather longer and more curved, enclosing an oblong-ovate space.” Some of these characteristics suggest a very close affinity of the specimen to *C. pallidipennis*, but the shape of the forceps is different (Burr 1910).

Cranopygia pallidipennis seems to be very close to *C. similis* and can be distinguished from the latter by a larger body size; the pattern of fuscous markings on the head, pronotum, and femora (Fig. 1b, e vs. Fig. 1g); a larger space enclosed by the distal part of the forceps (Fig. 1b vs. Fig. 1g); a less pronounced convexity at the outer angle of the parameres (Fig. 1c vs. Fig. 1h); and the presence of a single, long filamentous projection at the tip of the virgae (Fig. 1d vs. Fig. 1i). The last characteristic is likely a diagnostic feature distinguishing *C. pallidipennis* from *C. similis*. Unfortunately, we could not reexamine the male specimen from “Penang” described by Burr (1910) as it is currently missing; it was not found in the collections of the NHM (including Burr’s collection) or the MM. In conclusion, our study shows that *C. pallidipennis*

is a member of the contemporary earwig fauna of the island, whereas the identity of Burr's specimen of *Cranopygia* from "Penang" requires further investigation including determining the exact location from which it was collected.

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A new species of *Baenothrips* Crawford from China (Thysanoptera, Phlaeothripidae)

Chao Zhao¹, Xiaoli Tong¹

¹ Department of Entomology, College of Agriculture, South China Agricultural University, Guangzhou 510642, China

Corresponding author: Xiaoli Tong (xtong@scau.edu.cn)

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Abstract

A new urothripine species, *Baenothrips cuneatus* sp. n., is described from China. This is distinguished from its congeners by the following combination of characteristics: dorsal surface of head having a wedge-shaped reticulation extending from median to the posterior margin; antennal segments VII–VIII is closely joined with a complete suture; the mesoacrotergite strongly constricted in the middle; abdominal tergite I divided into 5 plates; width of membranous gap between ovispan on abdominal sternite IX approximately 1/3 of the apical width of segment IX.

Keywords

Baenothrips, China, fungus-feeding thrips, new species

Introduction

The genus *Baenothrips* Crawford currently comprises 11 species in the world, of which five are distributed in Asia (ThripsWiki 2016). These thrips are considered to be fungus-feeding, with most living in leaf litter, grass tussocks or dead twigs (Stannard 1970; Mound 1972; Okajima 1994). However, some species, such as *B. mouni* Stannard of Australia, can crawl up above soil level to grass stems, and are likely to be wind-dispersed (Mound 1972; Ullitzka and Mound 2014). The new species described below

has similar dispersive behaviour, and can be collected not only in leaf litter but also on fresh leaves or stems of grass, fern, and dicotyledons. Presumably this species normally inhabits leaf litter, but crawls up fresh plants occasionally and is then dispersed by wind.

Materials and methods

The thrips were extracted by using Tullgren funnels from leaf litter, or collected by beating vegetation over a white plastic tray using a small stick, and then sorted and preserved in 90% alcohol. Specimens were then mounted into Canada balsam on microscope slides. Structural details were examined with a ZEISS Imager A1 microscope, photos were taken by a Photometrics CoolSNAP camera, and the figures were subsequently processed with Adobe Photoshop CS6. All type specimens are deposited in the Insect Collection, South China Agricultural University (SCAU).

Taxonomy

Baenothrips cuneatus sp. n.

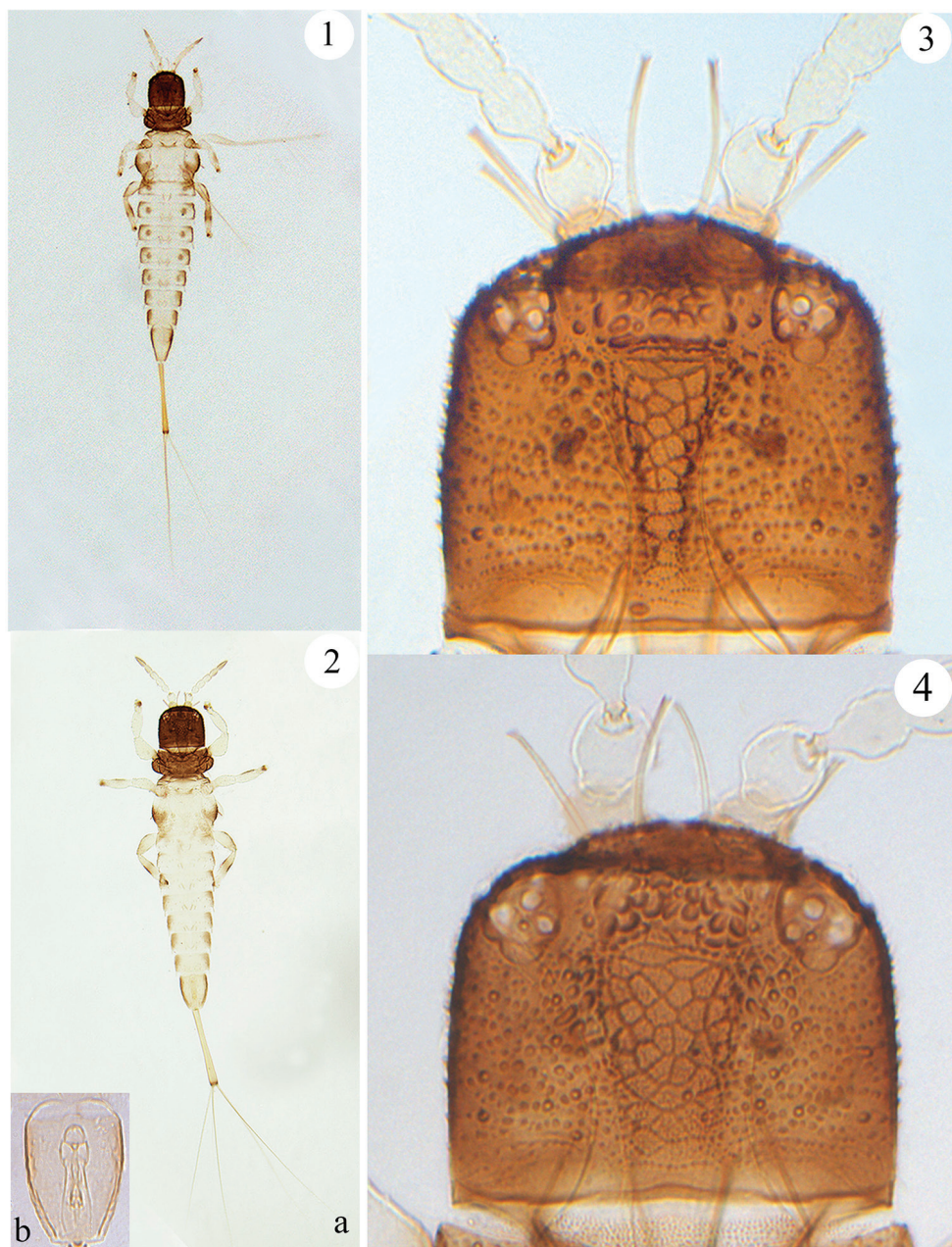
<http://zoobank.org/9CD835D4-F839-4FA7-A13E-CCCD48079809>

Figs 1–14

Material examined (All specimens were collected from leaf litter unless otherwise noted; females all macropterous, males all apterous).

Holotype. Female macroptera, **CHINA**, Guangdong province, Gaozhou County, Yuntan Town, Mt. Sanguanshan (21°55'10"N, 111°8'40"E), in leaf litter of *Acacia auriculiformis* (Fabaceae), 15.xii.2014, Chao Zhao (in SCAU).

Paratypes. 8 females 1 male, taken with holotype; 3 females 7 males, same locality and habitat as holotype, 5.ix.2015, Zhaohong Wang. **CHINA, Hunan:** 1 female, Yanling County, Shennong Valley (26°29'N, 114°1'E), on grass stem or leaf, 15.ix.2014, Chao Zhao. 1 female, Yanling County, Shennong Valley (26°29'N, 114°1'E), in leaf litter of *Cryptomeria fortune* (Taxodiaceae), 16.ix.2014, Chao Zhao. **Guangdong:** 1 male, Shixing County, The Chebaling National Nature Reserve (24°42'N, 114°11'E), 11.x.2002, Zhiwei Li; 3 females 1 male, Huizhou City, Mt. Nankunshan (23°38'N, 113°50'E), 11.xii.2002, Zhiwei Li; 1 female, Guangzhou City, Longdong Forest Park (23°14' N, 113°24' E), 5.xii.2004, 1 female, in leaf litter of *Acacia auriculiformis*, 1.xii.2006, Jun Wang; 1 female, Dongguan City, Mt. Yinpingshan (21°55'10"N, 111°8'40"E), on fresh leaf of *Stenoloma chusanum* (Lindsaeaceae), 10.ix.2014, Chao Zhao; 3 females, Guangzhou City, Mt. Maofengshan (23°17'N, 113°27'E), on fresh leaf or stem of *Dicranopteris dichotoma* (Gleicheniaceae), 4.i.2016, Chao Zhao; 3 females, Shenzhen City, Mt. Wutongshan (22°24'N, 113°17'E), on fresh leaf or stem of *Dicranopteris dichotoma*, 29.iv.2016, Chao Zhao. **Guangxi:** 1 female, Nanning City (22°48'N, 108°22'E), on fresh leaf or stem of *Pennisetum purpureum* (Poaceae), 3.x.2012 (Shulan Yang); 1 females,



Figures 1–4. *Baenothrips cuneatus* sp. n. **1** female habitus **2a** male habitus **2b** male genitalia **3** head of female **4** head of male.

Shangsi County, Shiwandashan National Forest Park (25°54'N, 107°54'E), on grass stem or leaf, 25.vii.2016, Chao Zhao. **Yunnan:** 1 female, Jinghong City, 5.iv.1987, Xiaoli Tong. **Hainan:** 1 male, Baisha County, Yinggeling National Nature Reserve, Yinggezui

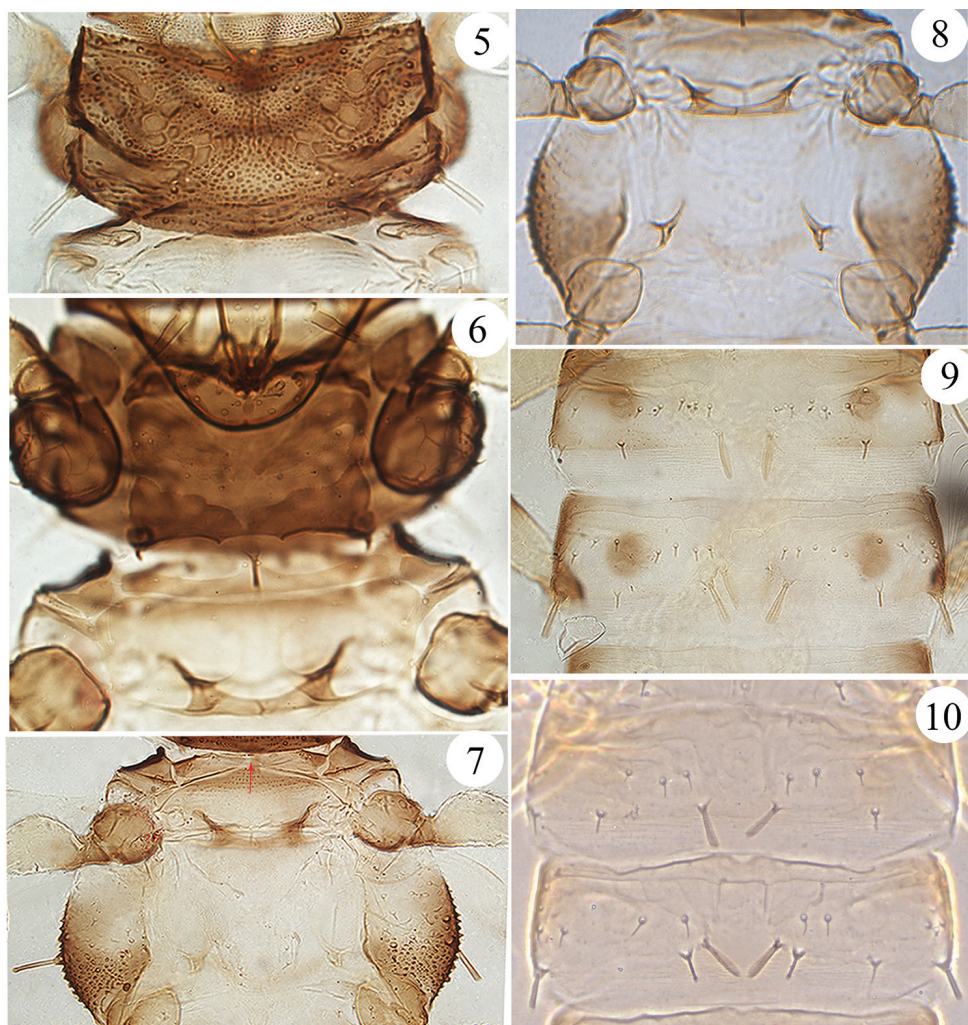
Protection Station (18°03'N, 109°54'E), on fresh leaf of *Argyreia acuta* (Convolvulaceae), 8.i.2016, Xiaoli Tong.

Description. Female macroptera (Fig. 1): Head and prothorax dark brown; pterothorax yellowish white with dark brown anteriorly and laterally; abdominal tergites I–IX yellowish white with brown laterally, of which tergites II–V each with a pair of light brown circular patches on either side; tube yellow with extreme apex dark brown. All coxae, trochanters and apical half of tarsi brown; fore and mid femora yellowish white except for inner base brown, hind femora pale yellowish brown with brown on dorsal margins; fore tibiae yellowish white, mid tibiae yellowish yellow shaded with light brown on outer margins, hind tibiae whitish but brown medially. Antennal segment I pale brown, segments II–VI yellowish white, segments VII and VIII pale brown.

Head (Fig. 3) almost as long as broad or a little shorter; head broadly rounded in front, with three pairs elongate cephalic setae on anterior margin; dorsal surface tuberculate and with a wedge-shape reticulation extending from middle to posterior margin; cheeks almost straight. Eyes with approximately eight facets dorsally and six ventrally, of which three dorso-lateral facets are distinctly larger than the others; three ocelli present, anterior ocellus placed between inner cephalic setae, posterior ocelli behind outer pair of cephalic setae and placed close to eyes. Antenna 8-segmented, arising ventrally (Fig. 13), segments VII–VIII closely joined with a complete suture; segment III with no sense cones, IV with two sense cones, each approximately two-thirds as long as the segment; segment V with one sense cone, situated outside of apex; segments VI and VII each with one sense cone dorsally. Maxillary stylets retracted to base of compound eyes, approximately one-third of head width apart medially.

Pronotum rectangular (Fig. 5), shorter than head, dorsal surface with irregular sculpture and wart-like tubercles; epimeral setae well developed. Mesoacrotergite strongly constricted medially by a very narrow bridge (Figs 7, 11); mesonotum sculptured with transverse dotted lines on anterior third; meta-epimeron bulging with one well developed seta. Fore wing bulging at base without basal setae; both fore wing and hind wing with a median vein or thickening, and with many, but not closely spaced, fringe cilia. Basantra weakly developed, largely membranous; ferna well developed, strongly narrowed posteromedially (Fig. 6); mesopresternum complete and transverse; mesoeusternum anterior margin entire. Mesosternal furcae fused in the middle; metasternal furcae placed laterally and widely separated (Fig. 8). All tarsi unarmed.

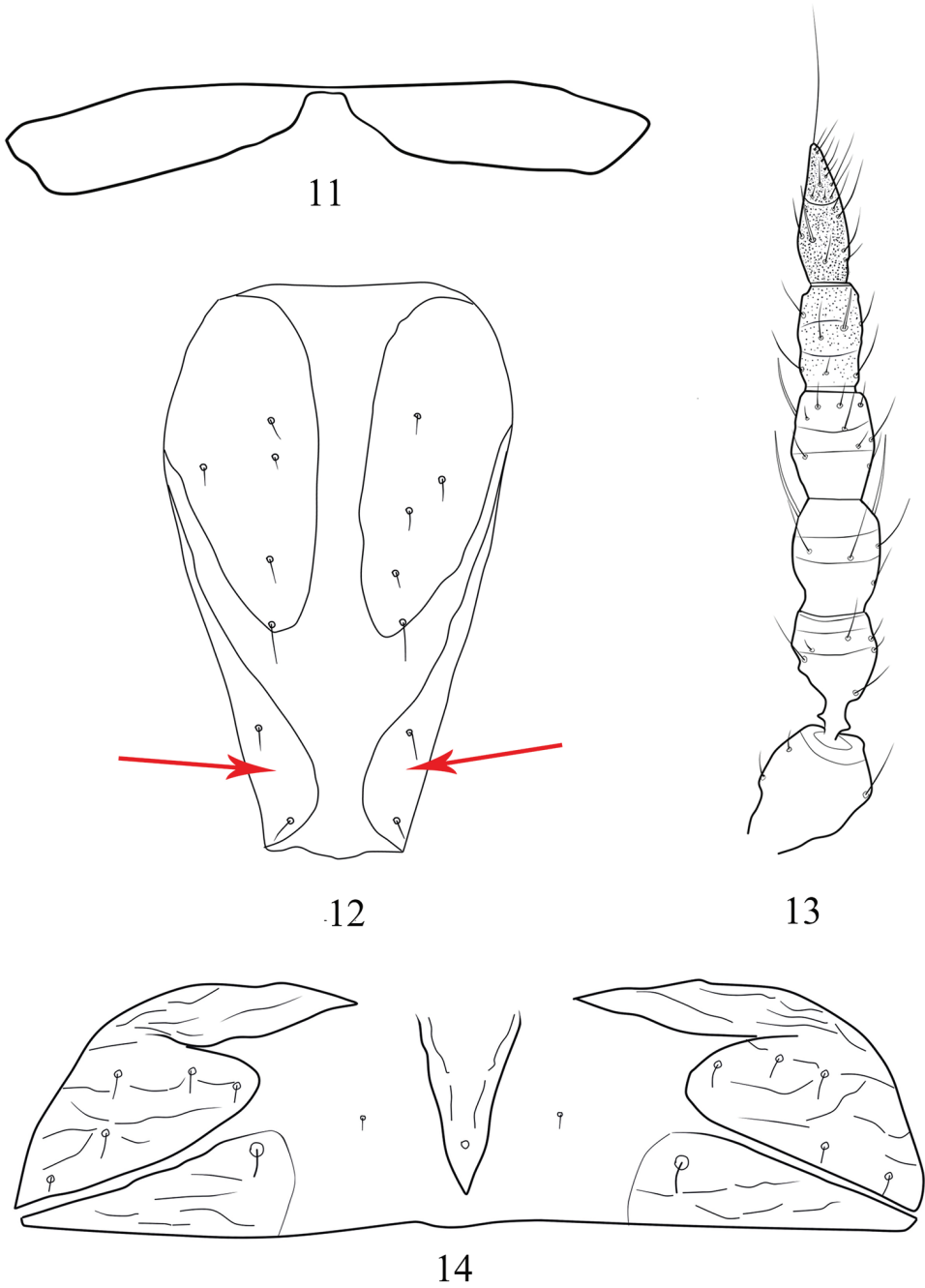
Abdominal tergite I divided into five plates, a slender median longitudinal plate bearing a campaniform sensillum (Fig. 14); tergite II with a pair of expanded wing-retaining setae; tergites III–VII with two pairs of wing-retaining setae, inner pair knife-like and outer pair fin-shaped (Fig. 9; cf. Bhatti 2002: fig 15a); tergites III–VIII posterolateral setae enlarged, each with a transverse row of 12–18 short setae medially; tergite IX 4.4 times as long as distal wide; ovispan slightly reduced, the width of membranous gap between ovispan approximately 1/3 of the apical width of segment IX (Fig. 12). Tube approximately twice as long as head with three pairs of anal setae; anal setae nearly 2.2 times as long as tube, but median dorsal pair half as long as the lateral two pairs.



Figures 5–10. *Baenothrips cuneatus* sp. n. **5** pronotum **6** ventral view of prothorax **7** dorsal view of pterothorax (arrow indicates mesoacrotergite constricted medially) **8** ventral view of pterothorax (show meso- and metasternal furcae) **9** abdominal tergites II–III of female **10** abdominal tergites II–III of male.

Measurements (holotype female in microns). Body length 1680. Head length 165; maximum width 170; anterior cephalic setae, median pair 73, lateral inner pair 65, outer pair 55. Pronotum length 100; median width 185; epimeral setae 27. Meta-thoracic epimeral setae 30. Abdominal tergite IX length 175, basal width 100, distal width 40. Tube length 315, basal width 20, apical width 30; anal setae, dorsal pair 335, lateral pairs 750. Antennal segments I–VIII length (width) as follows: 22 (28), 30 (29), 36 (25), 33 (24), 30 (21), 28 (19), 24 (14), 22 (10).

Male aptera (Fig. 2a): Head with only two pairs of elongate cephalic setae on anterior margin; wedge-shape reticulation of head wider than in female (Fig. 4); abdominal



Figures 11–14. *Baenothrips cuneatus* sp. n. (female) **11** mesoacrotergite **12** abdominal sternite IX (arrow indicates the ovispan) **13** antennal segments II–VIII **14** abdominal tergite I.

tergites III–VII without brown circular patches on either side; tergites II–VII with only one pair of wing-retaining setae (Fig. 10); abdominal tergite IX nearly three times as long as distal wide. Male genitalia as in figure 2b.

Measurements (paratype male in microns). Body length 1180. Head length 120; maximum width 140; two pairs of anterior cephalic setae 42. Pronotum length 80; median width 165; epimeral setae 20. Metathoracic epimeral setae 18. Abdominal tergite IX length 120, basal width 80, distal width 40. Tube length 225, basal width 15, apical width 25; anal setae, median dorsal pair 230, lateral pairs 550. Antennal segments I to VIII length (width) as follows: 16 (27), 25 (27), 35 (23), 27 (23), 35 (21), 24 (19), 25 (15), 17 (13).

Etymology. The specific epithet is from the Latin adjective “*cuneatus*” meaning wedge-shaped, and refers to the shape of reticulation on head.

Distribution. China (Hunan, Guangdong, Guangxi, Yunnan, Hainan).

Remarks. Only two species of the genus *Baenothrips* Crawford are validly recorded from China, *B. cuneatus*, and *B. ryukyuensis* Okajima. The record by Kudô (1978), of *B. asper* (Bournier) from China in Taiwan, was considered by Okajima (1994) to be a misidentification and to actually refer to *ryukyuensis*. Similarly, Bhatti (2002) suggested that the species *B. asper* is known only from Africa, and that the Asian records refer to some other species. Recently, *B. ryukyuensis* was recorded by Dang and Qiao (2014) from Fujian, China. Moreover, during sorting of specimens *Baenothrips* from China we found in our collections slide-mounted specimens labelled by Wang and Tong (2007) as *B. murphyi* (Stannard), and recognised that these actually represent *B. cuneatus*, the new species described above.

Baenothrips cuneatus sp. n. is most closely related to *B. asper* (Bournier) in colour pattern and several other features, but in the new species, dorsal surface of head having a wedge-shaped reticulation extending from median to the posterior margin; the mesoacrotergite is strongly constricted medially by a very narrow bridge (Figs 7, 11) as in *B. moundi* (Stannard) (cf. Bhatti 2002: fig 25) and the membranous gap (Fig. 12) between the ovispan on abdominal sternite IX is much wider than those in *B. asper* (Bournier) (cf. Bhatti 2002: fig 18). In addition, there are other five species of the genus occurring in Asia, some of them are also similar to *B. cuneatus* sp. n., but this new species can be distinguish from them by the below key.

Key to Asian species of *Baenothrips* (female)

- 1 Head with two pairs of prominent anterior cephalic setae.....2
- Head with three pairs of distinct anterior cephalic setae.....3
- 2 Two pairs of anterior cephalic setae situated laterally, and median pair of anterior cephalic setae absent; macroptera.....*B. quadratus*
- Only one lateral cephalic seta on either side, and one median pair of anterior cephalic setae present; aptera.....*B. indicus*

- 3 Antenna 8-segmented (suture between segments VII and VIII complete) ... 4
 – Antenna 7-segmented; except for epimeral setae, pronotum also having a pair of well-developed midlateral setae; macroptera or brachyptera ***B. minutus***
 4 Head with a wedge-shaped reticulation extending from median to the posterior margin; the mesoacrotergite is strongly constricted medially (Figs 7, 11); abdominal tergite I divided into five plates (Fig. 14); the width of membranous gap (Fig. 12) between ovispan is approximately 1/3 of the posterior margin of abdominal sternite IX; macroptera..... ***B. cuneatus* sp. n.**
 – Head reticulate just medially; the mesoacrotergite is not constricted medially; abdominal tergite I entire; the membranous gap between the ovispan is reduced to a longitudinal narrow cleft; macroptera or aptera **5**
 5 Three pairs of ocelli present, lateral ocelli placed close to eyes; basantra seemingly absent; macroptera ***B. murphyi***
 – Ocelli absent; basantra weakly developed; aptera..... ***B. ryukyuensis***

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This study was supported by the National Natural Science Foundation of China (31372236) and the Key Project for National Groundwork of Science & Technology (No.2013FY111500-5-3). We especially wish to acknowledge Zhaohong Wang, Zhiwei Li, Jun Wang, and Shulan Yang for collecting the specimens. Thanks are also due to the referees for their advice and constructive comments.

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Review of the genus *Genaemirum* Heinrich (Hymenoptera, Ichneumonidae, Ichneumoninae) with interactive identification keys to species

Pascal Rousse^{1,3}, Gavin R. Broad², Simon van Noort^{1,4}

1 Department of Natural History, Iziko Museums of South Africa, PO Box 61, Cape Town, 8000, South Africa **2** Department of Life Sciences, the Natural History Museum, Cromwell Road, London SW75 BD, UK **3** Department of Botany and Zoology, Evolutionary Genomics Group, Stellenbosch University, Private Bag X1, Stellenbosch 7602, South Africa **4** Department of Biological Sciences, University of Cape Town, Private Bag, Rondebosch, 7701, South Africa

Corresponding author: Simon van Noort (svannoort@iziko.org.za)

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Abstract

We describe *Genaemirum phagocossorum* Rouse, Broad & van Noort, **sp. n.**, a new ichneumonine parasitoid wasp reared from *Eucalyptus nitens* logs infested by the cossid moth *Coryphodema tristis*, which is considered a major pest of forestry and food crops in South Africa. This is the first plausible host association for the genus, and fits with the host association predictions of Heinrich. Two further undescribed species were found in the collections of the Natural History Museum in London and are described as *Genaemirum phacochoerus* Broad, Rouse & van Noort, **sp. n.** and *Genaemirum fumosum* Broad, Rouse & van Noort, **sp. n.** An identification key to the eight known species and a diagnosis for each species are provided, including photographs of all the primary type specimens. Online Lucid interactive identification keys are available at: <http://www.waspweb.org>.

Keywords

Africa, Afrotropical region, biocontrol, Ichneumonidae, Ichneumoninae, host, identification key, parasitoid wasp, species description, systematics

Introduction

“To find the details of the life history of [*Genaemirum doryalidis*] and its host, would be one of the most rewarding tasks of the Ethiopian ichneumonology”, concluded Heinrich (1967) after his description of the “monstruous” (sic) projections he observed on the genae of *Genaemirum doryalidis* Heinrich. *Genaemirum* Heinrich, 1936 is an endemic Afrotropical genus with five species known to date. The genus is characterized by the flattened and uncarinate scutellum, the long and evenly curved propodeum with median areas fused into a long and smooth mid-longitudinal surface, combined with highly specialized head structures. Both sexes exhibit a more or less strong expansion of the junction of the occipital and hypostomal carinae, females have a strong transverse carina across the frons and some also have the lower genae more or less expanded backwards. Almost nothing is known about the biology of *Genaemirum* species. Heinrich (1967) hypothesized that the extraordinary head structure would be an adaptation to an unusual biology and noted that he would not be surprised to see them emerging from a dry wood borer, based on the fact that the holotype of *G. doryalidis* was recorded as having been reared from a tree. We recently obtained an undescribed species of the genus, reared from a log infested with wood-boring moth larvae suggesting that Heinrich was in all likelihood right. We also take the opportunity to describe additional species that lay undescribed in the BMNH collection, provide an identification key to the eight known species, including online Lucid keys available at www.waspweb.org, and present high resolution images of all the primary type specimens.

Material and methods

Depositories

BMNH Natural History Museum, London, UK (Gavin Broad & David Notton).

MNHN Muséum National d'Histoire Naturelle, Paris, France (Claire Villemant & Agnèle Touret-Alby).

SAMC Iziko South African Museum, Cape Town, South Africa (Simon van Noort).

ZMHB Museum für Naturkunde, Humboldt Universität, Berlin, Germany (Frank Koch & Viola Richter).

ZSMC Zoologische Staatssammlung, München, Germany (Stefan Schmidt).

Photographs

At SAMC we used a Leica LAS 4.4 imaging system, which comprised a Leica® Z16 microscope with a Leica DFC450 Camera with 0.63× video objective attached. The

imaging process, using an automated Z-stepper, was managed using the Leica Application Suite V 4.4 software installed on a desktop computer. At BMNH, images were acquired using a Canon SLR EOS 5DSR with 65 mm macro lens mounted on a copy stand with an automated Z-stepper; images were aligned using Helicon Focus software version 6.6.1. Diffused lighting was achieved using techniques summarized in Buffington et al. (2005), Kerr et al. (2008), and Buffington and Gates (2009). All images presented in this paper, as well as supplementary images, are available at www.waspweb.org.

Results

Genaemirum Heinrich, 1936

Diagnosis (updated after Heinrich 1936, 1967). *Female*. Flagellum filiform, medium-sized and stout, not distinctly flattened and not to slightly widened beyond middle; head thick, temple long, wide and curved behind eyes; malar space very short, usually distinctly shorter than mandibular base; lower gena sometimes expanded backwards into more or less projecting protrusions; frons crossed by a laterally sinuate to acutely pointed transverse carina; oral and hypostomal carinae junction produced into a more or less strong triangular protuberance; mandible rather stout, upper tooth slightly to significantly longer than lower tooth; ventral margin of clypeus truncate to variably produced; mesoscutum moderately rounded with notaulus distinct on anterior third; scutellum flat to weakly convex, without lateral carina; propodeum long, in profile evenly and gently curved without distinct separation between anterior and posterior part, lateral areas curved down almost to base of hind coxa, median areas amalgamated into one elongate mid-longitudinal area which is not separated from post-scutellum; legs rather stout, hind coxa without scopa; fore wing with cu-a distal to Rs&M, areolet pentagonal and strongly narrowed anteriorly; first tergite with a distinct median field; second tergite and base of following tergites usually longitudinally sculptured; gastrocoelus deep, large; metasoma strongly oxypygous, apical margin of hypopygium remote from base of ovipositor sheath. *Male* (known for two species only). Sexual dimorphism very limited: flagellum more slender with tyloids, lower gena without protrusion, frons with transverse carina absent or very weak, pale markings more extensive.

Genotype. *Genaemirum mesoleucum* Heinrich, 1936.

Differential diagnosis. The gradual curve of the propodeum in profile is typical of the tribe Heresiarchini. The longitudinal confluence of the median propodeal areas, combined with the weakness of the basal furrow, is characteristic of several Afrotropical genera. *Genaemirum* is similar to *Coelichneumon* Thomson, 1893, absent from the Afrotropical region, in which the notauli are indistinct and the propodeum is shorter with areas basalis and superomedia separated. *Genaemirum* is also morphologically

similar to the Afrotropical genus *Afrocoelichneumon* Heinrich, 1938, in which the mid-longitudinal area of the propodeum is wider and the specialized structures of the female totally absent.

Biology. Heinrich (1967) did not speculate on exactly how the remarkable adaptations of the head could be associated with "some extraordinary biological features", but presumably the head is adapted to access the host in some unique way or is adapted for emerging from a particular substrate. Based on the oxygygous metasoma (the hypopygium is relatively short and ovipositor relatively long) and the biology of *Coelichneumon* species, *Genaemirum* species are likely to be idiobiont parasitoids of pupae. Many of the Carpenter moths (Cossidae), including the probable host of *P. phagocossorum*, pupate inside tunnels in wood (Gebeyehu et al. 2005, Plaut 1973), hence the head specializations exhibited by *Genaemirum* species are predicted to be an adaptation assisting the females to crawl down the galleries when searching for their host. It would be very interesting to see what the males look like in the species with very extravagant head ornamentation as this could shed light on the possible functional significance of the protuberances. However, in the two species where males are known (*G. varianum* and *G. phagocossorum*) the male head does not exhibit any morphological adaptations, suggesting that the underlying evolutionary drivers are acting on the females only. Selection for development of these facial protrusions would then stem from an increased functional ability to find hosts for oviposition, and are likely to have evolved to facilitate forward progress through the host caterpillars' frass that blocks their feeding tunnels. The females would need to negotiate these extended physical hurdles to reach the host pupae. The facial protrusions are very spade or blade-like in their form and we hypothesize that these protrusions act in a mechanical fashion, forcing the frass to open up, much like a road grader with an angled blade that pushes soil to the side.

Interestingly, Tom Huddleston's note in the BMNH copy of Heinrich's monograph indicates that some *Genaemirum* sp. individuals, identified by J.F. Perkins, were purportedly associated with *Eulophonotus myrmeleon* Felder (Lepidoptera: Cossidae). This ichneumonid genus is thus apparently associated with the cossid moth family. These specimens appear not to have been retained at BMNH and their identification is unknown, although Perkins apparently noted that these represented a species not included by Heinrich (1967).

Key to species (updated after Heinrich 1967)

Online Lucid identification keys are available at: www.waspweb.org



1 Male: known only for *G. varianum* (A) and *G. phagocossorum* (B).....2



– Female (a, b).....3



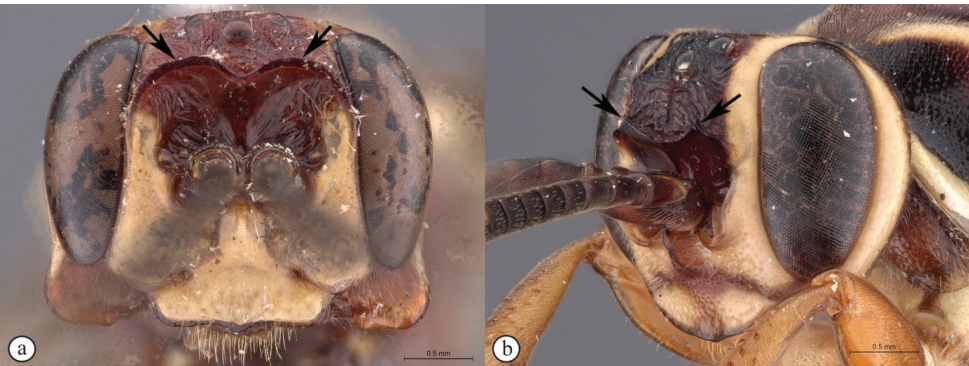
2 Metasoma yellowish-orange with tergite 1 dark reddish-brown (A); hind femur and tibia yellowish-orange (A); antennal scrobe extends to eye margins (B) *G. varianum* (Tosquinet)



– Metasoma uniformly dark reddish-brown (a); hind femur and tibia dark reddish-brown (a); antennal scrobe less extensive, ending an ocellar diameter from eye margins (b)..... *G. phagocossorum* Rousse, Broad & van Noort, sp. n.



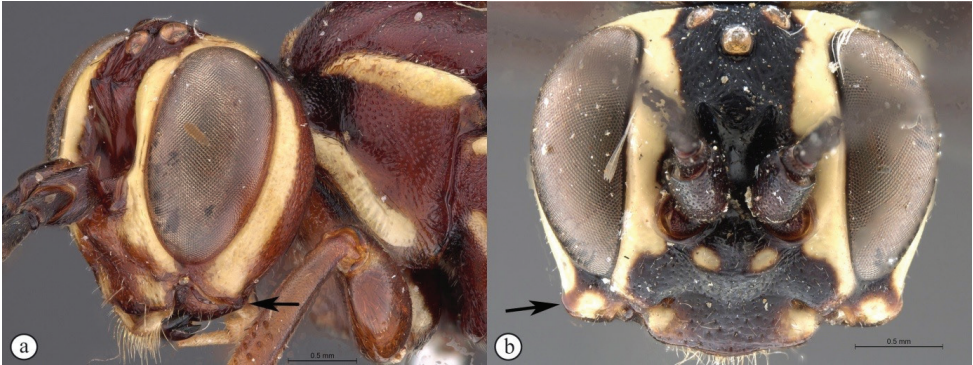
3 Frons with pronounced, horn-like projections pointed upward (A, B)4



– Frons with a bisinuate transverse lamella (a), that may have minor projections (b)7



- 4 Lower gena produced into a long spade-like protrusion (A, B); clypeus exceptionally expanded (A, B) 5



- Lower gena not expanded (a), or distinctly less expanded into a backward curved collar (b) 6



- 5 Clypeus apically slightly convex, gena moderately protruded (A); metasoma brownish-black (B) *G. doryalidis* Heinrich



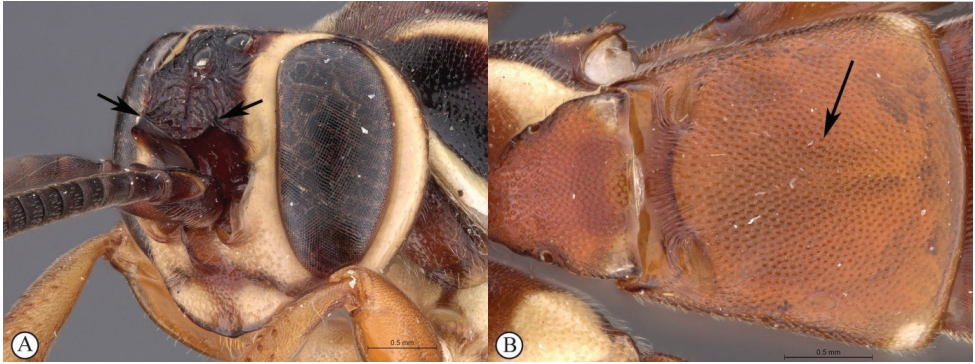
- Clypeus apically deeply emarginate, gena dramatically protruded (a); meta-soma yellowish-orange (b).....
..... *G. phacochoerus* Broad, Rousse & van Noort, sp. n.



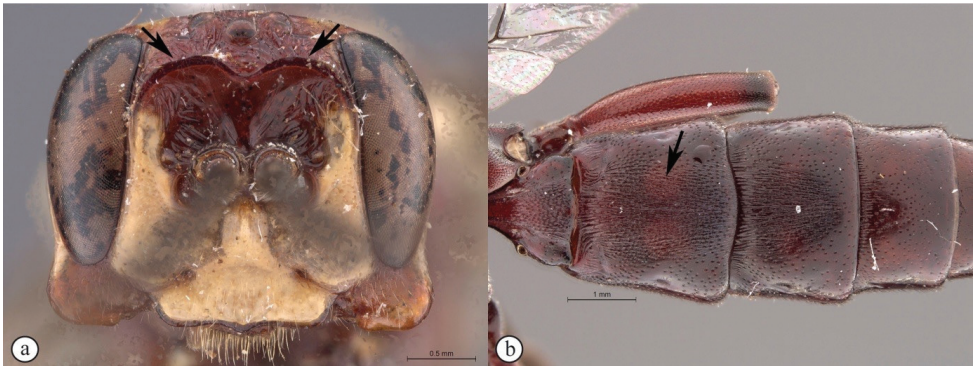
- 6 General coloration black (A); lower gena expanded into a backward curved collar (B).....*G. mesoleucum* Heinrich



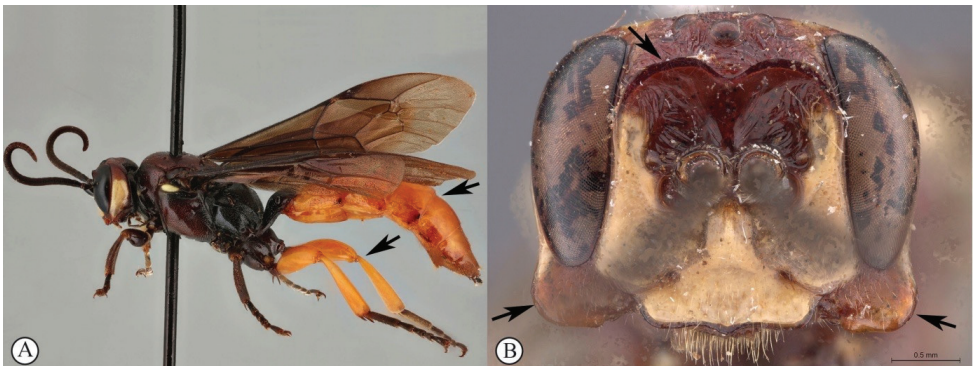
- General coloration dark red (a); lower gena not expanded (b).....
..... *G. vulcanicola* Heinrich



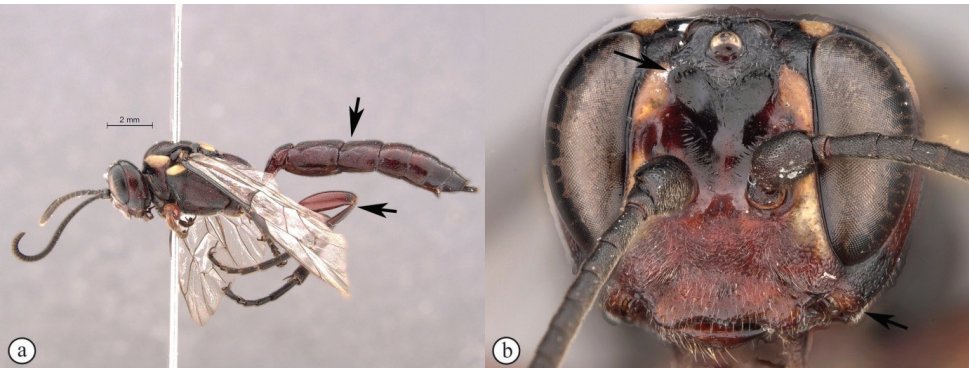
- 7 Frons with a forked, horn-like projecting carina above the antennal scrobes (A); second tergite medially punctate (B) *G. rhinoceros* Heinrich



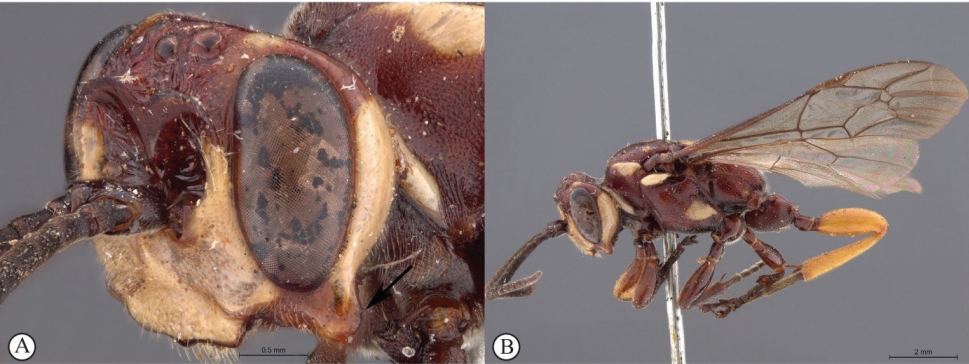
- Frons with a broad to acute cordate lamella above the antennal scrobes (a); second tergite medially longitudinally strigose (metasoma lacking in ♀ allotype of *G. varianum*, but ♂ holotype tergite is longitudinally strigose) (b) 8



- 8 Metasoma, hind femora and tibiae yellowish-orange (A); frons with a broad cordate lamella above the antennal scrobes (B)..... 9



- Metasoma, hind femora and tibiae reddish (a); frons with an acute cordate lamella above the antennal scrobes (b) *G. phagocossorum* Rousse, Broad & van Noort, sp. n.



- 9 Lower gena expanded into a backward curved, bluntly triangular, protuberance (A); wings hyaline (B) *G. varianum* (Tosquinet)



- Lower gena not expanded into a backward curved protuberance (a); wings infusate (b) *G. fumosum* Broad, Rousse & van Noort, sp. n.

Descriptions and diagnoses

Genaemirum phagocossorum Rouse, Broad & van Noort, sp. n.

<http://zoobank.org/64E4668F-C774-40B8-8D66-2FA090523F07>

Figs 1, 2

Type material. **HOLOTYPE** ♀: SOUTH AFRICA, Mpumalanga, Sappi Ndubazi plantation, near Machadadorp, N. 2006, B. Slippers, emerged from *Eucalyptus nitens* logs infested with cossid larvae of *Coryphodema tristis*, SAM-HYM-P025037a (SAMC). **PARATYPE**. 1♂ same label data, SAM-HYM-P025037b (SAMC).

Diagnosis. *Female*. Body length 16 mm. Black to dark reddish-brown overall with isolated yellow markings on head and mesosoma (pronotal shoulders, middle of mesoscutum, scutellum, dorsal section of mesopleuron below tegulae); vertex black with two small isolated lateral yellow spots, scrobe black dorsally and medially, dark reddish-brown laterally, separated from inner eye margins by yellow horizontal bands; lower face reddish-brown; legs black to dark reddish-brown; wings hyaline; antenna with 30 flagellomeres; lower gena not produced laterally; clypeus transverse, with ventral margin trisinuate; lower face reticulate, separated from upper face by a transverse ledge below toruli; upper frons and vertex smooth, with localised weak striations in an otherwise polished scrobe; scrobe dorsally demarcated by cordate raised sublamelliform carina; mesosoma sparsely punctate; metasoma sparsely punctate, polished, except for tergites 1-3, which are medially striate. *Male*. Body length 16 mm. Colouration similar to female except for face, which is dirty yellow with two black bands extending from toruli to clypeal-genal junction; vertex black with lateral yellow spots; gena with vertical yellow band adjacent to posterior eye margin; propodeum dorsally black; lower gena normal and frons without transverse carina; scrobe with horizontally curved striations; ocellar triangle reticulate, black; metasomal tergites more densely punctate than in female.

Differential diagnosis. The uniquely shaped cordate, sublamelliform raised carina dorsally demarcating the scrobe readily separates females of this new species from all the other described species, each of which has a diagnostically shaped horizontal carina, with various uniquely shaped projections in this region. The male is distinguishable from the only other known male (*G. varianum*) by the extent of the scrobe: extending to the inner eye margins in *G. varianum*, terminating laterally well before the inner eye margin in *G. phagocossorum*; scrobe sculpture, which is less extensive in *G. phagocossorum*; and overall body colour (body uniformly dark reddish-brown in *G. phagocossorum*; metasoma and hind femora and tibiae ochreous yellow, contrasting with dark reddish-brown head and mesosoma in *G. varianum*).

Etymology. From the latin “cossus” for “worm or grub found in wood”, which is the likely host (Cossidae), and “phago” = latin for “a glutton”. Noun in the genitive case.

Description. **FEMALE.** *Color.* Head dark reddish fading to black dorsally and on lower gena, with yellow markings: facial and frontal orbits and a postero-lateral isolated dot on vertex; mesosoma very dark reddish fading to black dorsally, with yel-

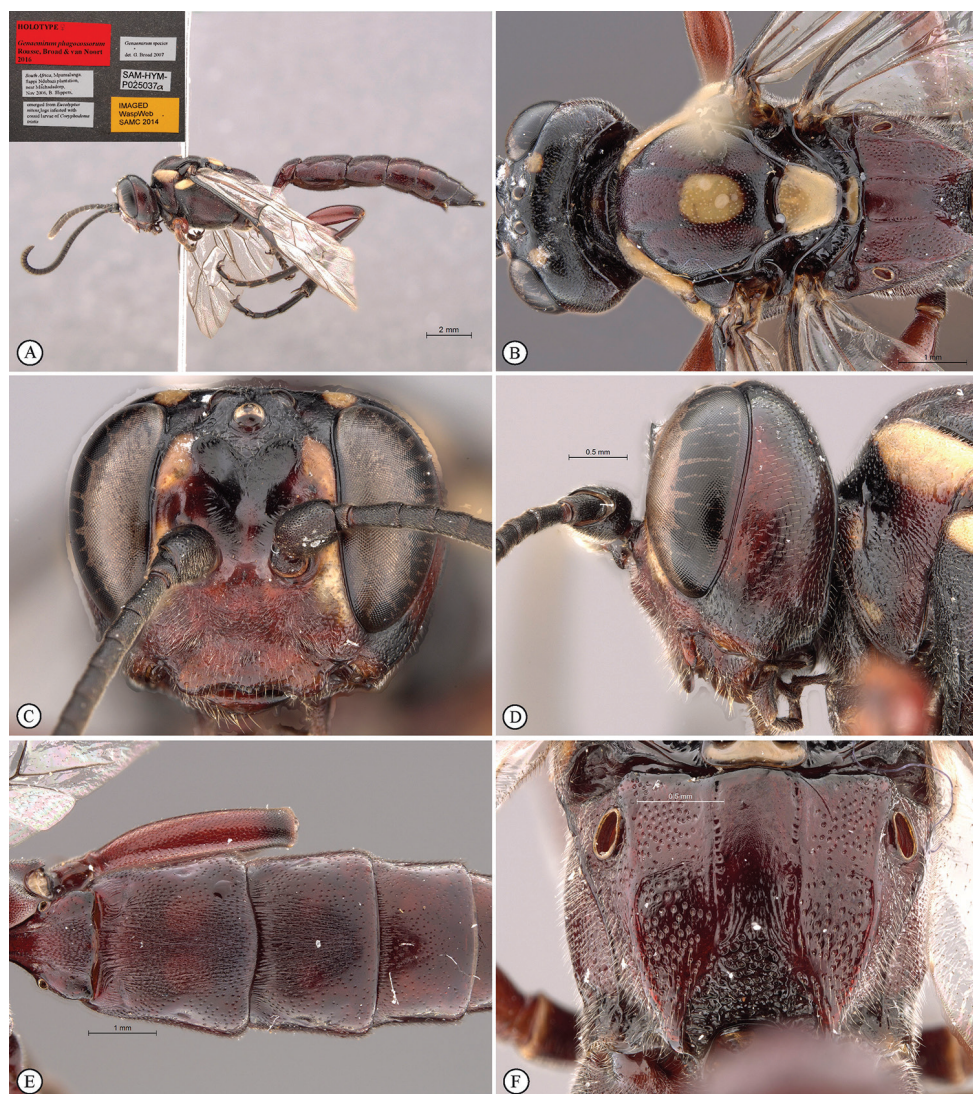


Figure 1. *Genaemirum phagocossorum* sp. n. Holotype female. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, mesosoma anterior-lateral view **E** metasomal tergites 1–4 dorsal view **F** propodeum, dorsal view.

low markings: dorsal margin of pronotum, subtegular ridge, centre of mesoscutum, scutellum and middle of metanotum; metasoma uniformly dark reddish; flagellum uniformly black; legs dark reddish, mid and hind tibiae and tarsi black; wings hyaline, venation testaceous to black.

Head. Mandible rather stout, mid-longitudinally densely punctate, teeth smoother with upper tooth about twice as long as lower tooth; malar space $0.5\times$ as long as mandible basal width; lower gena not expanded; occipital and hypostomal carinae joining

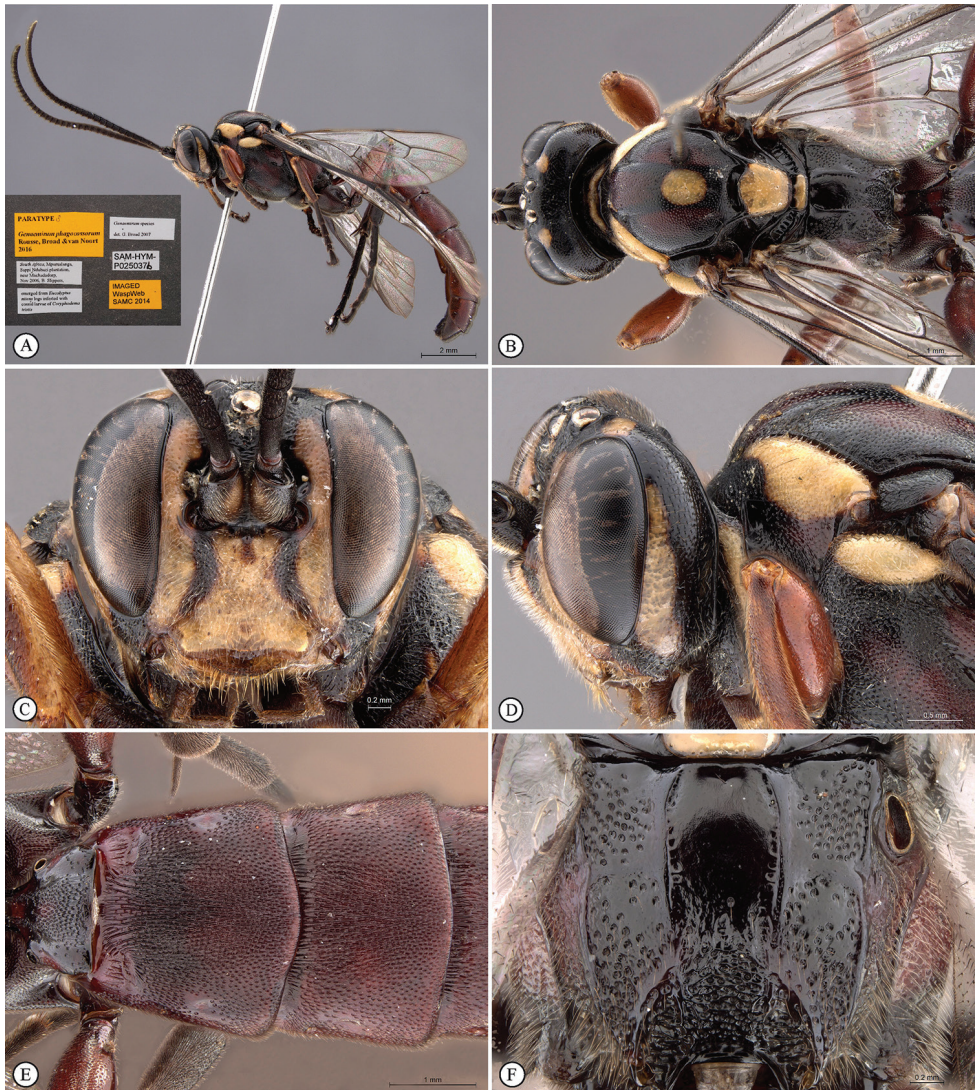


Figure 2. *Genaemirum phagocossorum* sp. n. Paratype male. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, mesosoma anterior-lateral view **E** metasomal tergites 1-4 dorsal view **F** propodeum, dorsal view.

at 0.6× basal mandible width before mandible, distinctly expanded at their junction into a blunt triangle; clypeus strongly transverse, about twice as wide as high, in profile flat, ventral margin with median and lateral lobes, unevenly punctate with punctation denser dorsally; face strongly transverse, about three times as wide as high, laterally punctate on coriaceous background, punctation denser medially on transversely rugose background; lower frons quite smooth, flat and steeply elevated above toruli, separated from upper frons by a bisinuate transverse carina; upper frons coarsely rugose; vertex

coriaceous with sparse punctures, punctation distinctly denser on inter-ocellar area; temple and gena densely punctate; temple moderately swollen behind eye; ocellar triangle wider than long, ocelli rather small, POL 1.0, OOL 1.3; antenna stout, widened slightly before middle, with 30 flagellomeres, basally elongate, flagellomeres 7–9 subquadrate, following flagellomeres transverse.

Mesosoma. Pronotum finely and densely punctate fading ventrally to coarsely longitudinally puncto-striate, pronotum collar enlarged and epomia strong; mesopleuron finely and densely punctate, somewhat rugose-punctate postero-ventrally, speculum barely smoother ventrally, posterior suture deeply crenulate, epicnemial carina nearly reaching pronotal margin below subtegular ridge, subtegular ridge strongly expanded; metapleuron densely and finely punctate, crenulate along pleural carina; mesoscutum evenly rounded, finely and densely punctate, notaulus distinct to anterior third, scuto-scutellar groove quite smooth; scutellum finely and more sparsely punctate, without lateral carina, quite flat in profile; propodeum typical of the genus, gently and evenly rounded in profile with median areas fused, carination distinct but very weak, densely punctate with punctation obsolescent mid-basally and distinctly coarser mid-posteriorly. *Legs*. Fore and mid tibiae with short and rather dense bristles along anterior faces, bristle sockets large and cupular.

Metasoma. Petiole with lateral and submedian dorsal carinae strong, abruptly enlarged into second tergite from level of spiracle; second tergite sparsely punctate laterally, medially longitudinally strigose; following tergites unevenly and sparsely punctate except tergite 2 medially and tergite 3 mid-basally longitudinally strigose; gastrocoelus deep, thyridia separated by 1.6× their own width; ovipositor sheath slightly protruding beyond metasomal apex.

MALE. Yellow markings more expanded, encompassing also mandible, clypeus, median face, genal orbits and pronotal collar; flagellum not widened with 33 flagellomeres, flagellomeres 7–14 with tyloids on outer surface and 6–32 with differentiated bristle mid-ventrally; lower frons transversely striate, transverse carina strongly attenuated; parameres simple; otherwise similar to female.

Biology. Reared from logs of *Eucalyptus nitens* (H. Deane & Maiden) Maiden (Myrtales: Myrtaceae), which were heavily infested with *Coryphodema tristis* (Drury) (Lepidoptera: Cossidae), but specific host association was not established. *Coryphodema tristis* is regarded as an agricultural pest in southern Africa because its host-plant range includes food crops, chiefly quince and apple trees (Rosales: Rosaceae, *Cydonia oblonga* Miller and *Malus pumila* Miller var. *domestica* Schneider). It is also considered to be a major forestry pest of *Eucalyptus nitens*, which is extensively cultivated in South Africa for the pulp and mining industry (Gebeyehu et al. 2005, Boreham 2006, Adam et al. 2013, Degefu et al. 2013). This likely host record suggests the potential for using *Genaemirum phagocossorum* sp. n. as a biocontrol agent of this pest species. However, the low number of reared specimens suggests that it is not a common parasitoid of this lepidopteran pest. See further discussion on biology under the genus treatment.

Distribution. South Africa.

***Genaemirum phacochoerus* Broad, Rousse & van Noort, sp. n.**

<http://zoobank.org/3A7FE578-617F-4ED3-B9EC-C4778D202B25>

Fig. 3

Type material. HOLOTYPE ♀: [TANZANIA] 'Mahali Peninsula. I 10.ix.1959. 2nd. Oxford U[niversity]. Exped[ition]. B.M. 1960-279.' 'Kungwe Camp: Forest clearing. 6'000ft.' (BMNH).

Diagnosis. *Female.* Body length 16 mm, fore wing length 13mm. Black mesosoma with large creamy-white markings on head and mesosoma and metasoma dull yellow beyond black first segment; face, large spot on upper vertex, lower edge of pronotum, scutellum, large oval patch on mesopleuron and spot on metapleuron all creamy-white; legs black except for dull reddish hind tibia; wings strongly infumate; antenna with 29 flagellomeres; lower gena produced laterally as a massive, rounded protuberance, concave and heavily rugose on outer side, with a triangular projection on its lower edge at half length; hypostomal carina produced as large, rounded triangular projection; clypeus slightly concave, corners elongate with edge deeply emarginate; lower face coriaceous, slightly concave, with pointed projection between antennal sockets; upper frons rugose; scrobe smooth, impunctate, with some weak rugae; scrobe dorsally demarcated by triangularly pointed projections; mesosoma mostly coriaceous, sparsely punctate; metasoma with sparse but distinct punctures, coriaceous, except tergites 2-3 medially strigose. *Male.* Unknown.

Differential diagnosis. The unique clypeus, which is deeply emarginate with long, sharp corners, and the exceedingly long, strongly sculptured genal protuberance, makes this a distinctive species, with the most extreme head ornamentation that we have seen in *Genaemirum* (or any ichneumonid). The European *Auritus elephas* (Brauns) has genae expanded in a similar, but less extreme, fashion; however, we have only seen illustrations of this species (Tereshkin 2004). The colour pattern (yellow metasoma and infusate wings) is also distinctive compared to *G. doryalidis*, which is the closest congener in its head ornamentation.

Etymology. The name is derived from the genus name for warthogs, after the resemblance of the head to that of a warthog. Noun in apposition.

Description. FEMALE. *Color.* Head black with face and large spot on vertex creamy-white, with narrow black border to clypeus and gena; mesosoma black, with creamy-white markings; anterior margin of pronotum (except medially), median 2/3 of mesopleuron, scutellum and large spot on posterior half of metapleuron; metasoma with first segment black, remainder dull yellow, paler posteriorly; flagellum uniformly black; legs black except hind tibia dull reddish brown, fore tibia brown on inner edge; wings infusate, venation black, pterostigma pale brown; setae mostly pale, inconspicuous, but many setae on 6th and 7th tergites black.

Head. Mandible rather stout, slightly concave on outer aspect, mid-longitudinally punctate, teeth smoother with upper tooth about 2.5× as long as lower tooth; malar space 1.2× as long as mandible basal width; lower gena massively expanded as an elon-



Figure 3. *Genaemirum phacochoerus* sp. n. Holotype female. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, mesosoma anterior-lateral view **E** metasomal tergites 1-4 dorsal view **F** propodeum, dorsal view.

gate protuberance, apically rounded, concave and rugose on outer aspect with triangular projection on lower edge; in frontal view, genae ventrally diverging so that maximum breadth is $1.1\times$ head width at widest point of eyes; ventral portion of occipital carina difficult to trace, one branch meets hypostomal carina far from base of mandible, another branch turned abruptly anterior then deflected to mandible base, delimiting strongly emarginate area on lower vertex; hypostomal carina distinctly expanded at apparent junction with occipital carina into a large, blunt, roughly equilateral triangle; clypeus about $0.9\times$ as wide as high (measured at maximum height of projections from

tentorial pits and width at tentorial pits), in profile slightly concave, not differentiated from face, ventral margin with elongate lateral lobes, face and clypeus coriaceous with punctures denser on clypeus, separated by 1.5–2× puncture width; upper face with conical projection between antennal sockets; lower frons quite smooth, flat and steeply elevated above toruli, with some rounded rugae forming a V-shaped slightly raised area medially, separated from upper frons by a transverse carina extended laterally into sharply pointed projections; upper frons coarsely rugose, rugose-striate around ocelli; vertex coriaceous with sparse punctures; temple distinctly narrowed behind eye; occipital carina raised, distinctly lamellar ventrally; ocellar triangle wider than long, ocelli rather small, POL 1.25, OOL 1.7; antenna stout, widened and slightly flattened medially, thinner apically, with 29 flagellomeres, first flagellomere 1.7× as long as apically wide, second 1.0× as long as wide, then widening towards middle with 8th flagellomere 0.7× as long as wide.

Mesosoma. Pronotum ventrally finely and densely punctate fading dorsally to sparsely striate, pronotum collar rugose-striate, epomia strong; mesopleuron bulging, strongly convex, mostly coriaceous, smooth and shining posteriorly, speculum barely differentiated, epicnemium finely and densely punctate, otherwise mesopleuron scarcely punctate, posterior suture deeply crenulate, epicnemial carina nearly reaching pronotal margin below subtegular ridge, dorsally fading into striations, area below strongly rounded, expanded subtegular ridge rugose-striate; metapleuron coriaceous with large punctures, denser dorsally, crenulate along pleural carina; mesoscutum evenly rounded, mesoscutum and scutellum (mesoscutellum) coriaceous with very fine, sparse punctures, notaulus narrow, deep, distinct to anterior third, scuto-scutellar groove quite smooth, deep and narrow, scutellar margin overhanging; scutellum with lateral carina to about 2/3 of length, quite flat in profile; propodeum typical of genus, gently and evenly rounded in profile with median areas fused, carination distinct, enclosing elongate central area that is 2.2× wider posteriorly than anteriorly, densely punctate with punctuation obsolescent mid-basally, coriaceous anteriorly and over entire area basalis+superomedia. *Legs.* Fore and mid tibiae with short and rather dense bristles along anterior faces, bristle sockets large and cupular.

Metasoma. Petiole with lateral and submedian dorsal carinae strong, abruptly enlarged into second tergite from level of spiracle, petiole coriaceous dorsally, more weakly sculptured on apex of postpetiole where sparsely punctate and faintly striate medially, tergite laterally strongly rugose; remainder of metasoma weakly coriaceous, more shining posteriorly, second tergite sparsely punctate laterally, medially longitudinally strigose; following tergites unevenly and sparsely punctate except tergite 2 medially and tergite 3 antero-medially longitudinally strigose, 4th tergite with short area of median, anterior striae; gastrocoelus deep, thyridia separated by 1.7× their own width; 6th and 7th tergites with strong setae; ovipositor sheath slightly protruding beyond metasomal apex.

MALE. Unknown

Biology. Unknown, but see discussion on biology under the genus treatment.

Distribution. Tanzania.

***Genaemirum fumosum* Broad, Rousse & van Noort, sp. n.**

<http://zoobank.org/75AB3798-E301-4AF0-BDC3-E5562E6F2A8D>

Fig. 4

Type material. HOLOTYPE ♀: [SOUTH AFRICA] 'NISSV. Nelspruit 4/2/72 E. de Villiers', '*Genaemirum* sp. ♀ det. T. Huddleston, 1972' (BMNH).

Diagnosis. *Female.* Body length 16 mm, fore wing length 11 mm. Dark red mesosoma with creamy-white subtegular ridge and black propodeum; face, clypeus, lower 2/3 of vertex, spot on anterior edge of pronotum, all creamy-white; legs dark reddish brown to black except for dull yellow hind femur and tibia; metasoma dull yellow beyond black first segment; wings strongly infumate; antenna with 27 flagellomeres; lower gena slightly produced laterally as distinct 'corners' to the face in frontal view, gena flattened and produced posteriorly; hypostomal carina raised; clypeus flat, corners slightly produced so medially concave, with pointed tooth centrally; lower face densely punctate, with blunt projection between antennal sockets; upper frons rugose; scrobe smooth, impunctate; scrobe dorsally demarcated by raised, arched lamella, medially incised; mesosoma largely punctate, except mesoscutum, smooth and shining; metasoma weakly coriaceous, with sparse but distinct punctures, tergites 2-3 medially strigose, 4th tergite strigose antero-medially, postpetiole medially striate. *Male.* Unknown.

Differential diagnosis. Amongst *Genaemirum* species with a bisinuate, raised lamella above the antennal scrobes, *G. fumosum* sp. n. can be distinguished from *G. phagocossorum* sp. n. and *G. varianum* on colour pattern and by the shape of the gena; unlike *G. phagocossorum* sp. n. the metasoma and hind legs are largely dull yellow, as in *G. varianum*, although *G. fumosum* sp. n. differs from the latter in the more restricted pale markings on the mesosoma and in the more strongly infusate wings, as well as the much more weakly produced gena. It shares with *G. phacochoerus* the overall colour pattern, including the infusate wings, but differs markedly in head structure.

Etymology. The name is derived from the Latin for "smoky", in reference to the infusate wings. Noun in apposition.

Description. FEMALE. *Color.* Head reddish brown with face and ventral 2/3 of vertex creamy-white, with narrow red border to clypeus; mesosoma dark reddish brown, with creamy-white subtegular ridge and small spot at ventral end of epomia, tegula, carinae at edge of scuto-scutellar groove, metascutellum, propodeum and metapleuron black; metasoma with first segment black, remainder dull yellow; flagellum uniformly black; legs with mid and hind coxae proximally black, fore and mid legs dark brown to black with fore tibia pale brown on inner side, mid tibia brown on inner side, hind leg with trochanter and trochantellus dark reddish brown, femur and tibia dull yellow, tarsus black; wings infusate, venation dark brown (apically) to black, pterostigma black; setae mostly pale.

Head. Mandible rather stout, slightly concave on outer aspect, mid-longitudinally punctate, teeth smoother with upper tooth about twice as long as lower tooth; malar space 0.45× as long as mandible basal width; lower gena flattened and triangularly produced posteriorly, forming a partial genal bridge across the hypostoma, anteriorly,



Figure 4. *Genaemirum fumosum* sp. n. Holotype female. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, mesosoma anterior-lateral view **E** metasomal tergites 1-4 dorsal view **F** propodeum, dorsal view.

gena produced as a low, pointed projection; occipital carina ventrally meeting hypostomal carina distant from mandible base by $1.25\times$ basal width of mandible; hypostomal carina raised, lamelliform; clypeus $2.6\times$ as wide as medially high, flat, not differentiated from face, ventral margin with weakly produced lateral lobes and strong, pointed, median tooth, face and clypeus shining, densely punctate, especially medially, with blunt projection between antennal sockets, face $3.9\times$ as wide as high; lower frons entirely smooth, flat and steeply elevated above toruli, separated from upper frons by a

smoothly curved lamella, raised laterally, incised medially; upper frons coarsely rugose-striate, including between ocelli, some punctures between lateral ocelli; vertex smooth, very faintly coriaceous, with very inconspicuous, sparse punctures; temple about as wide as eye, roundly narrowed behind eyes; occipital carina sharp, lamellate ventrally; ocellar triangle wider than long, ocelli rather small, POL 1.3, OOL 1.2; antenna stout, widened medially, thinner apically, with 27 flagellomeres, first flagellomere 1.3× as long as apically wide, second 1.0× as long as wide, then widening towards middle with 8th flagellomere 0.7× as long as wide.

Mesosoma. Pronotum densely punctate, shining with some rugosity posteriorly, ventrally, pronotum collar matt, epomia strong until just above transverse groove; mesopleuron a little bulging, mostly shining, densely punctate, speculum differentiated, unsculptured, epicnemium with finer, denser punctation, posterior suture deeply crenulate, epicnemial carina fading away distant from mid-height of pronotal margin, subtegular ridge rounded, expanded; metapleuron shining, densely punctate although punctation weaker centrally, short crenulations along pleural carina; mesoscutum evenly rounded, mesoscutum and scutellum (mesoscutellum) finely coriaceous, mesoscutum impunctate, scutellum with scattered punctures, notaulus narrow, distinct to anterior third, scuto-scutellar groove quite smooth, deep and narrow, scutellar margin overhanging; scutellum with lateral carina not extending beyond scuto-scutellar groove; propodeum typical of genus, gently and evenly rounded in profile with median areas fused, carination distinct except medially, enclosing elongate central area that is 1.7× wider posteriorly than anteriorly, shining and densely punctate with punctation obsolescent mid-basally, punctation very dense bordering pleural carina; *Legs*. Fore and mid tibiae with short and rather dense bristles along anterior faces, bristle sockets large and cupular.

Metasoma. Petiole with lateral and submedian dorsal carinae strong, abruptly enlarged into second tergite from level of spiracle, shining, postpetiole striate, punctate posteriorly, tergite laterally rugose-punctate; remainder of metasoma weakly coriaceous with distinct punctures, especially laterally on 2nd and 3rd tergites, medially longitudinally strigose; following tergites unevenly and sparsely punctate except tergite 4 antero-medially longitudinally strigose; gastrocoelus deep, thyridia separated by 2× their own width; 6th and 7th tergites with strong setae; ovipositor sheath slightly protruding beyond metasomal apex.

MALE. Unknown

Biology. Unknown, but see discussion on biology under the genus treatment.

Distribution. South Africa.

Genaemirum doryalidis Heinrich, 1967

Fig. 5

Material examined. Holotype ♀: Type [red bordered circular label], Holotype [red label], KENYA, Kenya Forest Department, K. Elburgon, L0.704, ex *Dovyalis abyssinica*,

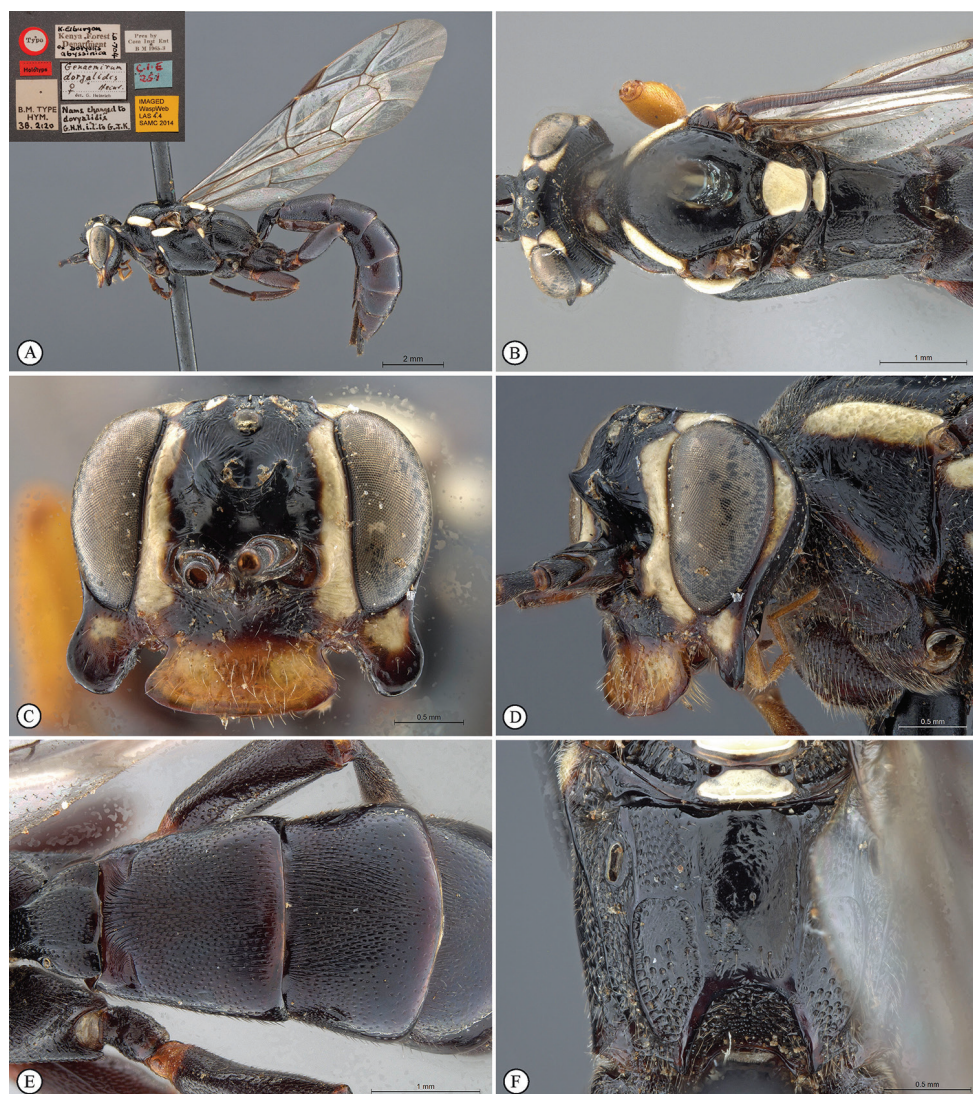


Figure 5. *Genaemirum doryalidis* Heinrich. Holotype female. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, mesosoma anterior-lateral view **E** metasomal tergites 1-4 dorsal view **F** propodeum, dorsal view.

Pres by Com Inst Ent BM 1965-3, C.I.E. 251, B.M. TYPE HYM. 3B.2120, *Genaemirum doryalidis* det. G. Heinrich, Name changed to *doryalidis* G.H.H. i.l. to G.J.K., Imaged WaspWeb LAS 4.4 SAMC 2014 [yellow label] (BMNH).

Diagnosis. *Female.* Body length 14 mm. Black with numerous white markings on head and mesosoma, fore leg orange from femur, and tergites 2–7 apically reddish; flagellum broken; lower gena extraordinarily expanded into flat, spade-shaped protuberance; clypeus strongly enlarged, considerably longer than face, widened and bent

upward toward apex, concealing mandible and labrum in frontal view; frons rugose with two horn-like protuberances pointing upward; basal tergites longitudinally striate medially. *Male*. Unknown.

Biology. Associated with *Dovyalis abyssinica* Warb. (Malpighiales: Salicaceae). See discussion on biology under the genus treatment.

Distribution. Kenya.

***Genaemirum mesoleucum* Heinrich, 1936**

Fig. 6

Material examined. Holotype ♀: Typus [red label], KENYA Camp III de l'Elgon, Zone des Bruyères, est 3.500 m, Museum de Paris, Mission de l'Omo, C. Arambourg, P.A. Chappuis & R. Jeannel, 1932–33, *Genaemirum mesoleucum* ♀ det. G. Heinrich, Imaged WaspWeb LAS 4.4 SAMC 2014 [yellow label] (MNHN).

Diagnosis. *Female*. Body length 14 mm. Black, with dorsal white markings on head and mesosoma; flagellum with a whitish median ring; antenna with 33 flagellomeres; hypostomal carina extended onto malar space, expanded into a backward curved blunt triangle over lower gena; clypeus transverse, apical margin subtruncate; lower frons smooth, separated from upper frons by a transverse acutely M-shaped carina; upper frons rugose; ventral junction of occipital and hypostomal carinae moderately expanded, triangular; tergites 1–4 longitudinally striate medially. *Male*. Unknown.

Biology. Unknown, but see discussion on biology under the genus treatment.

Distribution. Kenya.

***Genaemirum rhinoceros* Heinrich, 1967**

Fig. 7

Material examined. Holotype ♀: Holotype [red label] UGANDA, Zika Forest, Mengo, xi.18 '63, G.A. Lancaster, Typus Nr. Hym. 436 Zoologische Staatssammlung München [red label], Zoologische Staatssammlung München, Type-No.: ZSM-Hym-00254 [pink label], *Genaemirum rhinoceros* det G. Heinrich, Imaged WaspWeb LAS 4.4 SAMC 2015 [yellow label] (ZSMC).

Diagnosis. *Female*. Body length 15 mm. Head and mesosoma bright red interspersed with numerous large yellow markings; metasoma and legs yellowish-orange with coxae largely white; flagellum darker with a white median ring; antenna with 35 flagellomeres; hypostomal carina extended onto malar space, expanded into a backward curved blunt triangle over lower gena; clypeus lenticular, without differentiated ventro-lateral corners; face with a mid-longitudinal, horn-like, projecting lamella; lower frons smooth and short, separated from upper frons by a transverse M-shaped



Figure 6. *Genaemirum mesoleucum* Heinrich. Holotype female. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, pronotum lateral view **E** metasomal tergites 1-4 dorsal view **F** propodeum, dorsal view.

carina; upper frons with a differentiated rugose, triangular and shield-shaped surface; ventral junction of occipital and hypostomal carinae moderately expanded, triangular; tergites almost entirely punctate, without longitudinal sculpture except between gastrocoeli. *Male*. Unknown.

Biology. Unknown, but see discussion on biology under the genus treatment.

Distribution. Uganda.

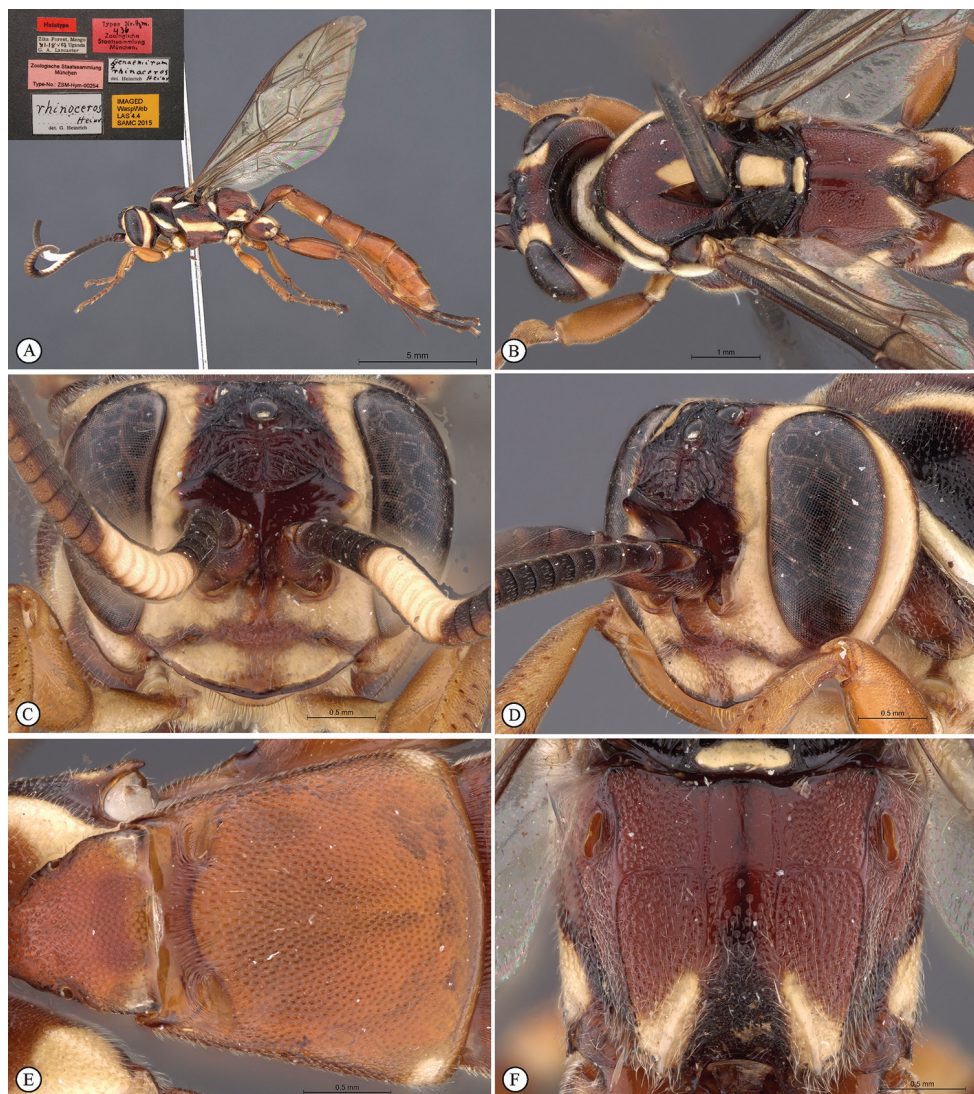


Figure 7. *Genaemirum rhinoceros* Heinrich. Holotype female. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, pronotum anterior-lateral view **E** metasomal tergites 1-2 dorsal view **F** propodeum, dorsal view.

Genaemirum varianum (Tosquinet, 1896)

Figs 8, 9

Amblyteles varianus Tosquinet, 1896: 97

Material examined. Holotype ♂: [South Africa] Type [red label], typus [red bordered label], Capland, Krebs., Zool. Mus. Berlin, 9213, ♂ *Amblyteles varianus* Tosquinet,

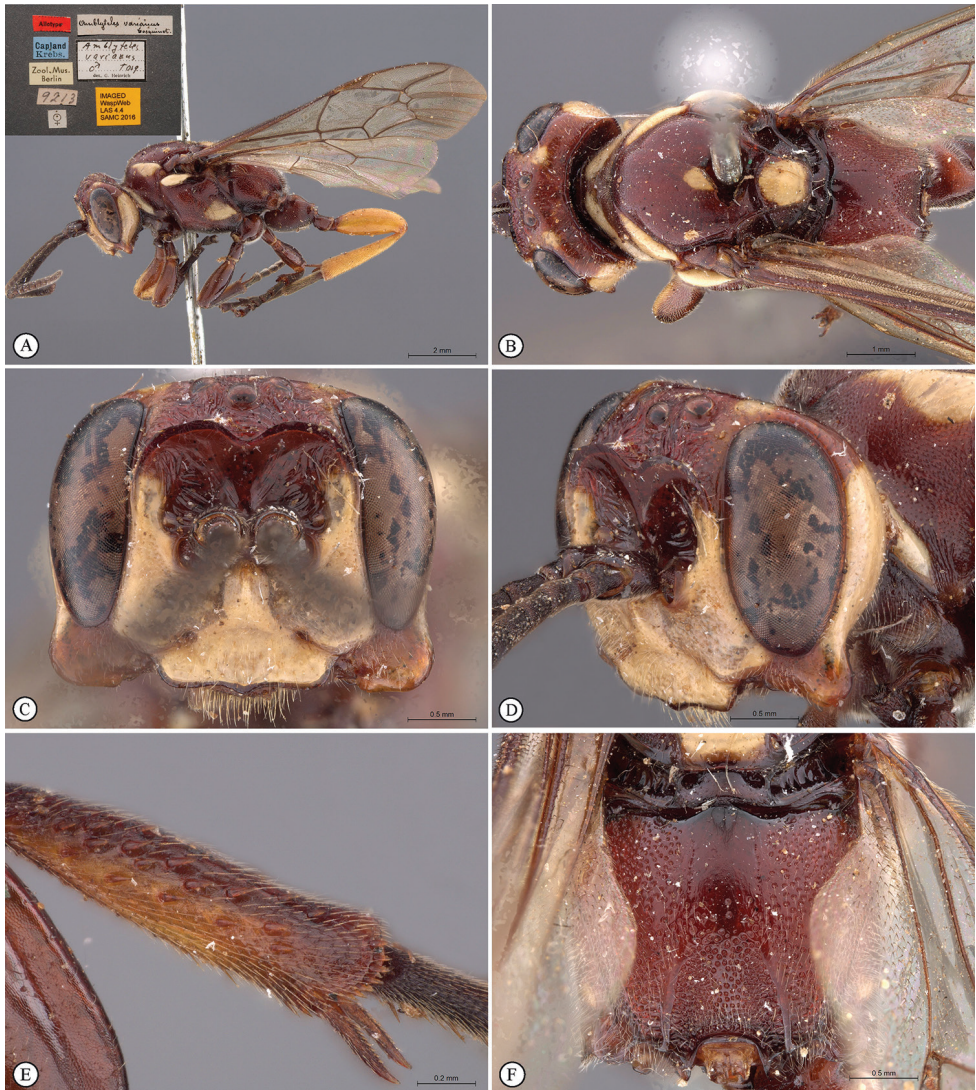


Figure 8. *Genaemirum varianum* (Tosquinet). Paratype female. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, pronotum anterior-lateral view **E** fore-tibial armature **F** propodeum, dorsal view.

Imaged WaspWeb LAS 4.4 SAMC 2016 [yellow label] (ZMHB). **Paratype** (Allotype) ♀: [South Africa] Allotype [red label] Capland, Krebs, Zool. Mus. Berlin, 9213, ♀ *Amblyteles varianus* det. G. Heinrich, Imaged WaspWeb LAS 4.4 SAMC 2016 [yellow label] (ZMHB).

Diagnosis. *Female.* Head and mesosoma red with white markings, mesosoma ventrally blackish; legs yellow with coxae red; antenna short with 26 flagellomeres; lower gena produced laterally in a blunt triangle curved backwards; ventral junction

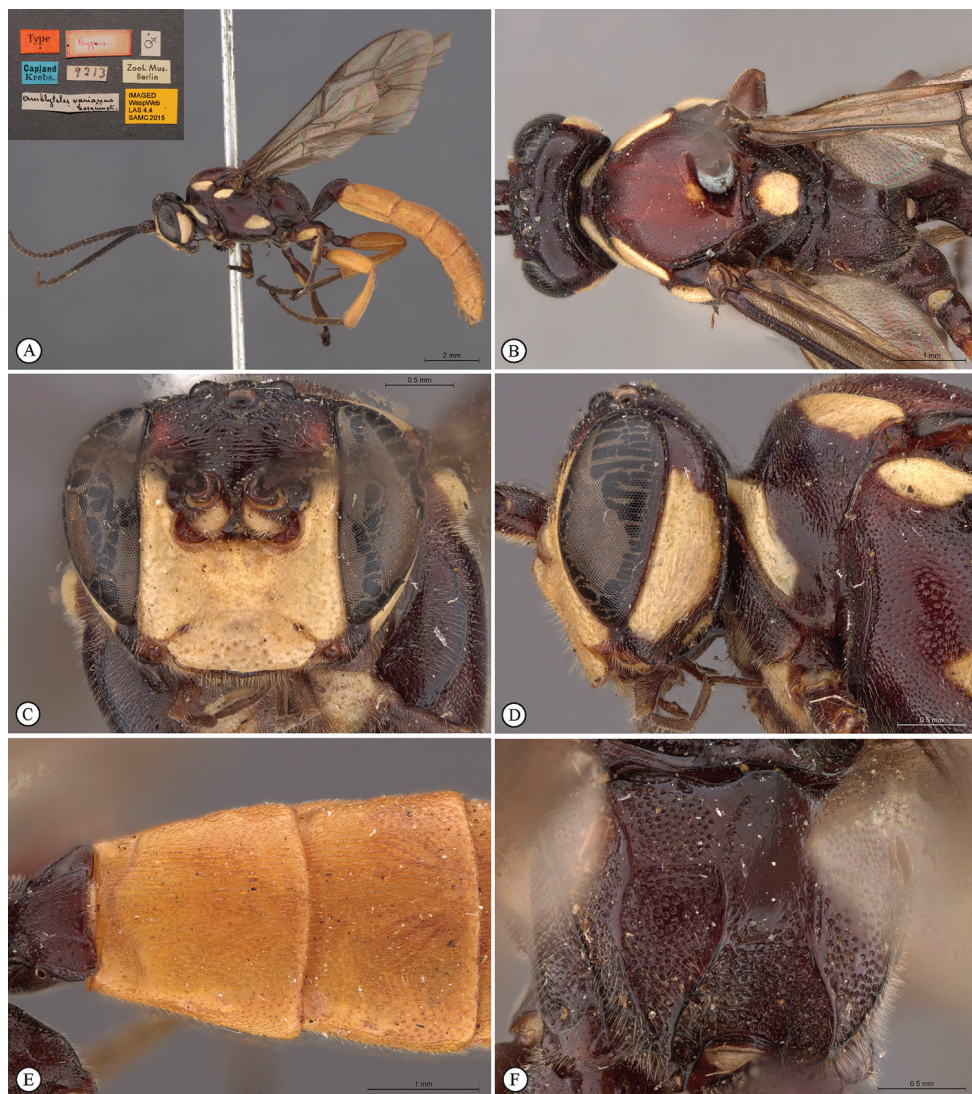


Figure 9. *Genaemirum varianum* (Tosquinet). Holotype male. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, mesosoma anterior-lateral view **E** metasomal tergites 1-4 dorsal view **F** propodeum, dorsal view.

of occipital and hypostomal carinae sharply expanded, triangular; clypeus transverse, about rectangular with ventral margin subtruncate, with a blunt median tooth; lower frons smooth, separated from upper frons by a transverse bisinuate carina; upper frons and vertex multi-directionally striate; mesosoma punctate; metasoma lacking in the type (and only known) female. *Male*. Body length 15 mm. Head and mesosoma black with numerous white markings, except for mesoscutum red and centrally white



Figure 10. *Genaemirum vulcanicola* Heinrich. Holotype female. **A** habitus lateral view (inset: data labels) **B** head, mesosoma, dorsal view **C** head anterior view **D** head, mesosoma anterior-lateral view **E** metasomal tergites 1-4 dorsal view **F** propodeum, dorsal view.

marked; metasoma yellow with tergite 1 black; legs yellow, basally and apically black, with white markings on fore and mid coxae; lower gena without expansion and frons without transverse carina, but ventral junction of carinae similarly pointed.

Biology. Unknown, but see discussion on biology under the genus treatment.

Distribution. South Africa.

***Genaemirum vulcanicola* Heinrich, 1967**

Fig. 10

Material examined. Holotype ♀: Holotype [red label] [TANZANIA] TANGANYIKA, Rungwe Mts., 2600 m, 12.XI.62, Typus Nr. Hym. 435 Zoologische Staatssammlung München [faded red label], Zoologische Staatssammlung München, Type-No.: ZSM-Hym-00253 [pink label], *Genaemirum vulcanicola* ♀ det. G. Heinrich, Imaged WaspWeb LAS 4.4 SAMC 2016 [yellow label] (ZSMC). 1 ♀, ‘Meru’, van Someren, VII.1943, V.G.L. van Someren collection, Brit. Mus. 1959-468 [there are towns called Meru in Kenya and Tanzania and van Someren’s collection is recorded only as being from East Africa, although Tanzania is perhaps more likely, as an ex-German colony] (BMNH).

Other material. A female from South Africa (Natal: Kloof, 1500ft, VIII.1926, R.E. Turner) in BMNH is smaller and paler red than other specimens and has more abundant yellow markings, but is structurally very similar to the holotype and non-type female examined. We tentatively refer this specimen to *G. vulcanicola*.

Diagnosis. *Female.* Body length 14 mm. Bright red overall with numerous yellow markings; flagellum darker with a white median ring; antenna with 37 flagellomeres; lower gena not expanded; clypeus transverse, about rectangular with ventral margin subtruncate; lower frons rugose, with two acute horn-like protuberances pointing upwards dorsally; ventral junction of occipital and hypostomal carinae expanded, pointed; tergites 1–4 longitudinally striate medially. *Male.* Unknown.

Biology. Unknown, but see discussion on biology under the genus treatment.

Distribution. South Africa, Tanzania.

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A preliminary account of the fly fauna in Jabal Shada al-A'la Nature Reserve, Saudi Arabia, with new records and biogeographical remarks (Diptera, Insecta)

Magdi S. El-Hawagry¹, Mahmoud S. Abdel-Dayem^{1,2},
Ali A. Elgharbawy², Hathal M. Al Dhafer²

1 Entomology Department, Faculty of Science, Cairo University, Giza 12613, Egypt **2** Plant Protection Department, College of Food and Agriculture Sciences, King Saud University, Riyadh 11451, PO Box 2460, Kingdom of Saudi Arabia

Corresponding author: Magdi S. El-Hawagry (elhawagry@gmail.com)

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Abstract

The first list of insects of Al-Baha Province, Kingdom of Saudi Arabia (KSA) was published in 2013 and contained a total of 582 species; an addendum to this list was published in 2015 adding 142 species and bringing the total number recorded from the province to 724 insect species representing 17 orders. The previous two studies excluded Jabal Shada al-A'la Nature Reserve (SANR), so the present study in SANR, as belonging to Al-Baha Province, are complementary to the previous two. The present study presents a preliminary list of Diptera (Insecta) in SANR, with remarks on their zoogeography, and is the first of a series of planned ecological and systematic studies on different insect orders as one of the outputs of a project proposed to study the entire insect fauna of SANR.

A total number of 119 Diptera species belonging to 87 genera, 31 tribes, 42 subfamilies, and representing 30 families has been recorded from SANR in the present study. Some species have been identified only to the genus level and listed herein only because this is the first time to record their genera in KSA. Fourteen of the species are recorded for the first time for KSA, namely: *Forcipomyia sahariensis* Kieffer, 1923 [Ceratopogonidae]; *Chaetosciara* sp. [Sciaridae]; *Neolophonotus* sp.1; *Neolophonotus* sp.2; *Promachus sinaiticus* Efflatoun, 1934; *Saropogon longicornis* (Macquart, 1838); *Saropogon* sp. [Asilidae]; *Spogostylum tripunctatum* (Pallas in Wiedemann, 1818) [Bombyliidae]; *Phycus* sp. [Therevidae]; *Hemeromyia* sp.; *Meoneura palaestinensis* Hennig, 1937 [Carnidae]; *Desmometopa inaurata* Lamb, 1914 [Milichiidae]; *Stomoxys niger* Macquart, 1851 [Muscidae]; and *Sarcophaga palestinensis* (Lehrer, 1998) [Sarcophagidae].

Zoogeographic affinities of recorded fly species suggest a closer affiliation to the Afrotropical region (46%) than to the Palearctic region (23.5%) or the Oriental region (2.5%). This supports the previous studies' conclusions and emphasizes the fact that parts of the Arabian Peninsula, including Al-Baha Province, ought to be a part of the Afrotropical Region rather than of the Palearctic Region or the Eremic Zone.

Keywords

Afrotropical, Al-Baha Province, Al-Sarah, Al-Sarawat Mountains, Arabian Peninsula, Eremic Zone, fly species, new records, Palearctic, Tihama

Introduction

Al-Baha Province (Fig. 1) is situated in the south-western part of the Kingdom of Saudi-Arabia (KSA) between the Holy Makkah and Asir provinces. It is the smallest province in KSA (approximately 10,362 km²), situated at 41–42° E and 19–20° N. It is characterized by natural tree cover (El-Juhany and Aref 2013) and agricultural plateaus. Huge and steep rocky mountains divide the province into two main sectors, a mountainous area known as 'Al-Sarat' or 'Al-Sarah' with an elevation of 1500–2450 m above sea level at the east forming a part of Al-Sarawat Mountains range, and a lowland coastal plain in the west, known as 'Tihama'. The second sector, Tihama, is divided into two districts, Al-Mekhwa and Qelwa (Alahmed et al. 2010, El-Hawagry et al. 2013, 2015). Jabal Shada al-A'la Nature Reserve (SANR) lies between latitudes 19.8149N–19.8763N and longitudes 41.2855E–41.3501E (Fig. 1). It is an isolated granite mountain massif made up of jagged spires and pinnacles, located in Al-Mekhwa district, 20 km to the south-west of Al-Mekhwa city, the capital of the district. It is a dissonant of the Sarawat Escarpment in the foothills of Tihama, measuring 68.62 square kilometers. Its location and its altitudinal range from 490 to 2,222 meters above sea level ensures high rainfall, a wide range of micro-climates, and a high level of biological diversity (SWA 2016).

In the lowland coastal plain, Tihama, the climate is hot in summer, warm in spring and mild in winter, with less than 100 mm of annual rainfall. In the mountainous area, Al-Sarah, the weather is generally cooler due to high altitude, in addition to the formation of clouds and fog accompanied by thunderstorms in winter, with a rainfall average of 405 mm annually (Ibrahim and Abdoon 2005; El-Hawagry and Al Dhafer 2015). The climate in SANR is intermediate between the climates in these two sectors, with a rainfall average of approximately 200 mm annually (Fig. 2).

SANR, as an isolated mountain massif, supports an exceptionally rich flora; with approximately 500 plant species recorded, including 63 key plant taxa including endemics and Afrotropical relicts, it is the site of highest botanical diversity known in Saudi Arabia. The exceptional floral diversity of SANR, together with the presence of griffon vultures and endemic birds of the southwestern mountains and carnivores such as, the Arabian red fox [*Vulpes vulpes arabica* Thomas, 1902], Arabian caracal [*Caracal caracal schmitzi* (Matschie, 1912)], striped hyaena [*Hyaena hyaena sultana* (Pocock,

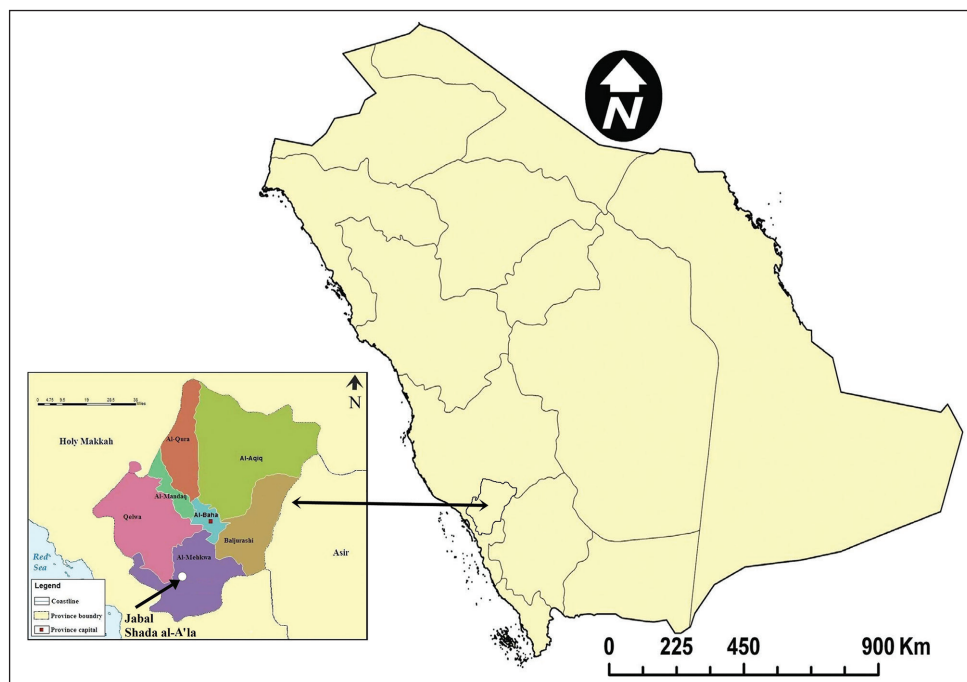


Figure 1. Map of Saudi Arabia showing Al-Baha Province and Jabal Shada al-A'la Nature Reserve.

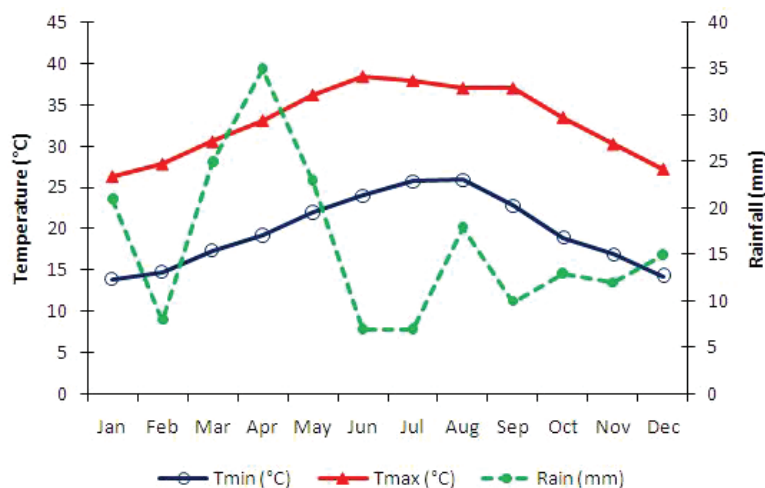


Figure 2. Monthly average temperatures and rainfall in 50 years (1950–2000). In Jabal Shada al-A'la Nature Reserve (Worldclim database: <http://www.worldclim.org/>).

1934)], Arabian wolf [*Canis lupus arabs* Pocock, 1934], sand cat [*Felis margarita harrisoni* Hemmer, Grubb & Groves, 1976], and reportedly the Arabian leopard [*Panthera pardus nimr* Hemprich & Ehrenberg, 1833], makes this small protected area a unique

treasure of biological diversity. Small communities on the mountain grow a distinctive variety of coffee and other crops in terraced fields (El-Hawagry et al. 2013; SWA 2016; UAEinteract 2016).

The purpose of this paper is to present a preliminary list of Diptera (Insecta) in SANR, Al-Baha Province, KSA, with remarks on their zoogeography. This is not the final list of Diptera that occur at SANR with the study serving as a basis for further investigations as many additional collected species are still unidentified and further studies are planned to be carried out at SANR. Also, this is the first of a series of planned ecological and systematic studies on different insect orders as one of the outputs of a project proposed to study the entire insect fauna of SANR.

El-Hawagry et al. (2013, 2015) studied the insect fauna of Al-Baha Province excluding SANR, so the present study and other future studies in SANR are complementary to the previous two studies. Studies on the fauna of SANR are of particular interest as this area lies in a part of the Arabian Peninsula which is thought by many authors to touch three of the main zoogeographical regions: the Palaearctic, the Afrotropical, and the Oriental (Hölzel 1998).

The Afrotropical Region is supposed to encompass all of Africa south of the Sahara, with the island of Madagascar and the nearby smaller islands. Many authors add parts of the Arabian Peninsula to the Afrotropical Region as well, but there seems to be no agreement as to how much (El-Hawagry et al. 2015). This may be deduced from the fact that the south-western and southern parts of the Arabian Peninsula including Al-Baha Province are strongly influenced by a subtropical to tropical climate with spring and summer rains (Abdullah and Al-Masroui 1998), and are thus dominated by a xeromesic tropical flora of palaeotropical origin, that in fact represents the impoverished northern part of an African flora (Ghazanfar and Fisher 1998; Hegazy et al. 1998). Examples of plant species with this conspicuous distribution pattern, linking south-west Arabia with the other side of the Red Sea, and commonly represented in SANR are: *Barleria bispinosa* (Forssk.) Vahl, *Blepharis ciliaris* (L.) B.L.Burt and *Hypoestes forskalii* (Vahl) R.Br. (Acanthaceae); *Aloe officinalis* Forssk. (Aloeaceae), *Aerva javanica* (Burm.f.) Juss. ex Schult., *Aerva lanata* (L.) A. L. Juss. ex Schultes and *Celosia* spp. (Amaranthaceae); *Adenium obesum* (Forssk.) Roem. & Schlt. and *Carissa edulis* (Forssk.) Vahl (Apocynaceae); *Commiphora quadricinta* Schweinf. and *Capparis cartilaginea* Decne. (Burseraceae); *Commelina forskalii* Vahl (Commelinaceae); *Conyza stricta* Willd., *Echinops* sp., *Psiadia punctulata* (DC.), *Pulicaria undulata* (DC.), *Rhamnus dispermus* (L.), *Tagetes minuta* L. and *Vernonia schimperi* DC. (Compositae); *Sansevieria ehrenbergii* Schweinf. ex Baker (Dracaenaceae); succulent *Euphorbia* spp. (Euphorbiaceae); *Acacia asak* (Forssk.), *Acacia etbaica* Schweinf. and *Indigofera spinosa* Forssk. (Fabaceae); *Asparagus africanus* Lam. (Liliaceae); *Hibiscus micranthus* L. and *Hibiscus deflersii* Schweinf. ex Cufod. (Malvaceae); *Ficus ingens* (Miq.) (Moraceae); *Commicarpus* spp. (Nyctaginaceae); *Aristida adscensionis* L., *Cenchrus ciliaris* L., *Eragrostis tenella* (L.) P. Beauv. ex Roemer & Schultes and *Pennisetum divisum* (Gmel.) Henr. (Poaceae); *Solanum incanum* L. (Solanaceae); *Grewia tembensis* Fresen and *Grewia tenax* (Forssk.) (Tiliaceae); *Cissus rotundifolia* (Forssk.) Vahl (Vitaceae); in addition to semi-evergreen

sclerophyllous woodlands of the Afromontane vegetation (Ghazanfar and Fisher 1998; Zohary 1973; Thomas 2016).

Sclater (1858) and Wallace (1876) proposed the classical zoogeographical regions and placed the northern border of the Afrotropics along the Tropic of Cancer, i.e. the northern limit of the Afrotropical Region was placed in Taif area, some 200 km north of Al-Baha Province (Hölzel 1998). Crosskey (1980) considered the northern boundaries of Yemen as the regional boundary between the Afrotropical and Palaearctic parts in the Arabian Peninsula. Extensive sampling of Insects in the Arabian Peninsula by many authors in Yemen, Oman, the United Arab Emirates and south-western mountains of KSA, have raised some interesting questions about the true extent of the Afrotropical Region in this important transitional zone. Authors indicate that Wallace's (1876) concept of the extent of the Afrotropical Arabian Peninsula is more accurate than Crosskey's (1980) limited concept of Yemen alone (Kirk-Spriggs and McGregor 2009, El-Hawagry et al. 2015). However, Uvarov (1938), Greathead (1980) and Larsen (1984) agreed that the south-western part of KSA including the study area should be united with the central Arabian deserts which are either considered as a part of the Palaearctic or by some authors as an autonomous Eremic Zone (also called the Saharo-Sindian faunal region).

Material and methods

Flies were collected from different localities in SANR over two successive years, 2014 and 2015 by the authors. Twelve collecting trips were made, six in 2014 in February, April, June, August, October and December, and six in 2015 in January, March, May, July, September and November. Collections were made in 6 different localities representing different altitudinal levels and habitats in SANR (Figs 13–18, Table 1). The collecting methods included sweep and aerial nets (randomly), bait traps (irregularly), light traps (6 traps, one in each locality, for one night in each trip), Malaise traps (6 traps, one in each locality, for one day in each trip), pitfall traps (90 traps, 15 in each locality, for three days in each trip), and vacuuming (one time in each locality, for 15 minutes in each trip). In addition, a few specimens were incidentally collected by hand.

All taxa are identified and arranged in alphabetical order. Dates of collection for each species are included for the purpose of mapping the activity periods of species in the study area. Each collection date is followed, between parentheses, by the method of collection used, and the latter is followed by the locality number from which the specimens are collected.

Zoogeographical affiliations of species reported in the study area were estimated using world catalogues and counted to calculate the percentage of Afrotropical, Palaearctic or Oriental elements.

Images of newly recorded species were made using a Leica MZ 125 stereo-binocular microscope (Leica Microsystems Ltd, St. Gallen, Switzerland) fitted with a digital camera (Q-imaging Micro Publisher 5.0 RTV; Zerene Systems LLC, Richland, WA, USA) at

Table 1. An overview of the collecting localities with their coordinates and common vegetation.

Locality no.	Coordinates (in decimal degrees)			The most common plants in the locality	
	Elevation (M)	Latitude (N)	Longitude (E)	Species	Family
1	1666	19.8429	41.3115	<i>Barleria bispinosa</i> (Forssk.)	Acanthaceae
				<i>Carissa edulis</i> L.	Apocynaceae
				<i>Conyza stricta</i> Willd.	Compositae
				<i>Psiadia punctulata</i> (DC.)	,,
				<i>Rhamnus dispermus</i> (L.)	,,
				<i>Aristida adscensionis</i> L.	Poaceae
				<i>Acacia etbaica</i> Schweinf	Fabaceae
				<i>Indigofera spinosa</i> Forssk.	,,
				<i>Hibiscus micranthus</i> L.	Malvaceae
				<i>Hibiscus deflersii</i> Schweinf. ex Cufod.	,,
2	1611	19.8402	41.3114	<i>Barleria bispinosa</i> (Forssk.)	Acanthaceae
				<i>Hypoestes forskalii</i> (Vahl)	,,
				<i>Aerva javanica</i> (Burm.f.)	Amaranthaceae
				<i>Capparis cartilaginea</i> Decne.	Burseraceae
				<i>Echinops</i> sp.	Compositae
				<i>Pulicaria undulata</i> (DC.)	,,
				<i>Tagetes minuta</i> L.	,,
				<i>Vernonia schimperi</i> DC.	,,
				<i>Cenchrus ciliaris</i> L.	Poaceae
				<i>Eragrostis tenella</i> (L.)	,,
				<i>Pennisetum divisum</i> (Gmel.)	,,
				<i>Indigofera spinosa</i> Forssk.	Fabaceae
				<i>Ficus ingens</i> (Miq.)	Moraceae
				<i>Commicarpus</i> spp.	Nyctaginaceae
				<i>Solanum incanum</i> L.	Solanaceae
3	1563	19.8388	41.3101	<i>Barleria bispinosa</i> (Forssk.)	Acanthaceae
				<i>Aerva javanica</i> (Burm.f.)	Amaranthaceae
				<i>Aerva lanata</i> (L.)	,,
				<i>Asparagus africanus</i> Lam.	Liliaceae
				<i>Commiphora quadricinta</i> Schweinf.	Burseraceae
				<i>Commelina forskalii</i> Vahl	Commelinaceae
				<i>Tagetes minuta</i> L.	Compositae
				<i>Aristida adscensionis</i> L.	Poaceae
				<i>Cenchrus ciliaris</i> L.	,,
				<i>Eragrostis tenella</i> (L.)	,,
				<i>Indigofera spinosa</i> Forssk.	Fabaceae
				<i>Solanum incanum</i> L.	Solanaceae
				<i>Grewia tembensis</i> Fresen	Tiliaceae
				<i>Grewia tenax</i> (Forssk.)	,,
				<i>Cissus rotundifolius</i> (Forssk.)	Vitaceae
4	1474	19.8452	41.3044	<i>Aerva javanica</i> (Burm.f.)	Amaranthaceae
				<i>Adenium obesum</i> (Forssk.)	Apocynaceae
				<i>Tagetes minuta</i> L.	Compositae
				<i>Cenchrus ciliaris</i> L.	Poaceae

Locality no.	Coordinates (in decimal degrees)			The most common plants in the locality	
	Elevation (M)	Latitude (N)	Longitude (E)	Species	Family
				<i>Acacia asak</i> (Forssk.)	Fabaceae
				<i>Acacia etbaica</i> Schweinf	„
				<i>Indigofera spinosa</i> Forssk.	„
				<i>Solanum incanum</i> L.	Solanaceae
5	1325	19.8511	41.3006	<i>Barleria bispinosa</i> (Forssk.)	Acanthaceae
				<i>Blepharis ciliaris</i> (L.)	„
				<i>Aerva javanica</i> (Burm.f.)	Amaranthaceae
				<i>Aerva lanata</i> (L.)	„
				<i>Acacia asak</i> (Forssk.)	Fabaceae
				<i>Acacia etbaica</i> Schweinf	„
				<i>Indigofera spinosa</i> Forssk.	„
				<i>Solanum incanum</i> L.	Solanaceae
6	1225	19.8627	41.3015	<i>Barleria bispinosa</i> (Forssk.)	Acanthaceae
				<i>Blepharis ciliaris</i> (L.)	„
				<i>Aloe officinalis</i> Forssk.	Aloeaceae
				<i>Psiadia punctulata</i> (DC.)	Compositae
				<i>Sansevieria ehrenbergii</i> Schweinf.	Dracaenaceae
				<i>Cenchrus ciliaris</i> L.	Poaceae
				<i>Acacia asak</i> (Forssk.)	Fabaceae
				<i>Solanum incanum</i> L.	Solanaceae

the Plant Protection Department, College of Food and Agriculture Sciences, King Saud University. Photo automontage was performed by Zerene stacker program version 1.04 (Innovative Solutions, Bucharest, Romania).

Many studies and keys have been consulted in order to identify, classify and estimate the zoogeographical affiliation of collected specimens and such studies are indicated after each taxon in the list, in addition to the following: Abdullah and Merdan (1995), Amoudi (1993), Dawah and Abdullah (2006), El-Hawagry (2015), El-Hawagry and Gilbert (2014), El-Hawagry et al. (2000), Evenhuis and Greathead (2015), Greathead (1980, 1988), Londt (2008), McAlpine (1981), Pape (1996), Pape and Thompson (2016), Soós and Papp (1984–1993), Unwin (1991).

Unidentified specimens (or photos of specimens) were sent to experts for identification, as indicated after each of these taxa in the list.

Flies of suborder Nematocera were examined and preserved in alcohol, while other flies were glued to pinned stiff paper points, and all are deposited at the King Saud University Museum of Arthropods, Riyadh, Saudi Arabia (KSMA).

Abbreviations used:

AF	Afrotropical
BT	Bait trap
HP	Hand-collecting
KSMA	King Saud University Museum of Arthropods, Riyadh, Saudi Arabia

LT	Light trap
MT	Malaise trap
NE	Nearctic
OR	Oriental
PA	Palearctic
PT	Pitfall trap
SANR	Jabal Shada al-A'la Nature Reserve
SW	Sweeping and areal nets
VC	Vacuuming

Results

A total of 119 fly species belonging to 87 genera, 31 tribes, 42 subfamilies, and representing 30 families was recorded from SANR through the present study. Some species have been identified only to genus and listed herein as the genera were not previously recorded from KSA.

Most of the recorded fly species are characteristic of the Afrotropical region. Table (2) indicates the zoogeographic affinities of recorded species suggesting a closer affiliation to the Afrotropical region (46%) than to the Palearctic region (23.5%) or the Oriental region (2.5%).

Table 2. Zoogeographic affinities of fly species of Jabal Shada al-A'la Nature Reserve (SANR).

Region	Affinities	
	No. of species	%
Afrotropical	55	46
Palearctic	28	23.5
Oriental	3	2.5
Cosmopolitan	14	12
Undetermined	19	16

List of species recorded at SANR to date

Order **Diptera**

Suborder **Nematocera**

Family **Bibionidae**

Dilophus tridentatus Walker, 1848

15 February 2014 (MT1), 5 May 2015 (SW1).

Identification: Haenni (1985).

Known distribution: AF.

Family **Ceratopogonidae**

Subfamily **Ceratopogoninae**

Tribe **Culicoidini**

Culicoides kingi (Austen, 1912)

23 August 2014 (LT2, LT5).

Identification: Alahmed et al. (2010), Boorman (1989).

Known distribution: AF.

Subfamily **Forcipomyiinae**

Forcipomyia sahariensis Kieffer, 1923

23 August 2014 (LT1).

Identification: Lewanczyk et al. (2009).

Known distribution: AF. First record from KSA.

Family **Culicidae**

Subfamily **Anophelinae**

Anopheles multicolor Cambouliu, 1902

23 August 2014 (LT2), 15 February 2014 (LT3).

Identification: Glick (1992).

Known distribution: PA.

Subfamily **Culicinae**

Aedes caspius (Pallas, 1771)

15 February 2014 (LT1, PT4).

Identification: Alikhan et al. (2014).

Known distribution: PA.

Culex pipiens Linnaeus, 1758

23 August 2014 (PT4).

Identification: Thielman and Hunter (2007).

Known distribution: Cosmopolitan.

Family **Sciaridae**

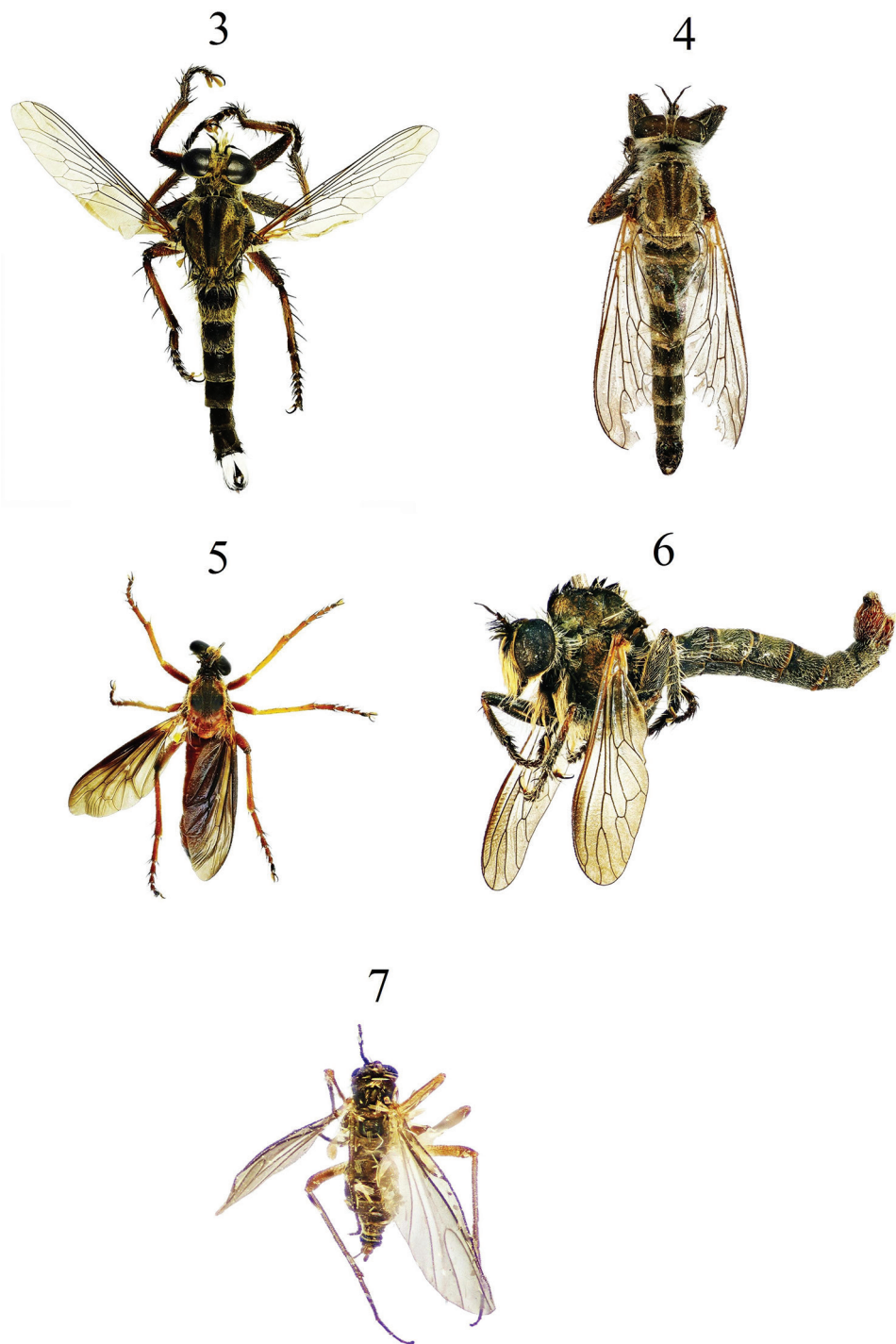
Chaetosciara sp. Fig. 7

15 February 2014 (MT1), 23 August 2014 (LT2).

Remark: This seems to be the first record of Sciaridae from KSA..

Identification: Steffan (1981) and Mohrig et al. (2012).

Known distribution: Undetermined.



Figures 3–7. **3** *Promachus sinaiticus* Efflatoun **4** *Neolophonotus* sp.1 **5** *Saropogon longicornis* (Macquart) **6** *Neolophonotus* sp.2 **7** *Chaetosciara* sp.

Suborder **Brachycera**

Infraorder **Asilomorpha**

Superfamily **Asiloidea**

Family **Asilidae**

Subfamily **Asilinae**

Tribe **Asilini**

Neolophonotus sp1. Fig. 4

14-15 February 2014 (MT1, MT3), 21 April 2014 (LT3), 27 January 2015 (MT2, MT3, MT5), 5 May 2015 (SW1), 27 July 2015 (LT2).

Remark: This seems to be the first record of this genus from KSA.

Identification: Dr. Jason G.H. Londt, from photos (personal communication).

Known distribution: Undetermined.

Neolophonotus sp2. Fig. 6

15 February 2014 (MT3), 15 November 2015 (MT3).

Remark: This seems to be the first record of this genus from KSA.

Identification: Dr. Jason G.H. Londt, from photos (personal communication).

Known distribution: Undetermined.

Subfamily **Apocleinae**

Promachus sinaiticus Efllatoun, 1934 Fig. 3

20 April 2014 (LT6), 3 June 2014 (LT2, MT4), 3-5 June 2014 (SW2), 15 November 2015 (MT6).

Identification: Efllatoun (1934, 1937).

Known distribution: PA. First record of the species from the KSA.

Subfamily **Dasypogoninae**

Tribe **Dasypogonini**

Saropogon longicornis (Macquart, 1838) Fig. 5

3 June 2014 (MT3).

Identification: Efllatoun (1934, 1937).

Known distribution: PA. First record from KSA.

Saropogon sp.

15 November 2015 (MT6).

Remark: This seems to be the first record of this genus from KSA.

Identification: Efllatoun (1934, 1937).

Known distribution: Undetermined.

Subfamily **Laphystiinae**

Trichardis leucocomus (Wulp, 1899)

3 June 2014 (MT5), 5 May 2015 (MT5).

Identification: Dr Torsten Dikow, from photos (personal communication).

Known distribution: PA.

Family **Bombyliidae**Subfamily **Bombyliinae**Tribe **Bombyliini***Bombylella delicata* Wiedemann, 1830

5 June 2014 (SW6), 28 July 2015 (SW3).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: AF.

Bombylius pallidipilus Greathead, 1967

15 February 2014 (MT1), 23 August 2014 (LT2).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: AF.

Systoechus horridus Greathead, 1980

21 April 2014 (LT2), 3 May 2015 (LT5), 14 November 2015 (LT6).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: PA.

Subfamily **Anthracinae**Tribe **Anthracini***Anthrax sticticus* Klug, 1832

22 April 2015 (LT).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: AF, PA.

Spogostylum candidum (Sack, 1909)

4 June 2014 (SW6).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: OR, PA.

Spogostylum isis (Meigen, 1820)

29 July 2015 (PT5).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: PA.

Spogostylum tripunctatum (Pallas in Wiedemann, 1818)

4-5 June 2014 (SW2), 2 September 2015 (LT6).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: PA. First record from KSA.

Tribe **Exoprosopini***Defilippia nigrifimbriata* (Hesse, 1956)

17 October 2014 (MT5).

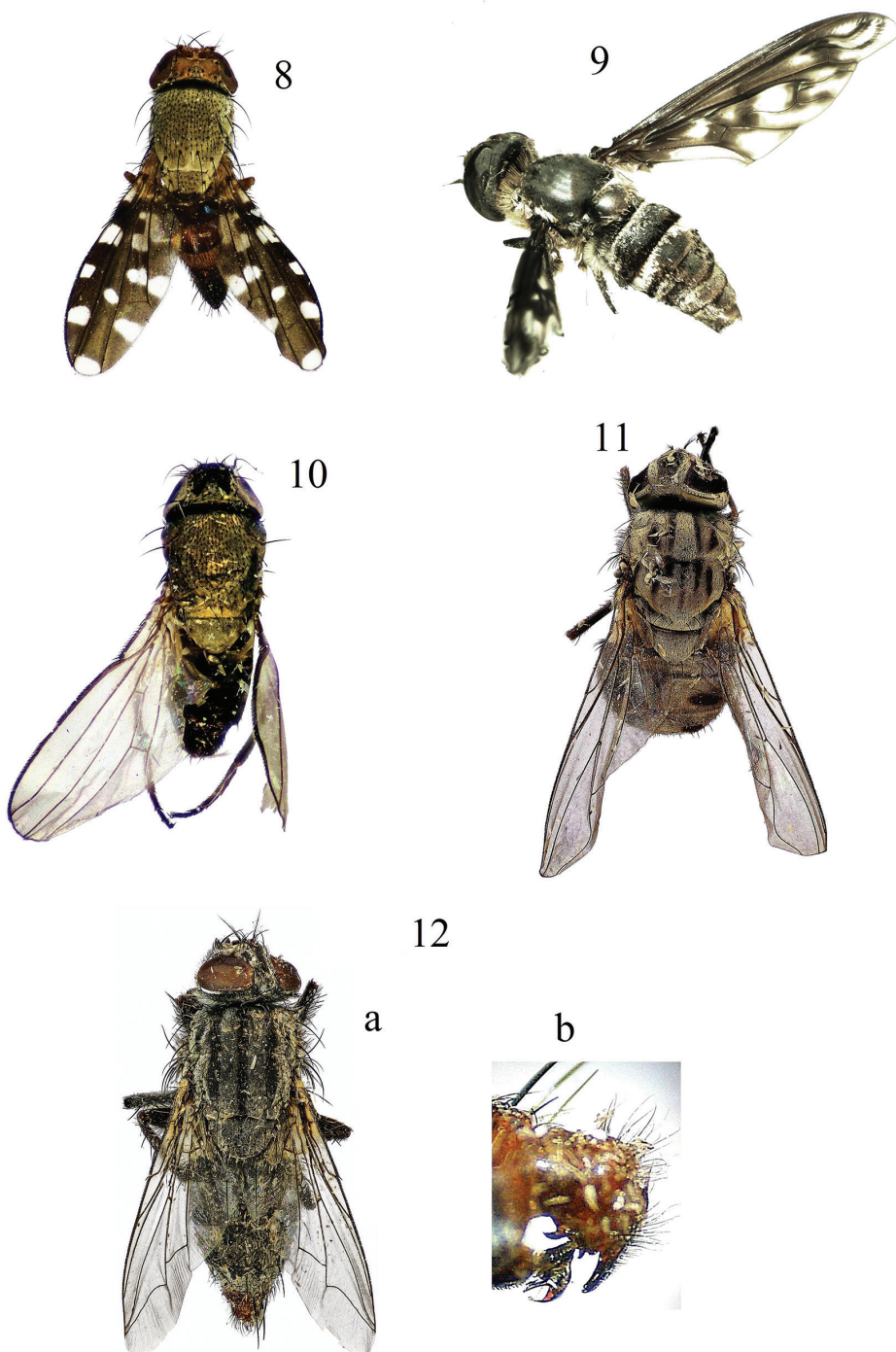
Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: AF.

Exoprosopa disrupta tihamae Greathead, 1980 Fig. 9

3 June 2014 (SW1).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).



Figures 8–12. 8 *Actocetor margaritatus* Wiedemann 9 *Exoprosopa disrupta tihamae* Greathead 10 *Desmometopa inaurata* Lamb 11 *Stomoxys niger* Macquart 12 **a** *Sarcophaga palestinesis* (Lehrer), habitus **b** same, male genitalia.

Known distribution: AF.

Heteralonia bisecta Greathead, 1988

29 July 2015 (PT5).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: AF.

Pterobates chalybaeus (Röder, 1887)

3 November 2014 (HP6).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: PA.

Tribe **Villini**

Exhyalanthrax triangularis Bezzi, 1924

27 January 2015 (MT5), 5 May 2015 (MT2, MT4), 15 November 2015 (MT4).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: AF.

Pachyanthrax circe (Klug, 1832)

5 May 2015 (MT4).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: AF.

Villa bivirgata Austen, 1937

3 June 2014 (SW4), 5 May 2015 (SW4).

Identification: Magdi El-Hawagry using Greathead (1980, 1988) and EL-Hawagry and Greathead (2006).

Known distribution: PA.

Villa paniscoides Bezzi, 1912

3 June 2014 (SW4), 27–28 July 2015 (SW1), 15 November 2015 (MT4).

Identification: Magdi El-Hawagry using Greathead (1980, 1988) and EL-Hawagry and Greathead (2006).

Known distribution: AF.

Tribe **Xeramoebini**

Desmatoneura sp.

4 June 2014 (SW4).

Identification: Magdi El-Hawagry using El-Hawagry and Evenhuis (2008).

Known distribution: Undetermined.

Petrorossia albula Zaitzev, 1962

5 June 2014 (SW2), 27 July 2015 (SW1).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: PA.

Petrorossia letho (Wiedemann, 1828)

5 June 2014 (SW4), 27 July 2015 (SW1).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: PA.

Petrorossia tropicalis Bezzi, 1921

3-5 June 2014 (SW2, SW4), 5 May 2015 (MT3), 27 July 2015 (SW4).

Identification: Magdi El-Hawagry using Greathead (1980, 1988).

Known distribution: AF.

Family **Therevidae**

Phycus sp.

1 June 2014 (LT5), 24 August 2014 (LT6).

Remark: This seems to be the first record of the genus from KSA.

Identification: Dr Martin Hauser (personal communication).

Known distribution: AF.

Superfamily **Empidoidea**

Family **Dolichopodidae**

Subfamily **Diaphorinae**

Asyndetus albifacies Parent, 1929

27 July 2015 (SW).

Identification: Grichanov (2007).

Known distribution: AF.

Subfamily **Dolichopodinae**

Dolichopus sp.

23 August 2014 (LT4), 10 December 2014 (LT6), 26 January 2015 (PT4), 27 July 2015 (LT6).

Identification: Grichanov (2007).

Known distribution: Undetermined.

Tachytrechus planitarsis Becker, 1907

23 August 2014 (LT2).

Identification: Grichanov (2007).

Known distribution: PA.

Superfamily **Nemestrinoidea**

Family **Nemestrinidae**

Trichopsidea costata Loew, 1858

10 December 2014 (LT6).

Identification: Narchuk (2007).

Known distribution: AF.

Superfamily **Tabanoidea**Family **Tabanidae***Haematopota pluvialis* (Linnaeus, 1758)

15 November 2015 (LT6).

Identification: Amoudi and Leclercq (1992) and Leclercq (1982, 1986, 2000).

Known distribution: PA.

Infraorder **Muscomorpha**Section **Aschiza**Superfamily **Platypezoidea**Family **Phoridae***Megaselia scalaris* (Loew, 1866)

23 April 2014 (PT2, PT3), 5 June 2014 (PT4), 2 March 2015 (PT4), 29 July 2015 (PT5), 23 August 2015 (LT3).

Identification: Magdi El-Hawagry.

Known distribution: Cosmopolitan.

Section **Schizophora**Subsection **Acalyptratae**Family **Carnidae***Hemeromyia* sp. 23 August 2014 (LT1).*Remark:* This seems to be the first record of the genus from KSA.

Identification: Sabrosky (1987).

Known distribution: Undetermined.

Meoneura palaestinensis Hennig, 1937

23 August 2014 (LT1, PT2).

Identification: Papp (1978).

Known distribution: PA.

Family **Chloropidae**Subfamily **Chloropinae***Pachylophus pellucidus* Becker, 1910

24 August 2014 (MT6).

Identification: Deeming and Al-Dhafer (2012).

Known distribution: AF.

Thaumatomyia notata (Meigen, 1830)

27 January 2015 (LT1).

Identification: Deeming and Al-Dhafer (2012).

Known distribution: AF, PA.

Subfamily **Oscinellinae***Anatrichus pygmaeus* Lamb, 1918

27 July 2015 (VC5).

Identification: Deeming and Al-Dhafer (2012).

Known distribution: AF.

Aphanotrigonum subfasciellum Collin, 1949

4 June 2014 (SW4), 24 August 2014 (LT6).

Identification: Deeming and Al-Dhafer (2012).

Known distribution: PA.

Lasiochaeta vulgaris (Adams, 1905)

15 February 2014 (MT1), 8 December 2014 (VC1, VC4), 5 May 2015 (MT4).

Identification: Deeming and Al-Dhafer (2012).

Known distribution: AF.

Polyodaspis robusta (Lamb, 1918)

15 February 2014 (MT1, PT1), 17 October 2014 (LT1), 27 July 2015 (VC2).

Identification: Deeming and Al-Dhafer (2012) for genus, and Lamb (1918) for species.

Known distribution: AF.

Scoliophthalmus micantipennis Duda, 1935

5 May 2015 (MT6).

Identification: Identification: Deeming and Al-Dhafer (2012).

Known distribution: AF.

Scoliophthalmus trapezoides Becker, 1903

5 May 2015 (MT6).

Identification: Identification: Deeming and Al-Dhafer (2012).

Known distribution: AF.

Subfamily **Siphonellopsinae**

Apotropina gregalis (Lamb, 1937)

23 August 2014 (LT5, LT6, PT2, PT3, PT4, PT5, PT6), 17 October 2014 (LT5), 8

December 2014 (VC4), 2-3 March 2015 (PT4, PT5), 17 July 2015 (LT3, MT4), 15

November 2015 (LT6).

Identification: Identification: Deeming and Al-Dhafer (2012).

Known distribution: AF.

Family **Chyromyidae**

Subfamily **Chyromyinae**

Somatiosoma eremicolum Ebejer, 2008

15 February 2014 (MT4).

Identification: Ebejer (2008).

Known distribution: AF.

Family **Conopidae**

Subfamily **Myopinae**

Tribe **Zodionini**

Zodion cinereum (Fabricius, 1794)

5 May 2015 (MT6).

Mei & Stuke J-H (2008) has been consulted to identify this species.

Identification: Mei and Stuke (2008).

Known distribution: PA.

Family **Diopsidae***Diopsis apicalis* Dalman, 1817

5 May 2015 (LT2, SW1).

Identification: Dawah and Abdullah (2008).

Known distribution: AF.

Sphyracephala beccarii (Rondani, 1873)

2 June 2014 (LT6), 3 June 2014 (LT3, LT4), 3 June 2014 (MT2), 27 January 2015 (LT4), 5 May 2015 (LT1, SW1), 15 November 2015 (LT6).

Identification: Dawah and Abdullah (2008).

Known distribution: AF.

Family **Drosophilidae**Subfamily **Drosophilinae**Tribe **Drosophilini***Drosophila melanogaster* Meigen, 1830

17–18 October 2014 (LT3, PT2), 8 December 2014 (PT2), 26–27 January 2015 (LT1, MT1, MT2, PT1, PT2), 2 March 2015 (PT1, PT2, PT4).

Identification: Magdi El-Hawagry.

Known distribution: Cosmopolitan.

Zaprionus indianus Gupta, 1970

2 March 2014 (PT5), 23 August 2014 (LT2), 18 October 2014 (PT1, PT2, PT4, PT5).

Identification: Amoudi et al. (1991).

Known distribution: OR.

Family **Ephydriidae**Subfamily **Discomyzinae**Tribe **Discomyzini***Actocetor indicus* (Wiedemann 1824)

23 April 2014 (PT4, PT5), 17 October 2014 (LT4).

Identification: Dawah and Abdullah (2006), Becker (1903) and Wiedemann (1824).

Known distribution: AF.

Actocetor margaritatus Wiedemann, 1830 Fig. 8

28 February 2014 (PT3), 23 August 2014 (PT1, PT2, PT4, PT5), 10 December 2014 (LT6), 5 May 2015 (LT4, SW1).

Identification: Dawah and Abdullah (2006), Becker (1903) and Wiedemann (1830).

Known distribution: AF.

Tribe **Psilopini***Psilopa nilotica* (Becker, 1903)

15 February 2014 (LT2, MT2), 4 June 2014 (SW4), 29 July 2015 (PT4, PT5).

Identification: Dawah and Abdullah (2006), Becker (1903).

Known distribution: AF, PA.

Subfamily **Hydrelliinae**

Notiphila ignobilis Loew, 1862

29 July 2015 (MT6).

Identification: Dawah and Abdullah (2006), Becker (1903).

Known distribution: AF.

Family **Lonchaeidae**

Subfamily **Lonchaeinae**

Tribe **Lonchaeini**

Silba virescens Macquart, 1851

15 February 2014 (SW6).

Identification: MacGowan & Friedberg (2009).

Known distribution: AF.

Family **Milichiidae**

Subfamily **Madizinae**

Desmometopa inaurata Lamb, 1914 Fig. 10

27 January 2015 (LT2), 29 July 2015 (PT4).

Identification: Deeming (1998).

Known distribution: AF. First record from KSA.

Desmometopa varipalpis Malloch, 1927

5 May 2015 (PT5), 29 July 2015 (PT6).

Identification: Identification: Deeming (1998).

Known distribution: AF.

Subfamily **Phyllomyzinae**

Phyllomyza sp.

15 February 2014 (LT2), 27 July 2015 (LT2).

Identification: Deeming (1998).

Known distribution: Undetermined.

Family **Pyrgotidae**

Campylocera ferruginea Macquart, 1843

15 November 2015 (LT6).

Identification: Dr Valery Korneyev, from photos (personal communication).

Known distribution: AF.

Eupyrgota latipennis (Walker, 1849)

3 June 2014 (LT2), 14 November 2015 (LT2).

Identification: Dr Valery Korneyev, from photos (personal communication).

Known distribution: AF.

Family **Sphaeroceridae***Rachispoda fuscipennis* (Haliday 1833)

15 February 2014 (PT2, PT3), 23 August 2014 (PT6), 18 October 2014 (LT3, PT1, PT2, PT3, PT4), 8–11 December 2014 (LT2, LT3, LT4, VC1, VC2).

Identification: Magdi El-Hawagry, compared with museum specimens.

Known distribution: PA.

Family **Tephritidae**Subfamily **Dacinae**Tribe **Dacini***Bactrocera zonata* (Saunders, 1842)

23 August 2014 (LT2), 5 May 2015 (SW1), 27 July 2015 (SW1).

Identification: Merz and Dawah (2005) and Efflatoun (1924).

Known distribution: OR.

Subfamily **Tephritinae**Tribe **Tephritini***Acanthiophilus helianthi* (Rossi, 1794)

23 August 2014 (LT2).

Identification: Merz and Dawah (2005) and Efflatoun (1924).

Known distribution: AF, OR, PA.

Dioxyna sororcula (Wiedemann, 1830)

15 February 2014 (MT4), 3 June 2014 (MT4), 8 December 2014 (LT5, VC1).

Identification: Merz and Dawah (2005) and Efflatoun (1924).

Known distribution: AF.

Goniurellia tridens (Hendel, 1910)

23 August 2014 (LT2).

Identification: Hendel (1910).

Known distribution: PA.

Trupanea stellata (Fuesslin, 1775)

3 June 2014 (LT2).

Identification: Merz and Dawah (2005) and Efflatoun (1924).

Known distribution: PA.

Family **Ulidiidae**Subfamily **Ulidiinae**Tribe **Ulidiini***Physiphora alceae* (Preyssler, 1791)

15 February 2014 (MT1, LT1), 21 April 2014 (LT1), 6 June 2014 (LT1), 23 August 2014 (LT1), 17–18 October 2014 (LT3, PT3), 27 January 2015 (MT1, MT3), 5 May 2015 (LT1), 27 July 2015 (LT1, SW1), 15 November 2015 (LT6, MT4).

Identification: Al Dhafer and El-Hawagry (2016).

Known distribution: Cosmopolitan.

Subsection **Calyptratae**

Family **Anthomyiidae**

Subfamily **Anthomyiinae**

Tribe **Anthomyiini**

Anthomyia pluvialis (Linnaeus, 1758)

15 February 2014 (MT1), 27 January 2015 (MT3), 4-5 May 2015 (MT3, SW1), 15 November 2015 (LT5).

Identification: Michelsen (2008).

Known distribution: PA.

Tribe **Hydrophoriini**

Delia platura (Meigen, 1826)

15 February 2014 (LT1, LT2, LT3, MT1), 23 August 2014 (LT2), 17 October 2014 (LT1, LT2), 27 January 2015 (LT2, LT3, MT2).

Identification: Meigen (1826).

Known distribution: Cosmopolitan.

Family **Calliphoridae**

Subfamily **Calliphorinae**

Calliphora croceipalpis Jaennicke, 1867

15 February 2014 (MT4).

Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: AF.

Calliphora vicina (Robineau-Desvoidy, 1830)

3 June 2014 (SW6).

Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: Cosmopolitan.

Subfamily **Chrysomyinae**

Chrysomya albiceps (Wiedemann, 1819)

4 June 2014 (SW1), 2 September 2015 (LT6), 15 November (LT3).

Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: AF.

Chrysomya putoria (Wiedemann, 1830)

3 June 2014 (SW4).

Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: AF.

Chrysomya regalis Robineau-Desvoidy, 1830

15 February 2014 (MT3), 4 June 2014 (MT6), 10 December 2014 (LT6). Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: AF.

Subfamily **Luciliinae***Lucilia sericata* (Meigen, 1826)

16 February 2014 (HP6), 21 February 2014 (LT3), 10 December 2014 (LT6).

Identification:

Known distribution: Cosmopolitan.

Subfamily **Polleniinae***Pollenia hungarica* Rognes, 1987

17 October 2014 (LT6).

Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: PA.

Pollenia rudis (Fabricius, 1794)

17 October 2014 (LT5).

Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: PA.

Family **Muscidae**Subfamily **Atherigoninae**Tribe **Atherigonini***Atherigona humeralis* Wiedemann, 1830

15 November 2015 (SW5).

Identification: Pont (1991).

Known distribution: AF.

Atherigona laevigata (Loew, 1852)

15 February 2014 (MT1), 8 December 2014 (VC4).

Identification: Pont (1991).

Known distribution: AF.

Atherigona reversura Villeneuve, 1936

15 February 2014 (MT3), 23 August 2014 (LT2, LT3, LT5), 17 October 2014 (LT4, LT5, MT2, MT4), 5 May 2015 (MT2), 15 November 2015 (MT4), 2 September 2015 (LT6).

Identification: Pont (1991).

Known distribution: OR.

Subfamily **Coenosiinae**Tribe **Coenosiini***Coenosia attenuata* Stein, 1903

15 February 2014 (MT4, PT4), 23 April 2014 (PT1), 23 August 2014 (LT2), 17 October 2014 (LT2, LT4, MT4), 18 October 2014 (PT5), 5 May 2015 (MT4), 15 November 2015 (MT4).

Identification: Pont (1991).

Known distribution: Cosmopolitan.

Coenosia humilis Meigen, 1826

5 May 2015 (MT6).

Identification: Pont (1991).

Known distribution: Cosmopolitan.

Tribe **Limnophorini**

Lispe nivalis Wiedemann, 1830

15 February 2014 (LT6).

Identification: Pont (1991).

Known distribution: AF.

Lispe pectinipes Becker, 1903

23 August 2014 (LT2, LT3), 17 October 2014 (LT5), 5 May 2015 (LT1, MT2), 14-15 November 2015 (LT4, LT5).

Identification: Pont (1991).

Known distribution: PA.

Subfamily **Muscinae**

Tribe **Muscini**

Musca albina Wiedemann, 1830

5 May 2015 (MT6).

Identification: Pont (1991).

Known distribution: AF, OR, PA.

Musca autumnalis De Geer, 1776

23 August 2014 (LT2), 5 May 2015 (MT2).

Identification: Pont (1991).

Known distribution: Cosmopolitan.

Musca calleva Walker, 1849

14 November 2015 (LT4).

Identification: Pont (1991).

Known distribution: AF.

Musca domestica Linnaeus, 1758

15 February 2014 (MT5, PT6), 3 June 2014 (MT2, SW6), 23 August 2014 (LT2, LT3), 5 May 2015 (MT6), 2 September 2015 (LT5), 15 November 2015 (LT6).

Identification: Pont (1991).

Known distribution: Cosmopolitan.

Musca lucidula (Loew, 1856)

3 June 2014 (MT6).

Identification: Pont (1991).

Known distribution: AF, PA.

Musca sorbens Wiedemann, 1830

5 May 2015 (MT1), 15 November 2015 (LT5).

Identification: Pont (1991).

Known distribution: AF.

Tribe Stomoxyini

Stomoxys niger Macquart, 1851 Fig. 11

15 February 2014 (MT4), 17 October 2014 (LT5).

Identification: Márcia et al. (2012).

Known distribution: AF. First record from KSA.

Subfamily Phaoniinae**Tribe Dichaetomyiini**

Dichaetomyia luteiventris (Rondani, 1873)

2 March 2015 (PT5).

Identification: Pont (1991).

Known distribution: AF.

Tribe Phaoniini

Helina coniformis (Stein in Becker, 1903)

15 February 2014 (MT5, PT2), 21 April 2014 (LT2), 17 October 2014 (LT1, LT5, MT1, MT2, MT3, MT4), 27 January 2015 (MT2, MT3), 14–15 November 2015 (LT4, LT5, MT4).

Identification: Pont (1991).

Known distribution: AF.

Helina lucida (Stein, 1913)

21 April 2014 (LT5).

Identification: Pont (1991).

Known distribution: AF.

Family Rhiniidae

Cosmina viridis Townsend, 1917

15–16 February 2014 (MT1, MT3), 17 October 2014 (LT5), 27 January 2015 (LT1, MT3), 4–5 May 2015 (SW4, MT2).

Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: AF.

Isomyia terminata (Wiedemann, 1830)

15 February 2014 (MT5, PT5).

Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: AF.

Rhinia apicalis (Wiedemann, 1830)

15 February 2014 (MT5), 3 June 2014 (SW4), 17 October 2014 (LT2, LT3, LT5), 14–15 November 2015 (LT4, LT5, LT6).

Identification: Setyaningrum and Al Dhafer (2014).

Known distribution: AF.

Family **Sarcophagidae**

Subfamily **Miltogramminae**

Taxigramma heteroneura (Meigen, 1830)

15 February 2014 (MT5), 3 June 2014 (SW4), 27 January 2015 (MT4), 5 May 2015 (MT4, SW1), 27-29 July 2015 (PT5).

Identification: Thomas Pape (personal communication) and the first author.

Known distribution: NE, PA.

Subfamily **Paramacronychiinae**

*Wohlfahrtia erythrocer*a Villeneuve, 1910

28 July 2015 (PT6).

Identification: Thomas Pape (personal communication) and the first author.

Known distribution: AF.

Wohlfahrtia nuba Wiedemann, 1830

3 May 2015 (PT5).

Identification: Thomas Pape (personal communication) and the first author.

Known distribution: AF.

Subfamily **Sarcophaginae**

Blaesoxipha algeriensis (Townsend, 1919)

23 August 2014 (LT5).

Identification: Thomas Pape (personal communication) and the first author.

Known distribution: PA.

Blaesoxipha rufipes (Macquart, 1839)

3 June 2014 (SW4).

Identification: Thomas Pape (personal communication) and the first author.

Known distribution: Cosmopolitan.

Sarcophaga adhamae (Lehrer and Abou-Zied, 2008)

21 April 2014 (BT6).

Identification: Lehrer and Abou-Zied (2008).

Known distribution: AF.

Sarcophaga africa (Wiedemann, 1824)

5 May 2015 (SW4).

Identification: Thomas Pape (personal communication) and the first author.

Known distribution: Cosmopolitan.

Sarcophaga babiyari (Lehrer, 1995)

3 June 2014 (LT6).

Identification: Thomas Pape (personal communication) and the first author.

Known distribution: AF.

Sarcophaga dux Thompson, 1869

15 February 2014 (MT1).

Identification: Thomas Pape (personal communication) and the first author.

Known distribution: Cosmopolitan.

Sarcophaga palestinensis (Lehrer, 1998) Fig. 12

21 February 2014 (LT1).

Identification: Thomas Pape (personal communication) and the first author.

Known distribution: PA.

Family **Tachinidae**

Subfamily **Exoristinae**

Tribe **Eryciini**

Drino lota (Meigen, 1824)

15–16 February 2014 (LT6, MT4, MT5, MT6, SW6), 17 October 2014 (LT4, LT5, LT6), 14–15 November 2015 (LT4, LT6).

Identification: Dawah (2011) and Tschorsnig and Herting (1994).

Known distribution: AF, PA.

Tribe **Exoristini**

Exorista larvarum (Linnaeus, 1758)

3 June 2014 (SW2, SW4).

Identification: Dawah (2011) and Tschorsnig and Herting (1994).

Known distribution: NE, PA.

Tribe **Goniini**

Gonia capitata (De Geer, 1776)

5 May 2015 (MT1). Identification: Dawah (2011) and Tschorsnig and Herting (1994).

Known distribution: PA.

Sturmia bella (Meigen, 1824)

15 February 2014 (MT1), 21 April 2014 (LT1), 3 June 2014 (SW4), 27–30 January 2015 (LT1, LT2, LT3), 27 July 2015 (LT5).

Identification: Dawah (2011) and Tschorsnig and Herting (1994).

Known distribution: OR, PA.

Subfamily **Phasiinae**

Tribe **Cylindromyiini**

Cylindromyia bicolor (Olivier, 1812)

7 June 2014 (SW4).

Identification: Dawah (2011), El-Hawagry et al. (2015) and Tschorsnig and Herting (1994).

Known distribution: PA.

Subfamily **Tachininae**

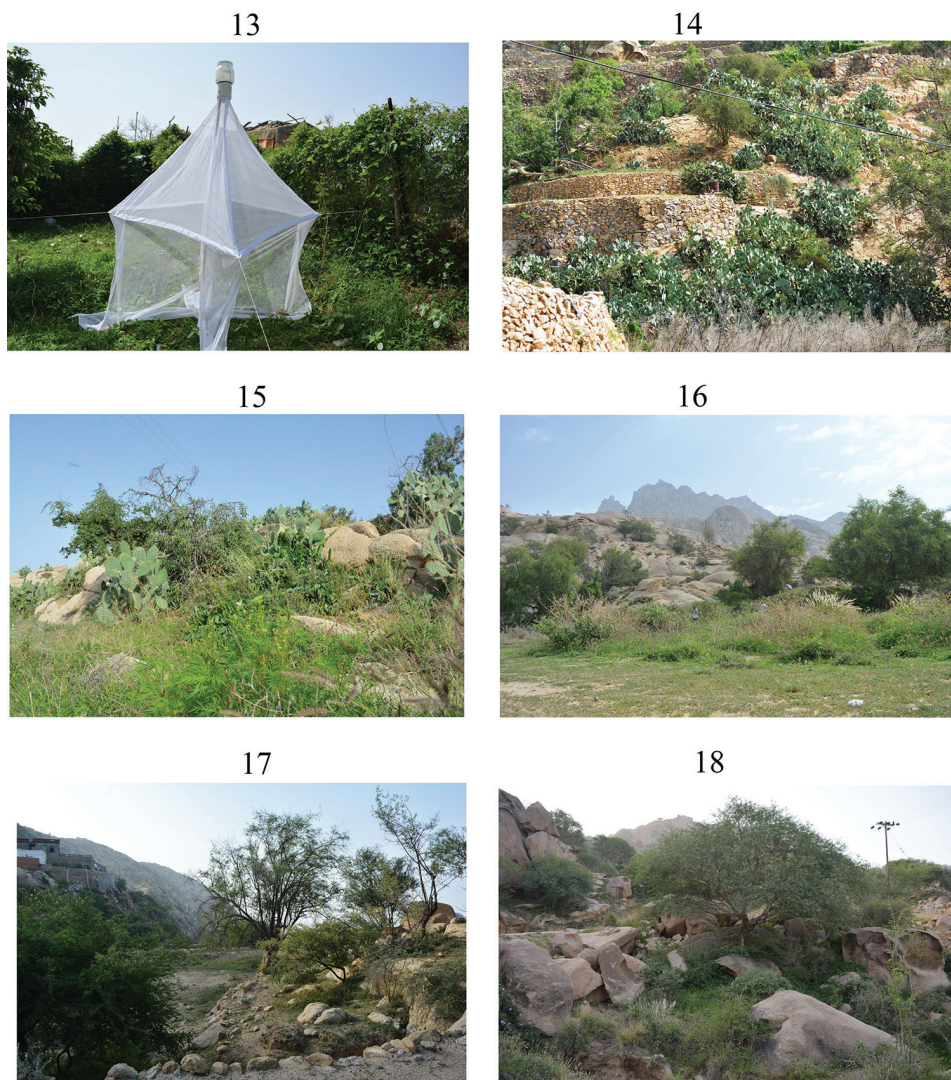
Tribe **Tachinini**

Dejeania bombylans (Fabricius, 1798)

10 December 2014 (LT6).

Identification: Dawah (2011) and Tschorsnig and Herting (1994).

Known distribution: AF.



Figures 13–18. 13 Collecting locality no. 1 14 Collecting locality no. 2 15 Collecting locality no. 3 16 Collecting locality no. 4 17 Collecting locality no. 5 18 Collecting locality no. 6.

Discussion

In terms of vegetation and speciation, the south-western part of KSA, including Al-Baha Province, is considered to be the most important part of the country and the Arabian Peninsula in general. Floristically and ecologically, this area is similar to the high altitude mountains of north-eastern and eastern parts of Africa, and like other areas in the south-western part of the Arabian Peninsula, contains montane woodlands and evergreen shrub lands, with strong Afromontane affinities (Bussmann and Beck 1995; Zohary 1973; Eig 1938).

Considering the insect fauna as a whole, El-Hawagry et al. (2013, 2015) attributed the extraordinary complex and the interesting insect fauna in Al-Baha Province to its geographical position at the junction of two of the world's main zoogeographical regions, the Afrotropical and the Palaearctic.

Many present day biogeographers think that the biogeographical divisions within the eastern and the northeastern parts of Africa should be extended towards east within the Arabian Peninsula as well, covering the high altitude regions of the southern Al-Sarawat Mountains, namely "Afromontane Archipelago" (Zohary 1973; Eig 1938). Bolton (1994), Eig (1938), El-Hawagry et al. (2013 and 2015) and Sharaf et al. (2012a, 2012b) concluded that the insect faunal composition in Al-Baha Province has an Afrotropical flavor as the Afrotropical elements were predominantly indicated, they tended to agree with those biogeographers who think that parts of the Arabian Peninsula, including Al-Baha Province, should be included in the Afrotropical region, but they couldn't indicate the northern border of this region exactly. All these facts seem to be reflected somehow on the fly faunal composition in Jabal Shada al-A'la Nature Reserve (SANR) as shown in the present results which obviously emphasize the fact that Al-Baha Province, as lying in the south-western part of the Arabian Peninsula, should be included in the Afrotropical Region rather than in the Palaearctic Region or the Eremic Zone.

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Iranocichla persa, a new cichlid species from southern Iran (Teleostei, Cichlidae)

Hamid Reza Esmaili¹, Golnaz Sayyadzadeh¹, Ole Seehausen²

1 Ichthyology and Molecular Systematics Lab., Department of Biology, College of Sciences, Shiraz University, Shiraz, Iran **2** Department of Fish Ecology & Evolution, EAWAG Centre for Ecology, Evolution and Biogeochemistry, 6047 Kastanienbaum, & Division of Aquatic Ecology, Institute of Ecology and Evolution, University of Bern, 3012 Bern, Switzerland

Corresponding author: Hamid Reza Esmaili (hresmaeil22@gmail.com)

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Abstract

Iranocichla persa **sp. n.** is described from the Shur, Hasanlangi and Minab River drainages flowing into the Persian Gulf at the Strait of Hormuz in southern Iran. It is distinguished from *I. hormuzensis*, from the Mehran River drainage, by nuptial males having a bright orange breast and lower part of the head (vs. black), a poorly developed or invisible (vs. distinctive) “*Tilapia*-mark” in the dorsal fin and very clear white spots making almost wavy bars or stripes on the caudal fin (vs. without or with very few white spots). Mitochondrial DNA sequence characters suggest that both *Iranocichla* species are closely related but form two distinct clades, diagnosable by several fixed mutations in ND2, D-loop and partially by COI sequences. Populations from Kol River drainage, which is situated in-between the Mehran and the Shur River drainages, are more similar to *I. hormuzensis* in terms of their male nuptial coloration but to *I. persa* **sp. n.** in their mitochondrial sequence characters. Their status requires further investigation.

Keywords

Barcode region, inland fish, Middle East, Persian Gulf

Introduction

The presence of a cichlid species in southern Iran was first noted by Behnke (1975) and these fishes were briefly described but not named by Saadati (1977) in his MS thesis. Coad (1982) described the Iranian cichlids as a new genus and species, *Iranocichla hormuzensis*, based on fishes from the Mehran River drainage and it was considered as the only cichlid fish of Iran (Esmaili et al. 2010, 2015). In 2013, HRE collected 82 *Iranocichla* individuals from all over its range. Schwarzer et al. (2016) analysed all these 82 individuals for their life coloration and 75 of them for their mitochondrial ND2 and D-loop sequences (2044 bp). Schwarzer et al. (2016) suggest the presence of three phenotypically distinct phylogeographic groups in *Iranocichla*. Fishes from the Mehran River drainage, which is the westernmost river inhabited by *Iranocichla*, form one of these clades corresponding to *I. hormuzensis*. Fishes from the Shur, Hasanlangi and Minab River drainages, in the eastern part of the range of *Iranocichla*, correspond to the majority of individuals of a second clade identified by Schwarzer et al. (2016), here described as *I. persa*. The third group identified by Schwarzer et al. (2016) inhabits the Kol River drainage, which is situated between the Mehran and Shur Rivers. Most of these fish form a third mitochondrial clade, closely related to the *I. persa* clade but some are part of the latter clade. Hence, this third group appears polyphyletic, albeit only a single haplotype in a single individual was shared with *I. persa*. Nuptial males from all three genetic groups can be differentiated by their coloration. Nuptial males of *I. hormuzensis* show a blue or black breast and head while those from the Shur, Hasanlangi and Minab have a bright orange breast and lower part of the head, a trait not known from any other Oreochromine cichlid. Nuptial males of the third molecular group resemble *I. hormuzensis* in these traits, although they differ from them in other coloration traits (see below), but are closer to *I. persa* in their mitochondrial sequences. Based on mitochondrial D-loop and ND2 datasets, the reciprocal monophyly of Mehran River populations (clade A) and of Shur, Rudan and Kol populations (clade B) was supported in Schwarzer et al. (2016). This is confirmed here with a set of mitochondrial cytochrome c oxidase subunit 1 (COI) sequences. These findings are discussed and the populations with an orange breast and head in nuptial males are described as a new species.

Material and methods

To study nuptial coloration, all fishes across the distribution range of the genus were collected during their reproductive season in March 2013 using cast and hand nets (Fig. 1). Nuptial males were photographed alive in a portable aquarium, immediately after being captured. After anaesthesia, fishes were either fixed in 10% formaldehyde or in 70% ethanol and all fishes were later transferred to and stored in 70% ethanol. Measurements were made with a dial caliper and recorded to 0.1 mm. All measurements were made point to point, never by projections. Methods for counts and measurements follow Coad (1982). Standard length (SL) was measured from the tip of

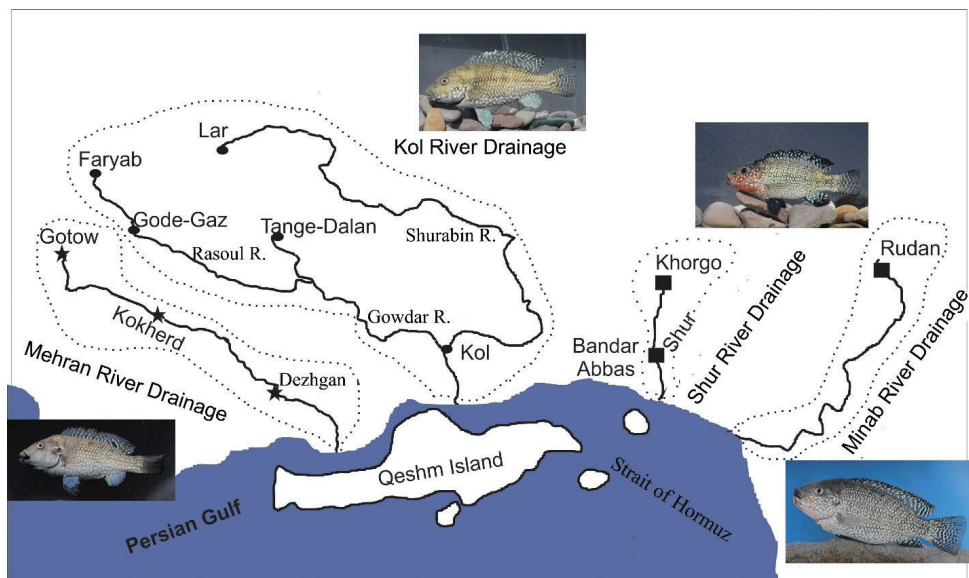


Figure 1. Geographic distribution map of *Iranocichla* populations in four river drainages of Iran. Symbols indicate our sampling sites and the different taxa. Asterisk = *I. hormuzensis*, rectangle = *I. persa* sp. n., circle = *Iranocichla* sp. "Kol".

the snout to the end of the hypural complex. The length of the caudal peduncle was measured from the insertion of the last anal-fin ray to the end of the hypural complex at mid-height of the caudal-fin base. The holotype is included in the calculation of means and SD. Abbreviations used: SL, standard length; HL, head length; FSJF, Fischsammlung J. Freyhof, Berlin; ZM-CBSU, Zoological Museum of Shiraz University, Collection of Biology Department, Shiraz.

DNA extraction and PCR. Genomic DNA was extracted using Macherey and Nagel NucleoSpin® Tissue kits following the manufacturer's protocol on an Eppendorf EpMotion® pipetting-roboter with vacuum manifold. The standard vertebrate DNA barcode region of the COI (cytochrome c oxidase subunit 1) was amplified using a M13 tailed primer cocktail including FishF2_t1 (5'TGTAAAACGACGGCCAGTCTGACTAATCATAAA-GATATCGGCAC), FishR2_t1 (5'CAGGAAACAGCTATGACACTTCAGGGT-GACCGAAGAATCAGAA), VF2_t1 (5'TGTAAAACGACGGCCAGTCAACCAAC-CACAAAGACATTGGCAC) and FR1d_t1 (5'CAGGAAACAGCTATGACAC-CTCAGGGTGTCCGAARAAYCARAA) (Ivanova et al. 2007). Sequencing of the ExoSAP-IT (USB) purified PCR product in both directions was conducted at MacroGen Europe Laboratories with forward sequencing primer M13F (5'GTAAAACGACGGC-CAGT) and reverse sequencing primer M13R-pUC (5'CAGGAAACAGCTATGAC).

Molecular data analysis. Data processing and sequence assembly was done in Geneious (Biomatters 2013) and the Muscle algorithm (Edgar 2004) chosen to create a DNA sequence alignment. Modeltest (Posada and Crandall 1998), implemented in the MEGA 6 software (Tamura et al. 2013), was used to determine the most appropriate

sequence evolution model for the given data, treating gaps and missing data with the partial deletion option under 95% site coverage cutoff. The model with the lowest BIC scores (Bayesian Information Criterion) is considered to best describe the substitution pattern. According to Modeltest, the Tamura-Nei model (Tamura and Nei 1993) with discrete Gamma distribution (5 categories (+G, parameter = 0.4292)), best represented the COI alignment, and was used to estimate the evolutionary history.

Maximum Likelihood (ML) phylogenetic trees were generated with 10,000 bootstrap replicates in RaxML software 7.2.5 (Stamatakis 2006) under the GTR+G+I model of nucleotide substitution, with CAT approximation of rate heterogeneity and fast bootstrap to explore species phylogenetic affinities. Bayesian analyses of nucleotide sequences were run with the parallel version of MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) on a Linux cluster with one processor assigned to each Markov chain under the most generalizing model (GTR+G+I) because over-parametrization apparently does not negatively affect Bayesian analyses (Huelsenbeck and Ranala 2004). Each Bayesian analysis comprised two simultaneous runs of four Metropolis-coupled Markov-chains at the default temperature (0.2). Analyses were terminated after the chains converged significantly, as indicated by the average standard deviation of split frequencies <0.01. Bayesian inference of phylogeny was conducted for 6,000,000 generations.

Results

COI barcode sequences are included for a total of 18 individuals of *Iranocichla* from its distribution range over four different river drainages (Mehran, Kol, Shur and Minab). Maximum Likelihood-based estimation of the phylogenetic relationships based on the mitochondrial COI barcode region placed the sequenced *Iranocichla* individuals into two closely related groups (Fig. 2). The four individuals from the Mehran River form one clade and the 14 individuals from the Kol, Shur and Rudan River drainages formed a second clade, fully consistent with the published data from other mitochondrial genes (Schwarzer et al. 2016).

Iranocichla persa sp. n.

<http://zoobank.org/B2A4CC63-A989-41F3-8E61-245E4B373B45>

Figs 3–5

Holotype. ZM-CBSU IP66, 89 mm SL; Iran: Hormuzgan prov.: Shur River approx. 30 km east of Bandar Abbas, 27°17'40.10"N 56°29'15.68"E; H. R. Esmacili, M. Masoudi, H. Mehraban, A. Gholamifard & N. Shabani, 12 March 2013.

Paratypes. All from Iran: Hormuzgan prov.: ZM-CBSU IP64, 2, 65–87 mm SL, same data as holotype. ZM-CBSU IP67–ZM-CBSU K1120, 20, 65–86 mm SL; Khorgo (Khorgu) hot spring approx. 50 km north east of Bandar Abbas, 27°31'21.3"N 56°28'12.7"E; H. R. Esmacili, M. Masoudi, H. Mehraban, A. Gholamifard & N.

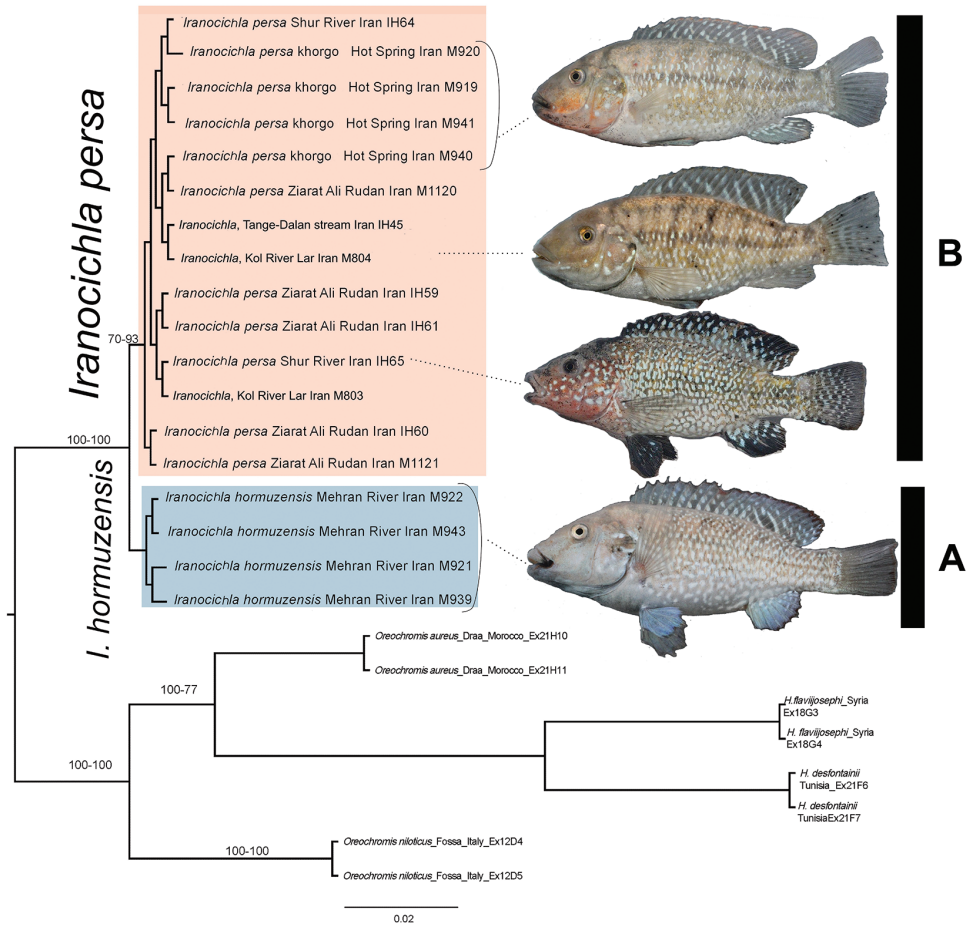


Figure 2. Maximum Likelihood estimation of the phylogenetic relationships of *Iranocichla* species based on the mitochondrial COI barcode region. Nucleotide positions with less than 95% site coverage were eliminated before analysis. Numbers of major nodes indicate bootstrap values from the Maximum Likelihood-method from 1000 pseudo-replicates, followed by Bayesian posterior probabilities.

Shabani, 12 March 2013. — ZM-CBSU IP59, 5, 74-88 mm SL; Rudan river at Ziarat Ali village, approx. 30 km north of Rudan, 27°45'44.42"N 57°14'34.33"E; H. R. Esmaili, M. Masoudi, H. Mehraban, A. Gholamifard & Shabani, 11 March 2013. —ZM-CBSU IP141, 5, 82-102 mm SL; Rudan river at Ziarat Ali village, approx. 30 km north of Rudan, 27°45'44.42"N 57°14'34.33"E; M. Masoudi & H. Mehraban, 9 April 2014. —FSJF 3468, 63-81 mm SL; Khorgo Hot spring approx. 50 km north east of Bandar Abbas, 27°31'21.3"N 56°28'12.7"E; H. R. Esmaili, M. Masoudi, H. Mehraban, A. Gholamifard & N. Shabani, 12 March 2013.

Materials used for molecular analysis. All from Iran: Hormuzgan prov.: ZM-CBSU M919, M920, M940, M941; Khorgo hot spring, 27°31'21.3"N 56°28'12.7"E (GenBank accession numbers: KY034435, KY034436, KY034437, KY034438).



Figure 3. *Iranocichla persa*, ZM-CBSU-IP66, male, holotype, 89.54 mm SL; Hormuzgan prov.: Shur River.

—ZM-CBSU M1120, M1121, ZM-CBSU-IH59, ZM-CBSU-IH60, ZM-CBSU-IH61; Rudan River at Ziarat Ali village, 27°45'44.42"N 57°14'34.33"E (GenBank accession numbers: KY034442, KY034443, KY034439, KY034440, KY034441). —ZM-CBSU-IH64, ZM-CBSU-IH65; Shur River, 27°17'40.10"N 56°29'15.68"E (GenBank accession numbers: KY034444, KY034445).

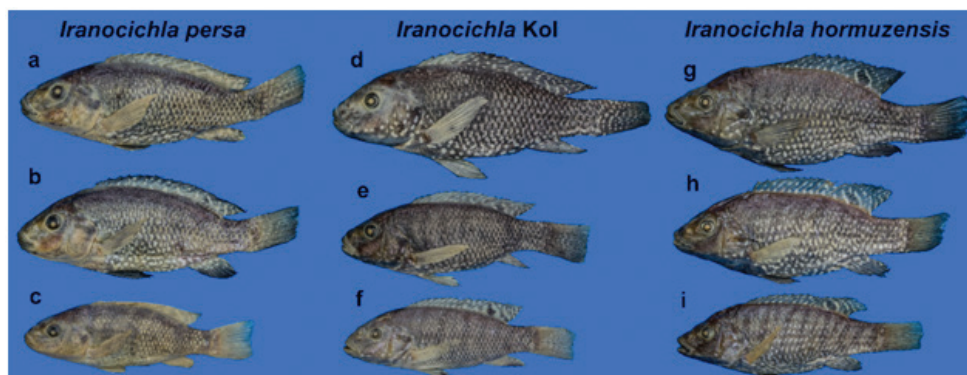


Figure 4. Males of the three *Iranocichla* taxa from Hormuzgan prov., Iran: *Iranocichla persa*; paratypes; **a** ZM-CBSU-IP75, 86 mm SL **b** ZM-CBSU-IP78, 82 mm SL **c** ZM-CBSU-IP69, 67 mm SL; Khorgo Hot spring. *Iranocichla* from Kol **d** ZM-CBSU-IP34, 113 mm SL **e** ZM-CBSU-IP38, 84 mm SL **f** ZM-CBSU-IH45, 78 mm SL; Kol River drainage. *Iranocichla hormuzensis* **g** ZM-CBSU-IH55, 90 mm SL **h** ZM-CBSU-IH51, 83 mm SL **i** ZM-CBSU-IH49, 72.2 mm SL; Mehran River drainage.

Diagnosis. *Iranocichla persa* is distinguished from *I. hormuzensis* by its nuptial coloration in males. In *I. persa*, the lower part of the head and breast are orange (vs. black), the background colour of the flank is grey with an orange hue (vs. black), each scale is furnished with an iridescent patch and these patches take up more space (vs. less) than the space between them, a poorly developed or invisible (vs. distinctive) “*Tilapia*-mark” in the dorsal fin, and very clear white spots making almost wavy bars or stripes on the caudal fin (vs. without or with very few white spots). Both species are also distinguished by multiple fixed molecular characters in mitochondrial ND2, D-loop (see Schwarzer et al. 2016).

Description. See Figure 3–5 for general appearance. Morphometric data are provided in Table 1. A small species with greatest body depth at approximately fifth dorsal-fin spine. Dorsal body profile convex from anterior part of dorsal fin to caudal peduncle. Ventral body profile straight or slightly convex between pelvic and anal fins. Dorsal head profile straight, slightly concave between nostrils and interorbital space. Head and eyes large. Mouth terminal, tip of upper and lower jaws at same vertical line (isognathous). Upper lip noticeably thickened, buccal region enlarged ventrally, oral teeth uniform in size and not enlarged medially.

Dorsal-fin base long, its origin at a vertical of pectoral-fin base, base of last dorsal-fin ray at vertical of posterior part of anal-fin base. Posterior dorsal-fin tip reaching to a point slightly in front of caudal-fin origin when folded back. Dorsal fin with 14–17 spines and $9\frac{1}{2}$ – $10\frac{1}{2}$ branched rays. Anal fin with 3 spines and $6\frac{1}{2}$ – $8\frac{1}{2}$ branched rays. Pelvic fin with 1 spine and 5 branched rays, not reaching to anus. Pectoral fin long with 11–12 branched rays, third branched ray being longest, reaching to vertical of 9th–11th dorsal-fin spine. Caudal fin truncate or slightly emarginated with 8+8 or 9+8 branched rays. Upper lateral line with 17–24 pored scales, starting from posterior tip of operculum to a vertical of 3rd–4th branched dorsal-fin ray. Lower lateral line with 9–13 pored scales, reaching

Table 1. Morphometric and meristic data of *Iranocichla persa*, (holotype, ZM-CBSU-IP66; paratypes, ZM-CBSU-IP59-IP65, IP67-IP78, K1120-K1127, n = 33).

	males (n = 18)				females (n = 15)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Standard length (mm)	66.6	102	82.5	8.5	63.7	88.7	73.0	7.7
In percentage of standard length								
Head length	33.8	37.0	34.9	0.9	33.5	37.6	36.1	1.0
Pre dorsal length	34.5	38.9	36.6	1.2	34.7	40.3	38.3	1.5
Post dorsal length	32.3	37.0	34.3	1.2	31.7	35.4	33.8	1.0
Dorsal fin length	49.6	53.7	51.4	1.1	46.3	52.0	49.3	1.7
Anal fin length	10.5	12.7	11.4	0.7	9.0	12.1	10.7	0.8
Pre-anal length	66.8	72.4	70.4	1.2	70.1	73.9	72.3	1.2
Pectoral fin length	21.4	29.4	25.7	2.1	23.0	27.1	24.7	1.2
Pelvic fin length	17.4	22.6	19.5	1.6	16.3	20.2	17.9	1.2
Pre-pelvic length	35.4	39.7	38.0	1.1	37.3	41.6	39.9	1.3
Maximum body depth	32.7	37.0	34.7	1.2	30.9	37.9	34.2	2.4
Body depth at dorsal fin origin	30.4	35.2	32.7	1.5	30.9	34.5	32.4	1.2
Minimum body depth	11.8	14.0	12.9	0.6	11.8	13.8	12.7	0.7
Distance between P&V	11.4	14.2	13.1	0.7	11.5	15.5	13.3	1.2
Distance between V&A	32.5	37.3	34.3	1.3	31.9	36.4	33.7	1.4
Caudal fin length	21.7	26.1	23.9	1.3	21.9	25.4	23.3	1.1
Caudal peduncle length	18.1	24.7	20.5	1.5	17.3	20.7	19.3	0.9
In percentage of head length								
Head depth	64.5	83.2	73.9	5.2	64.4	79.1	69.5	4.9
Head width	48.5	57.7	53.0	2.7	48.7	57.2	53.4	2.6
Preorbital distance	37.2	44.6	41.0	1.9	35.8	45.8	41.6	2.1
Postorbital distance	42.8	50.8	44.2	1.8	42.2	46.5	44.4	1.4
Interorbital distance	26.9	33.0	29.2	2.0	25.8	39.3	31.3	3.3
Eye diameter	16.7	20.8	18.8	1.1	16.5	20.2	17.9	1.1
Meristic characters								
Scales in upper lateral line	17	24	19.9	1.9	17	22	19.3	1.9
Scales in lower lateral line	9	13	11.2	1.4	9.0	13.0	10.4	1.2
Dorsal fin unbranched rays	14	17	15.4	0.8	14.0	17.0	15.3	0.8
Dorsal fin branched rays	9	10	9.7	0.5	9	10	9.6	0.5
Anal fin unbranched rays	3	3	3.0	0.0	3	3.0	3	0.0
Anal fin branched rays	6	8	6.7	0.6	6	7	6.7	0.4
Pelvic fin unbranched rays	1	1	1.0	0.0	1	1	1.0	0.0
Pelvic fin branched rays	5	55	5	0	5	5	5	0
Pectoral fin rays	12	12	12.0	0.0	11	12	11.9	0.2
Gill rakers	14	17	15.4	0.7	14	17	15.1	1.0

from a vertical of 3rd-4th branched dorsal fin rays to caudal-fin base. Scales cycloid or having very small ctenius-like structure, regularly arranged on flanks except that in a few larger individuals (≥ 85 mm SL; 3 out of 9 specimens), where scale rows are interspaced by irregularly set smaller scales, particularly on the upper flank. Head without scales in



Figure 5. *Iranocichla persa*, ZM-CBSU-IP64, male, paratype, 86.7 mm SL; Hormuzgan prov.: Shur River, ZM-CBSU-IP67, male, paratype, 75.8 mm SL; Hormuzgan prov.: Khorgo Hot spring, ZM-CBSU-IP73, female with eggs in her mouth, paratype, 76 mm SL; Hormuzgan prov.: Khorgo Hot spring.

some individuals, dorsal and anal fin bases without scales, no scale between the pectoral and pelvic fin bases and none on the belly and isthmus anterior to the pelvic fin. Upper margin of operculum without scales or with 1–2 large scales next to each other and sub-opercular bone without scales or with one scale at middle. Cheek without scales or with 1–3 rows of 1–7 almost non-imbricate scales. 11–12 rows of small scales on caudal-fin base, extending distally along more than half of the fin ray length in some individuals and extending distally along equal or less than half in some others.

Teeth in oral jaws regularly or irregularly arranged, 3–4 rows in both jaws (of the four examined, two individuals with 3 rows in upper and 4 in lower jaw). Number of rows decreases laterally to one row at rictus. Teeth in outer row widely spaced, spaces often nearly as wide as the crown, mostly bicuspid, major cusp with a protracted flank, but a few teeth tricuspid. Teeth in inner row tricuspid, central cusp largest (see Figs 6–8).

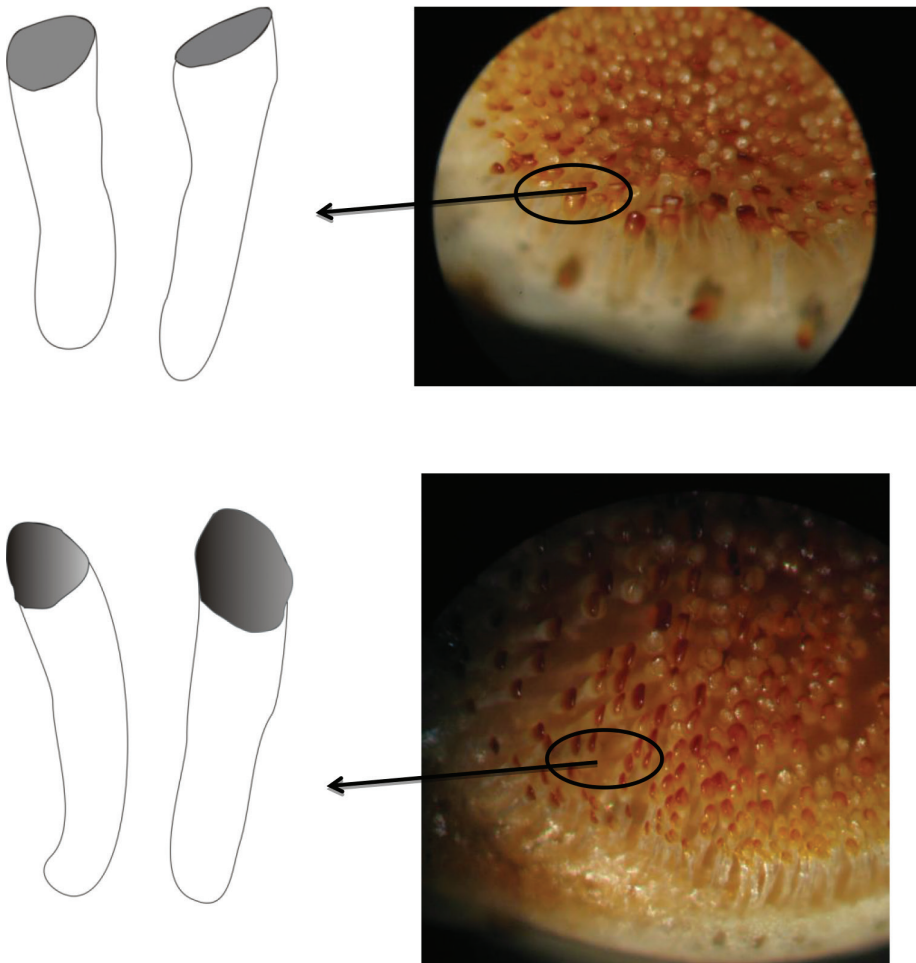


Figure 6. Lower and upper pharyngeal teeth of *Iranocichla persa*.

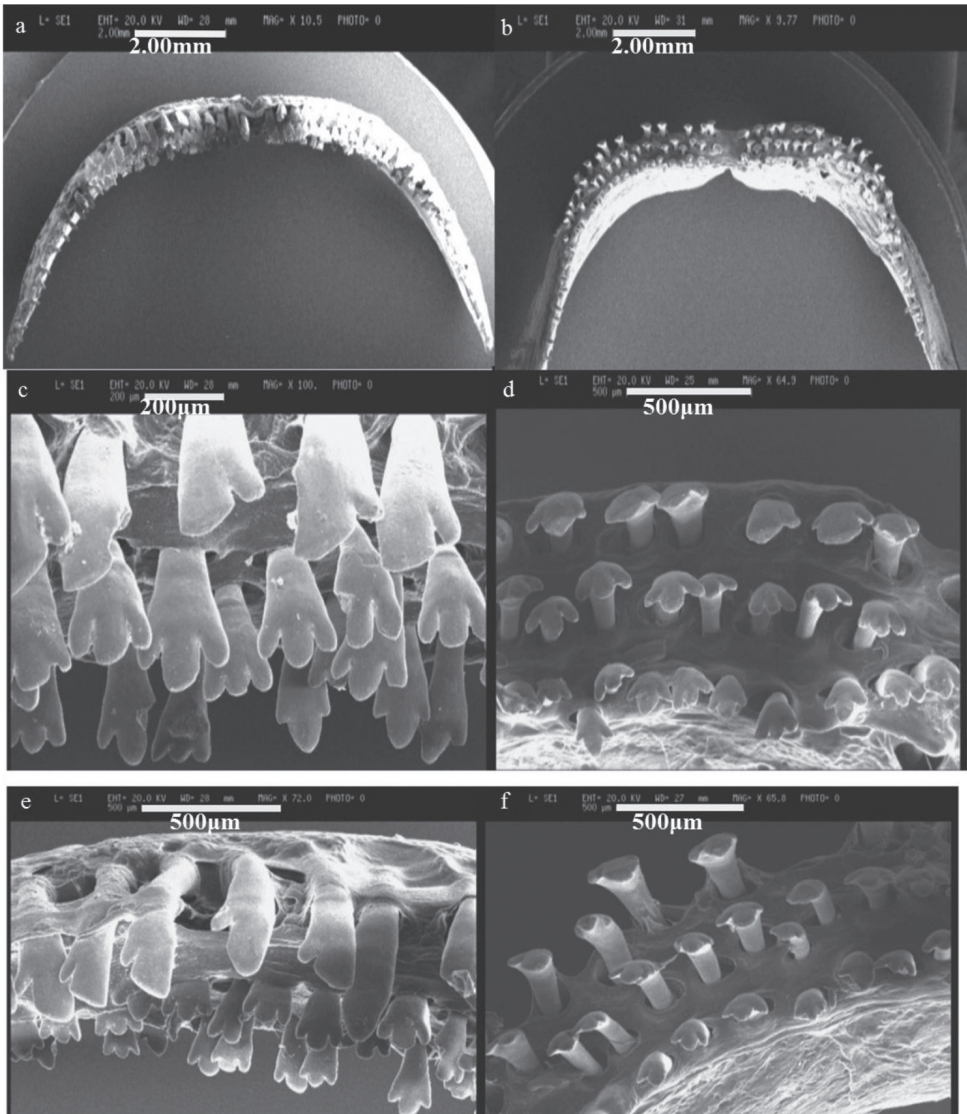


Figure 7. SEM photos of jaw teeth of *Iranocichla persa*; **a, c, e** upper jaw **b, d, f** lower jaw.

Sexual dimorphism. Nuptial males with an orange breast and lower part of head and few roundish white spots on cheek and operculum. Females have a longer head on average (33–38% SL vs. 34–37% SL), a wider interorbital distance (26–39% HL vs. 27–33% HL) and shorter pelvic fin (16–20% SL vs. 17–23% SL) as compared to males.

Colouration. In life. Background colour silvery grey or yellowish, a dark grey narrow saddle between eyes and a dark grey band at nape between uppermost parts of operculum. A dark grey, faint mid-lateral stripe between posterior eye margin and caudal-fin base and a second, often indistinct, dorso-lateral stripe between nape and

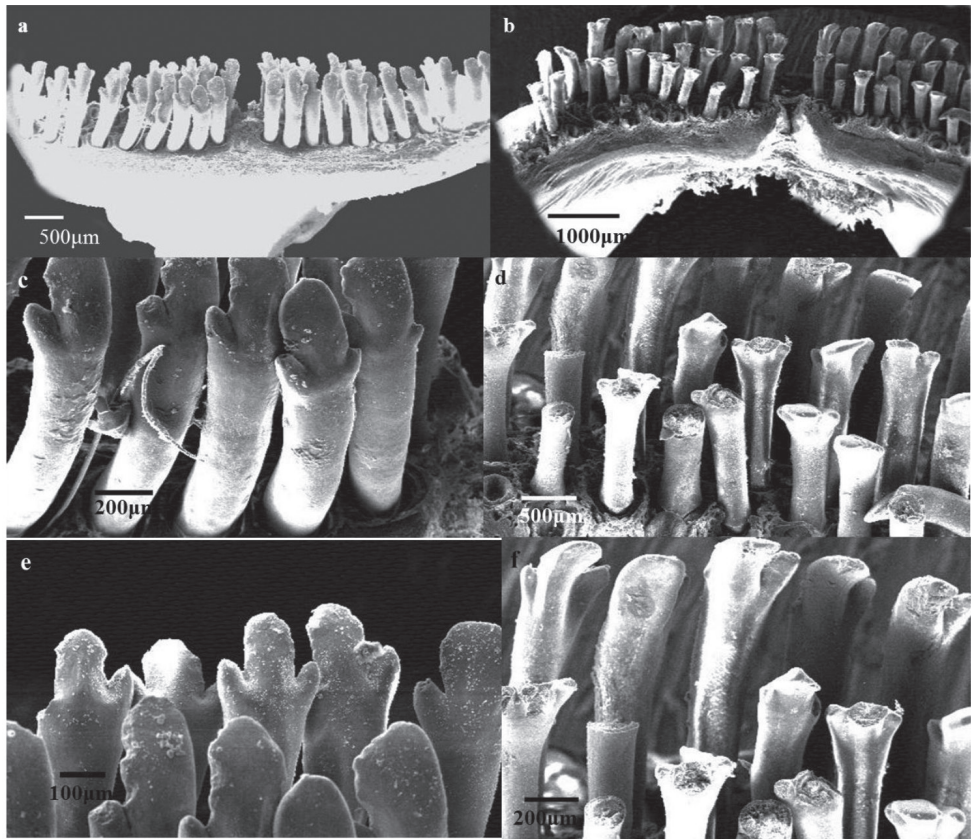


Figure 8. SEM photos of Jaws teeth of *I. hormuzensis*; **a, c, e** upper jaw **b, d, f** lower jaw.

“*Tilapia* mark”. Dorso-lateral stripe often dissociated into a marbled pattern. Mid-lateral stripe often dissociated into a series of vertically elongated large blotches at intersection with vertical bars. Body with 6–11 (mode 8) faint, wide, vertical bars, first bar at level of third dorsal-fin spine, last bar on posterior-most caudal peduncle. Bars most prominent above midlateral line, faded below. Bars almost or fully absent in nuptial males. Dorsal fin hyaline or grey with black “*Tilapia* mark” on posterior part of dorsal fin (absent in nuptial males). Caudal, anal, pelvic and pectoral fins grey or hyaline. Caudal fin with a series of 5–6 narrow vertical bars in some males, uniformly grey in other males and in all females.

Nuptial males with a prominent orange hue on flank. “*Tilapia* mark” absent. Lower head to upper eye margin orange, in some individuals with very small dark brown spots. Roundish white iridescent spots on cheek and operculum, Breast pale or orange. Breast and belly with very small dark brown spots in some individuals. Forehead and nape black in some individuals. Lips black at outer margin and orange at inner margin. Body except breast and nape with a prominent iridescent spot or small blotch on each scale. White blotches narrow, comma shaped, vertically elongated, most prominent on



Figure 9. Habitat of *Iranocichla persa*, Khorgo hot spring, Shur River drainage, Iran.

or restricted to posterior scale margins on upper flank above a horizontal line between pectoral-fin origin and posterior anal-fin base or a bit above that line. Below that line, iridescent spots and blotches on posterior scale margin roundish or ovoid, often irregularly shaped. On caudal peduncle and body behind a vertical line between last dorsal-fin spine and anal-fin origin, white spots narrow, restricted to posterior scale margin or along complete free scale margin, forming a reticulate pattern on caudal peduncle. Some individuals with irregularly x-shaped white blotches on anterior flank, roundish or ovoid on belly and comma-shaped, short vermiculate or roundish on dorsal and posterior flank. Dorsal fin with orange margin in most nuptial males, black in others. Dorsal fin rays hyaline, grey or black. Spines, membranes with white roundish or vertically elongated blotches, some fused to forward slanted narrow bars. Caudal fin grey or black with very clear white spots making almost wavy bars or stripes on the caudal fin. Anal fin grey with black distal anterior edge, with a few white, roundish, elongate or comma shaped blotches, most prominent on proximal and posterior parts of anal fin, absent on distal and anterior parts. Pelvic fin grey, light blue or black with few or no white spots or blotches. Pectoral fin hyaline or with black rays.

Distribution. *Iranocichla persa* is known from the Shur (Fig. 9), Hasanlangi and Minab River drainages flowing to the Persian Gulf at the Strait of Hormuz (Fig. 1).

Etymology. The species is named for Persia, the ancient name of Iran.

Remarks on populations from the Kol River drainage. The Kol River drainage is situated geographically between the Mehran River drainage, inhabited by *I. hormuzensis*, and the Shur River drainage, inhabited by *I. persa* (Fig. 1). The Kol popula-



Figure 10. *Iranocichla* from Kol River drainage: ZM-CBSU IP25 male, 71.3 mm SL; Hormuzgan prov.: Faryab hot spring, Kol River drainage, ZM-CBSU-IP34 male, 112.9 mm SL; Hormuzgan prov.: Gode-Gaz Spring, Kol River drainage.

tions (Figs 4,10) show some morphological characters resembling *I. hormuzensis* and others resembling *I. persa*. Nuptial males from the Kol River drainage resemble *I. hormuzensis* in having a black breast and lower part of the head (vs. orange in *I. persa*). On the other hand, nuptial males from the Kol River drainage resemble *I. persa* in having only a much faded “*Tilapia*-mark” in the dorsal fin or none at all (vs. bold in *I. hormuzensis*) (see Figs 3, 4, 10, 11), and in having very clear white spots making almost wavy bars or stripes on the caudal fin (vs. without or with very few white spots in *I. hormuzensis*) (Figs 4, 11). There is one exception, these are fishes from the Faryab hot spring, which is a quite isolated small spring situated in the upper most reaches of the Kol River drainage (Fig. 1). In the Faryab hot spring, males resemble the nuptial coloration of those from Mehran River, albeit being nearly black with iridescent blue spots on caudal and dorsal fin being connected to stripes. However, our two males in breeding dress from this hot spring were smaller than those sampled from any of our other sites and larger male individuals from Faryab are needed to rule out an ontoge-



Figure 11. *Iranocichla hormuzensis*, ZM-CBSU-IH54 male, 93.6 mm SL, ZM-CBSU-IH50 female with eggs, 83.4 mm SL Hormuzgan prov.: Dezhgan, Mehran River.

netic effect on the presence of “Tilapia-mark”. The nuptial males from the Shur and Minab River drainages have an orange edge to the dorsal fin. Nearly no differences in individual morphometric and meristic characters were found between the populations from the Kol and those from the Shur and Minab River drainages (Tables 1–3). The Kol populations resemble the latter and differ from *I. hormuzensis* in having a slightly more decurved dorsal head profile and a less pointed snout (Fig. 4).

From a genetic point of view, according to Schwarzer et al. (2016), who used ND2 and D-loop sequences, the western Kol River populations combined (Kol, Gode-Gaz, Faryab, Tange-Dalan) but also Gode-Gaz and Faryab each on its own, were genetically more diverse than *Iranocichla* populations of other drainages, having 15 different haplotypes, none of which was shared with any other drainage system and making two clades separated by a minimum of 4 mutations. All of them belonged to clade B of Schwarzer et al., but while one of the clades was unique to the Kol drainage populations, sharing a relatively recent common ancestral haplotype with the *I. persa* haplotype clade, the other Kol river clade was shared with *I. persa*, albeit with many

Table 2. Morphometric and meristic data of *Iranocichla* sp. from Kol River drainage (Gode-Gaz stream) (ZM-CBSU34-40, H1547-H1551; n = 12).

	males (n = 7)				females (n = 5)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Standard length (mm)	83.4	109	95.2		59.6	69.7	63.0	
In percentage of standard length								
Head length	35.0	36.3	35.6	0.5	37.4	38.7	38.1	0.6
Pre dorsal length	35.6	37.4	36.3	0.8	38.5	40.2	39.6	0.8
Post dorsal length	36.1	40.0	38.6	1.5	36.3	39.5	38.3	1.3
Dorsal fin length	51.9	56.7	53.4	1.6	50.2	53.5	51.1	1.3
Anal fin length	10.6	12.2	11.6	0.5	8.8	11.1	10.0	0.9
Pre- anal length	73.1	77.4	74.9	1.6	75.3	76.9	75.8	0.6
Pectoral fin length	26.5	30.8	27.9	1.4	28.6	30.0	29.5	0.6
Pelvic fin length	21.2	23.7	22.3	0.9	18.8	22.2	20.5	1.4
Pre- pelvic length	38.6	41.7	40.4	1.1	40.3	42.2	41.1	0.7
Maximum body depth	35.4	37.0	36.3	0.6	34.1	36.4	35.6	1.0
Body depth at dorsal fin origin	34.2	35.8	35.2	0.6	33.0	34.7	34.0	0.7
Minimum body depth	13.2	14.0	13.5	0.3	11.5	13.4	12.4	0.7
Distance between P&V	13.7	15.5	14.3	0.6	12.1	13.7	12.8	0.6
Distance between V&A	35.6	40.1	37.6	1.5	36.5	39.4	38.1	1.3
Caudal fin length	23.2	25.9	24.8	0.9	25.9	27.1	26.3	0.4
Caudal peduncle length	16.7	18.1	17.3	0.5	16.7	18.3	17.4	0.7
In percentage of head length								
Head depth	83.8	87.4	85.3	1.2	77.4	90.7	83.4	5.0
Head width	50.9	53.9	52.3	1.1	49.9	52.8	51.8	1.1
Preorbital distance	38.8	43.5	41.5	1.6	39.9	40.5	40.2	0.2
Postorbital distance	44.2	47.1	45.6	1.1	42.9	44.0	43.3	0.4
Interorbital distance	28.6	30.8	29.8	0.9	31.2	31.8	31.7	0.3
Eye diameter	17.2	20.5	18.4	1.0	17.8	18.8	18.4	0.4
Meristic characters								
Scales in upper lateral line	17	23	20.6	2.1	17	21	19	1.6
Scales in lower lateral line	9	12	11	1.0	10	12	11.4	0.9
Dorsal fin unbranched rays	15	16	15.6	0.5	15	16	15.4	0.5
Dorsal fin branched rays	9	10	9.3	0.5	9	10	9.4	0.5
Anal fin unbranched rays	3	3	3	0.0	3	3	3	0.0
Anal fin branched rays	5	7	6.1	0.9	6	7	6.6	0.5
Pelvic fin unbranched rays	1	1	1	0.0	1	1	1	0.0
Pelvic fin branched rays	5	5	5	0.0	5	5	5	0.0
Pectoral fin rays	11	12	11.3	0.5	11	12	11.4	0.5
Gill rakers	14	16	14.9	0.9	14	16	15.4	0.9

distinct haplotypes. Based on these results, Schwarzer et al. (2016) concluded that the nearly complete lack of haplotype sharing between the rivers, combined with distinct differences in male nuptial coloration, suggests the existence of two younger allopatric species within Clade B (Kol, Shur and Minab River systems): a red headed species in

Table 3. Morphometric and meristic data of *Iranocichla hormuzensis* from Mehran River (ZM-CBSU K1128-K1143, IH2-IH7, n = 22).

	males (n = 10)				females (n = 12)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Standard length (mm)	82.3	100.6	91.8	5.2	59.0	84.4	72.3	7.3
In percentage of standard length								
Head length	34.3	36.8	35.9	0.7	35.3	37.0	36.3	0.5
Pre dorsal length	35.7	39.3	38.0	1.1	38.1	40.1	39.0	0.6
Post dorsal length	34.0	37.6	35.3	1.0	32.8	36.3	34.7	0.8
Dorsal length	48.2	52.6	51.2	1.5	47.6	49.8	48.8	0.6
Anal length	9.1	12.2	10.7	0.9	9.4	10.3	9.8	0.3
Pre Anal length	69.2	72.2	71.1	0.8	71.1	73.3	72.7	0.6
Pectoral fin length	22.7	27.7	26.8	1.5	24.9	26.8	25.8	0.7
Pelvic fin length	16.3	19.9	18.4	1.1	15.9	18.1	17.3	0.6
Pre Pelvic length	38.9	41.5	40.0	0.9	40.7	43.6	41.9	0.7
Maximum body depth	32.3	39.2	35.7	1.8	31.9	37.5	34.5	1.4
Body depth at dorsal fin origin	31.7	36.9	33.9	1.5	31.5	34.4	33.0	0.9
Minimum body depth	13.0	14.2	13.6	0.4	12.0	13.2	12.5	0.4
Distance between P&V	12.8	15.5	13.7	0.9	12.4	13.8	12.9	0.4
Distance between V&A	30.6	34.6	33.1	1.2	31.3	33.6	32.5	0.8
Caudal fin length	21.9	23.9	23.1	0.6	21.7	25.1	23.0	0.9
Caudal peduncle length	19.4	21.2	20.2	0.6	19.3	22.0	20.5	0.9
In percentage of head length								
Head depth	60.2	69.2	65.2	2.9	64.4	72.4	69.1	2.3
Head width	48.1	59.0	53.7	3.5	52.3	61.6	56.1	2.4
Preorbital distance	40.0	43.1	42.1	0.9	41.2	43.9	42.3	0.7
Postorbital distance	42.1	45.9	44.0	1.2	42.5	48.4	46.2	2.2
Interorbital distance	25.7	36.8	32.0	3.6	33.1	36.9	34.4	0.9
Eye diameter	17.3	20.8	18.4	1.1	15.6	20.0	17.5	1.3
Meristic characters								
Scales in upper lateral line	16	21	18.2	1.8	15.0	21.0	18.2	2.1
Scales in lower lateral line	9	14	11.9	1.7	10.0	13.0	11.7	1.1
Dorsal fin unbranched rays	15	16	15.2	0.4	15.0	16.0	15.2	0.4
Dorsal fin branched rays	9	11	10.2	0.6	9.0	10.0	9.8	0.4
Anal fin unbranched rays	3	3	3.0	0.0	3.0	3.0	3.0	0.0
Anal fin branched rays	5	7	6.0	0.9	5.0	7.0	6.1	0.8
Pelvic fin unbranched rays	1	1	1.0	0.0	1.0	1.0	1.0	0.0
Pelvic fin branched rays	5	5	5.0	0.0	5.0	5.0	5.0	0.0
Pectoral fin rays	12	12	12.0	0.0	12.0	12.0	12.0	0.0
Gill rakers	14	17	15.9	1.0	15.0	17.0	15.8	0.7

Shur, Hasanlangi and Minab (described as *I. persa* here) and a dark black one in the Kol river. The divergence of these forms is more recent and the western Kol populations appear to be para- or polyphyletic assemblages in their mitochondrial genes, possibly suggesting an old stable population or a case of more recent secondary contact

Table 4. Teeth formula of *Iranocichla*. 1 = unicuspid; 2 = bicuspid; 3 = tricuspid.

Species	ZM-CBSU Number	Locality	Sex	SL (mm)	Upper jaw teeth formula	Lower jaw teeth formula
<i>I. persa</i>	25	Khorgo	M	81	14(1)+26(2)	2(1)+17(2)+2(3)
<i>I. persa</i>	SEM	Khorgo	M	60.7	12(1)+34(2)+1(3)	19(2)+4(3)
<i>I. persa</i>	147	Ziyarat Ali	F	73.7	43(2)+1(3)	1(1)+23(2)
<i>I. persa</i>	148	Ziyarat Ali	M	94.8	25(1)+29(2)+1(3)	5(1)+18(2)
<i>I. sp. Kol</i>	3	Lar	M	90.3	9(1)+36(2)+3(3)	5(1)+5(2)+4(3)
<i>I. hormuzensis</i>	295	Bastak-Mehran	M	76.7	4(1)+27(2)+12(3)	3(1)+21(2)+1(3)
<i>I. hormuzensis</i>	325	Bastak-Mehran	F	72.4	41(2)+20(3)	26(2)
<i>I. hormuzensis</i>	394	Kokherd	F	80.5	14(1)+32(2)+1(3)	20(2)
<i>I. hormuzensis</i>	398	Kokherd	M	82	8(1)+26(2)+3(3)	17(2)+1(3)

and admixture with gene flow from the Shur River into the Kol River. The eastern arm of the Kol river harbours only one of the two haplotype clades, but Schwarzer et al. (2016) had limited sampling from that river arm. Note that the persistence of two divergent haplotype clades only in the western arm of the Kol River does not seem to be associated with any obvious phenotypic polymorphism within these sites, hence we do not see evidence for more than one species in any one river.

Comparative materials

Specimens from Kol River drainage. ZM-CBSU IP24, 10, 39–71 mm SL; ZM-CBSU k1144, 5, 30–58 mm SL; Hormuzgan prov.: Faryab Hot Spring at Faryabe-Sanguyeh village, approx. 30 km north of Bastak city, 27°26'01.0"N 54°16'43.0"E. — ZM-CBSU IP34, 11, 67–113 mm SL; Hormuzgan prov.: Gode-Gaz (Gowde-Gaz) stream approx. 15 km east of Bastak city at Gode- Gaz village, 27°17'28.8"N 54°29'20.7"E. — ZM-CBSU IP45, 1, 78 mm SL; Hormuzgan prov.: Tange-Dalan stream, 27°23'14.6"N 55°00'14.0"E. — ZM-CBSU IP79, 3, 89–100 mm SL; Fars prov.: Lar stream, approx. 25 km east of Lar city, 27°38'19.0"N 54°41'33.2"E. — ZM-CBSU IP82, 1, 87 mm SL; Iran: Hormuzgan prov.: Kol River approx. 15 km north of Bandare-pol, 27°07'19.5"N 55°44'55.4"E.

***Iranocichla hormuzensis*.** All from Iran: Hormuzgan prov.: ZM-CBSU IH2, 11, 73–102 mm SL; Mehran River at Kokherd, approx. 50 km south-east of Bastak, 27°04'50.1"N 54°28'24.4"E. — ZM-CBSU K1128, 8, 68–101 mm SL; Mehran River at Kokherd, approx. 50 km south-east of Bastak, 27°04'50.1"N 54°28'24.4"E. — FSJF 3467, 82 mm SL; ZM-CBSU IH13, 11, 59–89 mm SL; ZM-CBSU K1136, 8, 59–84 mm SL; Mehran River at Gotow (Gotab), approx. 20 km south-west of Bastak, 27°08'37.2"N 54°15'44.70"E. — ZM-CBSU-IH46, 12, 68–94 mm SL; Mehran River at Dezhgan, approx. 35 km west of Bandare-Khamir, 26°52'55.4"N 55°16'20.8"E.

Material used for molecular COI analysis

Specimens from Kol River drainage. All from Iran: — ZM-CBSU-IH45, Tange-Dalan stream, 27°23'14.6"N 55°00'14.0"E (GenBank accession number: KY034448). — ZM-CBSU M803, M804; Kol River at Lar, 27°38'19.0"N 54°41'33.2"E (GenBank accession numbers: KY034446, KY034447).

***Iranocichla hormuzensis*.** All from Iran: ZM-CBSU M921, M922, M939, M943; Mehran River at Kokherd, 27°04'50.1"N 54°28'24.4"E (GenBank accession numbers: KY034431, KY034432, KY034433, KY034434).

Comparative material from GenBank

Oreochromis niloticus FJ348104.1, *Oreochromis niloticus* KJ554049, *Oreochromis niloticus* KJ553958, *Oreochromis aureus* KJ553787, *Oreochromis aureus* KJ553805, *Sarotherodon galilaeus* HM882887.1, *Sarotherodon galilaeus* FJ348122.1, *Astatotilapia burtoni* EU888024, *Astatotilapia desfontanii* KJ553606, *Astatotilapia desfontanii* KJ553501, *Astatotilapia desfontanii* KJ553392, *Astatotilapia desfontanii* KJ553501.

Discussion

Female and juvenile *Iranocichla persa*, *I. hormuzensis* and those from Kol River drainage are difficult to distinguish from each other based on morphology, and males are best distinguished when they are territorial and show their nuptial coloration. Outside the breeding period, adult males can be distinguished based on differences in the retention of the “Tilapia-mark”, the iridescent spotting of the fins and differences in head shape. Both species are distinguishable by multiple fixed substitution between their mitochondrial lineages, as seen in their ND2, D-loop and COI sequences, suggesting a relatively old divergence of ~160 and 318 kya years (Schwarzer et al. 2016) between two readily diagnosable species, *I. hormuzensis* and *I. persa*.

The populations from Kol River drainage including Lar, Faryab, Gode-Gaz (Rasoul), Tange-Dalan, Kol River itself, whose haplotypes are either nested in the *I. persa* mitochondrial clade, or very closely related to it, show some phenotypic trait mosaic between the two species. Hence, male breeding coloration differs remarkably between the species and these differences coincide with major drainage system differences (Fig. 1). Based on available and presented data including the haplotype network and demographic history reconstruction conducted by Schwarzer et al. (2016), low genetic diversity and little haplotype sharing, those authors proposed two possible scenarios for allopatric speciation of *Iranocichla* between the major river drainages (clades A, B): (I) *Iranocichla* populations persisted throughout the Pleistocene in the Mehran and Kol River systems, but remained isolated ever since their first split ~160 and 318 kya.

(II) Shur and Mehran River drainages (including Rudan River) were only colonized during or after the Last Glacial Maximum (LGM) from the Kol river drainage, most likely through occasional long distance dispersal through the Strait of Hormuz. Alternatively, *Iranocichla* of clade B may have entered the Shur River system earlier and persisted both in Shur and Kol River drainage during droughts in the LGM. They may then have colonized the Rudan River in the Minab River system from Shur and also recolonized the Kol River system from the Shur during or just after the LGM. This would explain the central position within clade B of Shur haplotypes in the haplotype network and the existence of and admixture between two haplotype clades in the western arm of the Kol River system. Yet another possibility is that Shur and Kol river systems were colonized at the same time (the reconstructed most recent common ancestor haplotype of all Kol, Shur, and Rudan haplotypes is extinct or absent in our data) and started to diverge into a western Kol and an eastern Kol/Shur clade, and that the western Kol afterward was colonized a second time from the east through river capture of the eastern Kol which may once have drained toward the Shur as indicated by the river topology of the eastern Kol (Fig. 1). Subsequently more recent bottlenecks of eastern Kol and Shur populations could have led to their divergence in haplotype frequencies without much sequence divergence (see Schwarzer et al. 2016). The exact taxonomic status of the Kol River populations awaits further research.

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